Journal of Applied Ecology
October 2013, Volume 50, Issue 5, Pages 1081-1092
http://dx.doi.org/10.1111/1365-2664.12140

Impact of increasing deployment of artificial floating objects on the spatial distribution of social fish species

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Abstract:

1. Approximately 300 pelagic fish species naturally aggregate around floating objects (FOBs) at the surface of the oceans. Currently, more than 50% of the world catch of tropical tuna comes from the industrial tuna fisheries around drifting FOBs. Greater understanding of the complex decision-making processes leading to this aggregation pattern and the impact of the massive release of artificial FOBs by fishermen on the spatial distribution and management of tuna is needed.

2. We analyse how the interplay between social (relationships between individuals) and non-social (responses to the environment) behaviours may affect the spatial distribution of a population in a multi-FOB environment. Taking the example of tropical tunas associating with FOBs and using differential equations and stochastic simulations, we examine how, when increasing the number of FOBs, fish aggregation dynamics and the distribution of the population among patches are affected by the population size, level of sociality and the natural retentive and/or attractive forces of FOBs on individual tuna.

3. Our model predicts that, depending on the species' level of sociality, fish will be scattered among FOBs or aggregated around a single FOB based on the number of FOBs deployed in a homogeneous oceanic region.

4. For social species, we demonstrated that the total fish catch is reduced with increasing FOBs number. Indeed, for each size of population, there are a number of FOBs minimizing the total population of fish associated with FOBs and another number of FOBs maximizing the total population of associated fish.

5. *Synthesis and applications*. In terms of fisheries management, the total catch volume is directly linked to the total number of floating objects (FOBs) for non-social species, and any limit on the number of sets would then result in a limit on the total catch. For social species (e.g. tuna), however, increasing the number of FOBs does not necessarily lead to an increase in the total catch, which is a non-intuitive result. Indeed, our model shows that, for specific values of the parameters, deploying a greater number of FOBs in the water (all other parameters being constant) does not necessarily help fishermen to catch more tuna, but does increase the level of fishing effort and bycatch.

Keywords: behaviour-based modelling ; Bycatch ; FAD ; FOB ; sustainable fishery ; tuna

1. Introduction

In the wild, the spatial distribution of individuals is most often patchy (Parrish & Hamner 1997), resulting from animals' reactions to biotic or abiotic factors, which are themselves often patchy, or from the interactions of conspecifics with each other, in the case of social species (Parrish & Hamner 1997; Parrish & Edelstein-Keshet 1999; Krause & Ruxton 2002; Stephens *et al.* 2002). These two processes structure scientific investigations of the spatial dynamics of wild animals; ecologists usually favour the importance of environmental stimuli, whereas ethologists often emphasize the relationships between conspecifics. However, these two approaches are non-exclusive.

Advances in the understanding of the spatial dynamics of fish illustrate this dichotomy. Ecologists generally try to interpret the observed distributions of fish as a result of interactions between fish and their environment (Pitcher 1992; Bertignac, Lehodey & Hampton 1998), while ethologists have extensively studied the schooling behaviour of fish, focusing on the mechanisms by which local interactions between members of the same school control the motion of the school (Viscido, Parrish & Grunbaum 2004; Hemelrijk & Hildenbrandt 2008; Couzin 2009; Capello *et al.* 2011). The functionality of aggregates that tropical tunas often form around floating objects (FOBs) were studied at short scales by ethologists while ecologists favour longer and larger scales. For years, it has been reported that tropical tunas (mainly skipjack, *Katsuwonus pelamis*, yellowfin, *Thunnus albacares*, and bigeye, *T. obesus*, tunas) naturally aggregate around objects floating at the surface of the ocean, such as logs, and debris, among others (Uda 1936; Hunter & Mitchell 1967), but the reasons that tunas associate with FOBs are still unknown. The first hypothesis to explain these fish aggregations came from ecologists, who proposed that tunas were feeding on smaller fish that were associated with the FOBs (Kojima 1956; Bard, Stretta & Slepoukha 1985). Tunas, however, do not seem to generally feed on prey associated with drifting FOBs (Ménard *et al.* 2000). Later, ecologists advanced the indicator-log hypothesis (Hall 1992): natural FOBs (e.g., logs) could be indicators of productive areas, either because most of them originate in nutrient rich areas, such as river mouths, or because they aggregate in rich frontal zones offshore. In the late 1990s, ethologists suggested that tunas could associate with FOBs for social reasons (Dagorn & Freon 1999; Freon & Dagorn 2000). Floating objects could act as meeting points where individuals or small schools could gather to form larger schools, providing advantages to their members (Pitcher and Parrish 1993).

A better understanding of this associative behaviour is of increasing importance because this behaviour is intensively exploited by fishermen (largely on tropical tuna purse seine vessels) to facilitate their catch of tropical tunas. Initially, tropical tuna purse seine vessels began fishing for tunas that were aggregated around natural FOBs, such as logs. However, since the 1990s, fishermen have been using man-made floating objects, called fish aggregating devices (FADs), to facilitate the capture of these species. Globally, several thousands of FADs (usually rafts made of bamboo sticks that are equipped with satellite buoys that allow fishermen to relocate them) are regularly deployed by fishermen in the oceans (Moreno *et al.* 2007; Dagorn *et al.* 2013). The use of FADs has largely contributed to an increase in the total catch of tuna: the catch of tropical tunas around drifting FADs by purse seine vessels has accounted for almost 50% of the tuna catch in the Pacific Ocean and 25% in other oceans (Fonteneau, Pallares & Pianet 2000; Dagorn *et al.* 2012b).

Several authors have modelled the dynamics of tuna aggregations around FOBs (Clark & Mangel 1979; Hilborn & Medley 1989; Dagorn, Bach & Josse 2000). Surprisingly, although tropical tunas are known to school, a form of social behaviour (Norris & Schilt 1988), all of these studies considered fish units that were independent, with no interaction between conspecifics (Robert *et al.* 2013). The fact that tunas school does not indicate, however, whether their social behaviour plays a key role in the aggregations that they form around FOBs. While recent studies (Soria *et al.* 2009; Capello *et al.* 2011) have described the role of social behaviour in the aggregations of small, pelagic fish species (e.g., the bigeye scad, *Selar crumenophthalmus*) around FADs, the influence of the social behaviour of tunas on the dynamics of their aggregations around FOBs is still poorly understood. Using a system of differential equations, we studied the patterns that were generated by fish interacting with each other while joining and leaving FOBs, as opposed to independent fish. In addition, due to the strong non-linearity of the model, we also performed stochastic simulations, where the random aspects of processes are automatically incorporated. This approach where all individuals behave independently in the limit of parameters values allows us to investigate the main effects arising from fluctuations. One of the main tasks requested by the Regional Fisheries Management Organizations (RFMO), who are in charge of the management of tuna fisheries, is an assessment of the consequences of the increasing number of FOBs in the ocean due to the release of large numbers of FADs. Consequently, we specifically examined the effects of an increase in the number of FOBs on the aggregation dynamics and distribution of tunas among FOBs when including or excluding social interactions from the model.

2. The model

The model consists of a system of *p+1* interconnected populations: x_i is the fraction of the total population (*N*) around the FOB *i*, one of the *p* FOBs, and x_e is the fraction of the total population (*N*) outside the FOBs (Fig. 1). All FOBs are identical (same design or same potential to attract/retain fish) and are located in a homogeneous environment. The population outside the FOBs is homogeneously distributed within this environment and the total fish population stays constant in the area (the recruitment and arrival of new fish in the population = mortality of fish). The differential equations describing the evolution of the fraction of the population around each FOB (x_i) through time can be written as in Eq 1,a:

$$\frac{dx_i}{dt} = R_i x_e - Q_i x_i \qquad i = 1, \dots, p \qquad (1, a)$$

$$x_e + \sum_{i=1}^{p} x_i = 1 \qquad (1, b)$$

R_i (Q_i) is the probability of joining (leaving) the FOB *i*. (Eq 2) and these probabilities depend on the interaction between the fishes. The model neglects the social interaction between fish outside the FOBs. It made the assumption that the interaction between fish implies that the greater the number of individuals around the FOB *i* X_i $(=Nx_i)$, the greater the probability R_i of joining this FOB (Eq 2,a) and the lower the probability of leaving it. (Eq 2,b).

$$R_i = \mu(1 + \beta N x_i) \qquad (2, a)$$

$$Q_i = \theta(1 + \varepsilon N x_i) \qquad (2, b)$$

μ is the kinetic constant of joining the FOB *i* (when a FOB is "empty") *and* θ is the maximal probability of leaving the FOB *i* per time unit. β and ε are the strengths of the social interaction and we assume, to simplify the analysis, that these strengths are the same (β = ε) for the both probabilities (joining and leaving). When β= o, it corresponds to the case of independent/asocial fish and R_i and Q_i are constant ($R_i=\mu$; $Q_i=\theta$).

In biological terms, we assume that the social interaction is proportional to the population size. The influence of a large number of individuals with a small β is equivalent to the influence of a small population with a large β. Consequently, the parameter b corresponds to large populations and/or large values of β (Eq 3).

$$b = \beta N \quad (3)$$

Dividing Equation 1 by μ, we define a new time $\tau = \mu t$ and the ratio $g = \frac{\theta}{\mu}$ and we obtain:

$$\frac{dx_i}{d\tau} = (1 + bx_i)x_e - \frac{gx_i}{1 + bx_i} \quad (4, a)$$

$$1 = x_e + \sum_{i=1}^{p} x_i \quad (4, b)$$

<u>Monte Carlo simulations</u>

To understand the main effects arising from the fluctuations in the non-linear process of aggregation, we used Monte Carlo simulations including stochasticity in the simulation. The simulations were based on the same mechanisms that were defined in the differential system of equations (Eq. 4a,b). The following steps summarize our analysis. (1) Initial conditions: the number of individuals around each FOB is fixed at 0, and the number outside the FOBs equals N; (2) Decision process: p+1 states are possible for each individual around each FOB i (i=1,...,p) and outside the FOBs. At each time step (t), the position of each individual is checked. Then, its probability of leaving (joining) FOB i is given by Q_i (R_i) (Eq. 2a,b). Its change of state at time t

depends on the comparison between the calculated value Q_i (R_i) and a random number that is sampled from a uniform distribution between 0 and 1. If its value is less than or equal to Q_i (R_i), the individual leaves (joins) FOB *i*.

The probabilities Q_i and R_i, of moving are updated at each simulation step in relation to the number of individuals already present on site *i*. The process is repeated for a sufficient number of steps to reach the stationary state. Monte Carlo simulations are run 1000 times with a population of 1000 individuals during 1000 time steps. The simulation results allowed us to follow the progress towards the stationary state for FOB *i* in relation to time. The distributions of the numbers of individuals present in FOB *i* in relation to time and at the stationary state were calculated.

3. Non-social system

This model includes the scenario consisting of the absence of interaction between individuals (b =0). Trivially, as each individual settles randomly under one of the p FOBs, the model has only one stationary symmetrical solution ($x_1=x_2=...=x_p$). The populations around each FOB are identical and can be expressed as a function of g and p (Eq. 5a,b). The total fraction of the population associated with the p FOBs is $T = p*x_i$.

$$x_i = \frac{1}{g+p} \quad i = 1, \dots, p \quad (5, a)$$

$$T = \frac{p}{g+p} \quad (5, b)$$

4. Social systems

a. The case of one FOB

In the case of one FOB (p =1), at the stationary state Eq. 4a is

$$\frac{dx}{dt} = 0 = (1 + bx)x_e - \frac{gx}{(1+bx)} \qquad \text{(6a)}$$

or $(1 + bx)^2 x_e = gx = 0$ (6b)

with $x_e = 1 - x$ (6c)

The solutions of this algebraic equation are the stationary states of Eq. 4. This equation has only one stationary solution, except for $b>8$ and $g-<g<g+$, where three stationary states exist: two stable and one unstable.

$$g_{\pm} = (1 + bA_{\pm)})^2 \left(A_{\pm}^{-1} - 1\right) \quad (7,a)$$

$$A_{\pm} = 0.25 \pm (0.0625 - 0.5b^{-1})^{0.5} \quad (7,b)$$

Based on Eq. 7a,b, we show in Figure 2a the zones were the model has one or three stationary solutions.

Figure 2b, describing x_1 as a function of g for 3 values of b, shows a classical hysteresis effect. For small values of g ($g<g-$), i.e., a strong tendency to associate with the FOB and/or a weak tendency to leave it, a large fraction of the population aggregates around the FOB. However, for large values of g (g >g+), a small fraction aggregates around the FOB. For $g-<g<g+$ *and* $b>8$, the system adopts one of the two stable states based on its history and random events (i.e., a large or small population around the FOB). The medium value is a threshold that is always unstable.

Similarly, Figure 2c, describing x_i as a function of b for 3 values of g, shows a similar hysteresis behaviour. Indeed, when increasing b (keeping g constant), the aggregated population around the FOB increases. For large values of g, we observe two stable states: a small population or a large one aggregated around the FOB.

b. The case of two FOBs

With two FOBs ($p=2$), the model has two families of stationary states (Figure 3a,b). The first family corresponds to an equal but small number of individuals around both FOBs ($x_1=x_2$). The solutions for the second family are asymmetrical states with unequal numbers of individuals on each site ($x_1>x_2$ or $x_1<x_2$) (Figure 3a,b). This result implies that one of the sites (FOB) is selected by the majority of the population.

The detailed analysis of the solutions indicates that the symmetrical solution (equal distribution of fish under the 2 FOBs) is stable for $b<2$, for $2<b<6$ and $g>4b-8$, and for for $b>6$ and $g>(1+0.5b)^{0.5}$ (Figure 3g,h).

In contrast, the system exhibits an asymmetric stable steady state ($x_1>x_2$ or $x_1<x_2$) when $b>2$ and $g< 4b-8$. In such a scenario, the selection of one FOB occurs through amplification (Figure 3c,d).

Finally, one symmetrical and one asymmetrical solution are stable for $b>6$ and $4b-8<g<(1+0.5b)^2$ (see Figure 3e,f). In this case, the initial condition (or randomness, for the stochastic model) determines which steady state will be reached.

If we convert back into biologically meaningful variables, the stable stationary states for this model for a large population (N) and/or strong social interactions β demonstrate that for two FOBs, one FOB captures the whole population (Figure 3b,c). For small values of N and/or β or a large value of g, the population is equally distributed between the two FOBs. The greater b (smaller g), the greater is the clustering asymmetry.

c. Generalization to p FOBs

For b>0 and p FOBs, the model has three zones of stationary states: one with a single, homogeneous, symmetrical steady state solution $x_1=x_2=...=x_p$, a second zone with an asymmetrical steady state solution $x_1>x_2=...=x_p$ (or: $x_2>x_1=x_3=...=x_p$, … ; $x_p> x_1=...=x_{p-1}$) and a zone where both solutions are stable and coexist (Figure 4a,b).

For instance, for b=10, g=20 and an increasing p, the model shifts from an asymmetrical steady state to a symmetrical one via the bistability situation, where the symmetrical and asymmetrical solutions are stable. Indeed, for these values of the parameters b and g, we observed the asymmetrical solution $x_1>x_2$ (or $x_1<x_2$) for p=2 (Figure 3a), the bistability solution for p=10 (Figure 4a) and the symmetrical solution for p=25 (Figure 4b). This result highlights the tendency of fish to scatter due to an increasing number of FOBs, similar to what happens when there is no social interaction between fish (see the Discussion section).

As shown in Figure 4c,d, when the number of FOBs is small (<10) and g=10, one FOB is randomly selected (with a frequency of 1/p). When the steady state is reached, the population around this "winning" FOB x_i is high, nearly the entire population (Figure 5a). However, when the numbers of FOBs increases, both solutions are initially stable (asymmetrical and symmetrical solutions). For very large numbers of FOBs, we do not observe such selection, and the fish are equally distributed among all of the FOBs. For g≥34, the asymmetrical steady state disappears and only the symmetrical steady state exists. In each of these three cases (g=10, g=34, g=60), not surprisingly, there is agreement between theoretical (Figure 4c,e,g) and simulated results (Figure 4d,f,h).

5. Non-social vs. social systems: a case study

The level of fish association to FOBs, as well as the asymmetrical or symmetrical pattern, can deeply influence the pattern of fishing effort. In this respect, we present an example of the variation in these parameters through a comparison of the influence of the number of FOBs (p) on the total fraction of the population under FOBs (T, Figure 5a) and on the maximum fraction of the population observed under one FOB (x_{i_max}, Figure 5b) for different values of b (inter-attraction between fishes and/or population size, Figure 5, see Eq. 3a).

For a small number of FOBs (p<60) in a non-social system (b=0), the proportion of the population associated with FOBs (T) increases with p. Individuals are equally distributed among FOBs and x_{i_max} decreases with p (Figure 5a,b). In a social system, according to the value of b, if T is always higher than 75%, whatever the number of FOBs (p), then the distribution of fish among FOBs switches abruptly at a critical value of p, from an asymmetrical state with a high x_{i_max}, corresponding to the selection of one FOB by the population, to a symmetrical state, where individuals are scattered between FOBs in identical small groups (Figure 5a,b).

However, for a large number of FOBs (p>60), for non-social (b=0) or social fish (b=10, b=20), more than 80% of the individuals are equally distributed among FOBs, with the remaining 20% outside the FOBs. Consequently, the number of fish associated with each FOB is very small, and $x_{i\_max} \cong \frac{\sum_{i=1}^{p} x_i}{p}$.

Discussion

The dynamics and distribution of tunas within an array of FOBs can be studied using the theoretical ambit of metapopulation analyses and the spatial distribution of populations in multi-patch environments (Gotelli & Kelley 1993). In this study, we examined how aggregation dynamics are affected by the size of the fish population, the level of sociality between individuals, the total number of aggregation sites available (i.e., FOBs) and the natural retentive/attractive forces of FOBs on single individuals. We demonstrate that, depending on the values of these parameters, we could firstly predict that within a homogeneous oceanic region, the fraction of the population associated to FOBs can strongly varied and secondly, that the different FOBs will be equivalently occupied or that only one of them will be selected. Moreover, for some particular values of the parameters, the history of the system could lead to either of these two solutions (bistability).

Distribution of non-social fish among FOBs

Trivially, without social interactions (b = 0), as individuals respond individually to a unique stimulus (i.e., the FOB), the fraction of the population associated with FOBs will slowly increase with the number of FOBs. In this context, aggregation corresponds to the summation of all individuals responses. This has been the common vision of tuna aggregations around FOBs. Moreover, if FOBs are equivalent in quality, the proportion of the population associated with each of them will be identical and inversely proportional to their number (Eq. 5). The total number of individuals associated with FOBs will only depend on g, the intrinsic retention power of FOBs. These results are in agreement with previous studies that have modelled the behaviour of fish around FOBs (Clark & Mangel 1979; Hilborn & Medley 1989; Dagorn *et al.* 2000).

In this case, the aggregation pattern of individuals is influenced more by the sum of individual responses (Fraenkel & Gunn 1961) than by a true collective decision process (Camazine 2001; Halloy *et al.* 2007; Sumpter 2010). If FOBs differ in quality (i.e., some naturally attract or retain more fish than others), a non-homogeneous situation exists. In such a case, the most favourable FOBs will aggregate a large percentage of the population, and each FOB will be characterized by its own value of g. The FOB with the highest quality (i.e., the lowest value of g) will aggregate the most individuals.

Distribution of social fish among FOBs

When fish of the same species interact with each other (i.e., when the presence of conspecifics under a FOB influences the probability of reaching or staying around this FOB), our model and simulations show a different pattern. Indeed, for social species with a constant population size in an area with two or more FOBs of the same quality, the aggregative patterns predominantly arise from an amplification process that depends on the number of fish associated with each FOB (x_i) and on the level of social interactions between fish and/or the population size (b, see Eq. 1a). This observation indicates that the greater is the number of fish around a FOB and/or the higher the inter-attraction between fish, the lower is the probability that a fish will leave it and/and the greater the probability that a fish will join it. Nonetheless, for high numbers of FOBs (Figure 4a), the scattering of the population among all FOBs precludes the amplification process from occurring, and the system shifts back to an equal distribution, which could be considered suboptimal in terms of fish exploitation if the number of fish around each FOB is too small (Auger *et al.* 2010). This complex dynamic changes the common vision of the aggregation processes for non-social fish. Even for social species, an equal distribution of fish among FOBs can be obtained for some particular values of the parameters. Indeed, for a constant population of fish (the recruitment and arrival of new fish in the population = mortality of fish), we observe a shift from the selection of one FOB to an equal distribution of fish among all FOBs when the number of FOBs increases (Figure 6). This observation corresponds to the steady-state, so it may only be reached after an infinite length of time. For a small number of FOBs or a medium number associated with a large social interaction, the aggregation of fish under one FOB is the only one stable solution. Increasing the number of FOBs should, in general, lead to the vast majority of fish associating with all FOBs (Figure 6). This pattern of equal distribution is also obtained if the number of FOBs is medium or large and the social interactions between conspecifics are small (Figure 6). However, in this case, only a small proportion of the population is associated with FOBs. This pattern is due to the low probability of having enough individuals together around a FOB at the same time, which is required to initiate the amplification process that will lead to the selection of only one FOB.

In summary, it is noteworthy that for social species, the largest total number of individuals associated with FOBs can be reached in two different situations, depending on the size of the population and the number of FOBs. When few FOBS are present, there is selection, and a large proportion of the population is aggregated around one FOB. When there are many FOBs, there is an equal distribution of fish among all of the FOBs, each of them being occupied by a small number of individuals. Trivially, our model shows that for small or intermediate numbers of

FOBs, the population around a FOB is higher for social species, in comparison to non-social ones, or social situations with a scattered population among a large number of FOBs (Figure 5). Another important result is that for each size of population of fish (for social species, again), there is a number of FOBs that minimizes the total population of fish associated with FOBs, and another number of FOBs that maximizes the total population of associated fish.

What can we say in terms of management? The release of thousands of FADs into the ocean by purse seine vessels drastically increases the number of floating objects. Indeed, concerning the Indian Ocean, the number of FOBs has at least double since the introduction of FADs and in Somalia area for instance, the multiplication factor has reached as high as 20 or 40 (Dagorn *et al.* 2012b; Dagorn *et al.* 2013). In the Mozambique Channel and Chagos area, few FADs are deployed by fishers because the density of FOBs is naturally high i.e. they regularly drift in from both the eastern coast of Africa and Madagascar. The consequences of this increase differ between social and non-social species. Firstly, for social species only, above a critical number of FOBS, fish are less associated to FOBs. If implications for purse seine fishery are evident, this higher proportion of the population non-associated with FOBs could have ecological impact on social species by preventing them to access to potential benefits resulting from FOBs association (see Introduction section). Secondly, as already highlighted by previous studies (Auger et al. 2010), a very large number of FOBs in comparison to the local abundance of the fish population results in a small number of fish aggregated under each object, which confirms our theoretical results. This pattern is shared by both non-social and social models, under the specific conditions of a small inter-attraction between fish for the latter. This situation would reduce the catch uncertainty (almost all FOBs have fish) but lead to an increase in the number of sets needed to reach a commercially viable level of total catch. Fishing on FOBs contributes to the catch of other species that naturally aggregate around these objects, called bycatch (Romanov 2002; Amandè *et al.* 2010). In the ecosystem approach to fisheries (Pikitch *et al.* 2004), such non-desirable catch should be minimized, knowing that some of those species are threatened (e.g., pelagic sharks Gilman (2011)). It appears that the total amount of bycatch is more dependent on the number of fishing sets (fishing effort) rather than the total amount of tuna caught, which led scientists to consider whether the fishery could reduce its impacts on the ecosystem by avoiding targeting small tuna schools around FOBs, i.e., catching the same total amount of tuna with a smaller number of sets (Dagorn *et al.* 2012a). Limiting the number of sets on FOBs is one of the possible means advanced to mitigate the impact of fishing on FOBs (Dagorn *et al.* 2012b). Therefore, any increase in the number of fishing sets would counteract the reduction of bycatch. For non-social species, the total amount of catch of target species is directly linked to the total number of FOBs, and any limit on the number of sets (e.g., to limit bycatch) would then result in a limit on the total catch. For social species, however, increasing the number of FOBs does not necessarily lead to an increase in the total catch, a result that is not intuitive for many people, including fishermen. Our model shows that, for some particular values of the parameters, deploying a greater number of FADs in the water does not necessarily help fishermen catch more tuna, all other parameters being constant. However, it does increase the number of fishing sets, which certainly increases the bycatch (Dagorn *et al.* 2012a).

Interestingly, the model properties and behaviours are unchanged if we increase the grain by considering small schools of fish as the basic units instead of individual fish (e.g., in Dagorn *et al.* (2000)). This approach is more realistic, but would require modelling social interaction between fish not only when they are at FOBs but also when they are not associated with FOBs. Our model describes how the change in the number of FOBs, which can be adjusted by managing the number of FADs that are deployed by fishermen, could affect the spatial distribution of fish. Such spatial distribution could then impact some key behavioural and biological parameters of the species, in particular for social species. We consider that assessing the effects of the deployment of FADs on the distribution of fish within an array of FOBs is a key step in evaluating the impacts of FADs on the ecology of species, and our model could provide a framework to guide future experiments.

This study identified tropical tunas as the main species of interest because they are the target species of large-scale fisheries in all oceans. Fish aggregations, however, often comprise several fish species (Romanov 2002; Taquet *et al.* 2007; Amandè *et al.* 2010), and our model could easily be used to investigate the effects of increasing the number of FOBs on these other species, both social and non-social. Moreover, fish around a FOB could display some interspecific relationships (e.g., predator-prey interactions). Our model could be adapted to the dynamics of two interacting species, with one species influencing the presence or residence time of the other species around a FOB.

There is no doubt that our analysis and model have some weakness. Indeed, in our analysis, we mainly focused on the stationary solutions of the model in a constant environment. Second, the space is not explicitly modelled. However, a preliminary analysis of the dynamics of a spatial version of the model indicates that our main conclusions remain valid, e.g., in terms of the influence of the number of FOBs and the size of the population of fish on the selection of a single FOB by the population.

This model highlights the need for experiments to characterize the role of the social behaviour of tunas (or other species) in their association with FOBs. Various types of dataset should be used to parameterize our model and to confront output to data. Each of these databases displays advantages and disadvantages, no one being perfect at this time. As a case study, we used observer's data on board commercial purse seine trip (Data Collection Framework – Obstuna database http://sirs.agrocampus-ouest.fr/atlas_thoniers/). This choice was mainly driven by the fact that logbook do not provide information on "empty" FOBS, data are only available for fished FOBs. Even with observer database, fish biomass associated to FOBs is probably underestimated. Indeed, if this biomass does not reach a threshold determine by fishers FOBs are visited but not fished. Nevertheless, we can illustrate with these unsatisfactory data one of our social model predictions i.e. the decreasing pattern in the occupancy rate (e.g the number of fished FOBs divided by the total number of FOBs) when increasing the number of FOBs (Figure 7). To confirm such preliminary results, it would be useful to link them to local abundance of the population using total catches of tuna, including all fleet, available at the RFMOs level. To quantify more precisely the occupancy pattern of FOBs in a given area, another source of data, soon available to scientists, consist in the tuna biomass estimates provided by the satellite linked sonar buoys that fishermen recently deployed around their FOBs.

These preliminary results stress the need to collect accurate data on the number of

FOBs in the ocean and to better characterize fish behaviour at FOBs (Dagorn *et al.* 2012a; Dagorn *et al.* 2012b). Here, we have shown the sensitivity of the aggregation patterns to the individual behaviour (probabilities of leaving and joining a FOB), population size and number of FOBs. However, we assert that the main challenges concerning the questions addressed in this paper and the model predictions are not theoretical, but experimental ones. Specifics experiments are required to provide data needed to calibrate the model parameter (especially g and b). Recent experiments could bring important information to quantify the extent to which social interactions modulate the probability of leaving and reaching a FOBs or a network of FOBs (Robert *et al.* 2013).

Acknowledgments

J.L. Deneubourg is Senior Research Associate of the FRS-FNRS. This study was achieved with financial support from the Commission of the European Communities, specific RTD programme of Framework Programme 7, "Theme 2-Food, Agriculture, Fisheries and Biotechnology" through the research project MADE (Mitigating adverse ecological impacts of open ocean fisheries).

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Figure 1. Model of aggregation process.

Figure 2. Diagrams of solutions For 1 FOB. (a) Space parameters : number of solutions as a function of the parameters g and b (b) Fraction of the total number of individuals around the FOB (x_1) in relation to g for b=5, b=10, and b=20. Solid lines: stable solutions; dashed lines: unstable solutions. (c) Fraction of the total number of individuals around the FOB (x_1) in relation to b for g=10, g=50, and g=100. Solid lines: stable solutions; dashed lines: unstable solutions.

Figure 3. Diagrams of solutions for 2 FOBs. (a) Space parameters: number of solutions as a function of the parameters g and b (b) fraction of the total population around the FOBs as a function of g for a network of 2 FOBs. Stochastic simulation: for b=10 and 2 FOBs: Distribution of experiments according to the fraction of the total population associated with the FOB 1 for g= 10 (c), 34 (e) and 60 (g). Case study of the stochastic simulation of the time evolution of the fraction of the total population associated to each FOBs For g= 10 (d), 34 (f) and 60 (h).

Figure 4. Diagrams of solutions for p FOBs. Space parameters: number of solutions as a function of the parameters g and b for p=10 (a) and p=25 (b) Fraction of the total population around the FOBs (b=10) in relation to p for g=10 (c), g=34 (e), and g=60 (g). Stochastic simulation: mean fraction of the simulated total population around the FOBs (b=10) in relation to p for g=10 (d), g=34 (f), and g=60 (h).

Figure 5. Stochastic simulation. For b=0, b=10 and b=20 and a constant g=10 (a) Influence of the number of FOBs (p) on the maximum number of individuals observed under one FOB (X_{i_max}), (b) Influence of the number of FOB (p) on the total number of individuals under FOBs (T).

Figure 6. Diagram synthetizing the influence of the number of FOBs (p) and the social interaction (b) on the spatial pattern of fish (aggregation of homogeneous distribution).

Figure 7. Boxplot of the proportion of fished FOBs as a function of the number of observed FOBs. Observer's data in the Atlantic and Indian Ocean between January 2006 and august 2010 (Obstuna database: http://sirs.agrocampus-ouest.fr/atlas_thoniers). Number of FOBs observed was calculated on a 2° squared and on a monthly base.

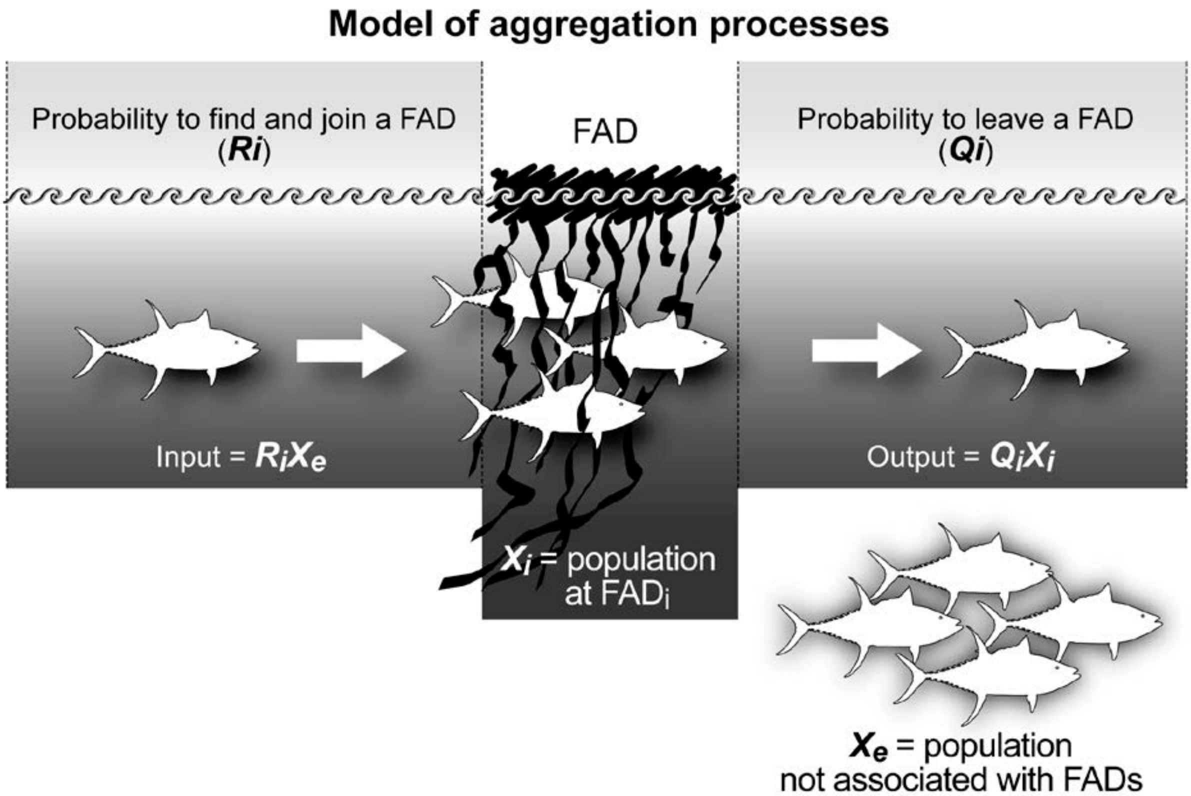

Model of aggregation processes
Probability to find and join a FAD
(Ri)
FAD
Probability to leave a FAD
(Qi)
Input = R_iX_e
Output = Q_iX_i
X_i = population
at FAD$_i$
X_e = population
not associated with FADs

Fig.1

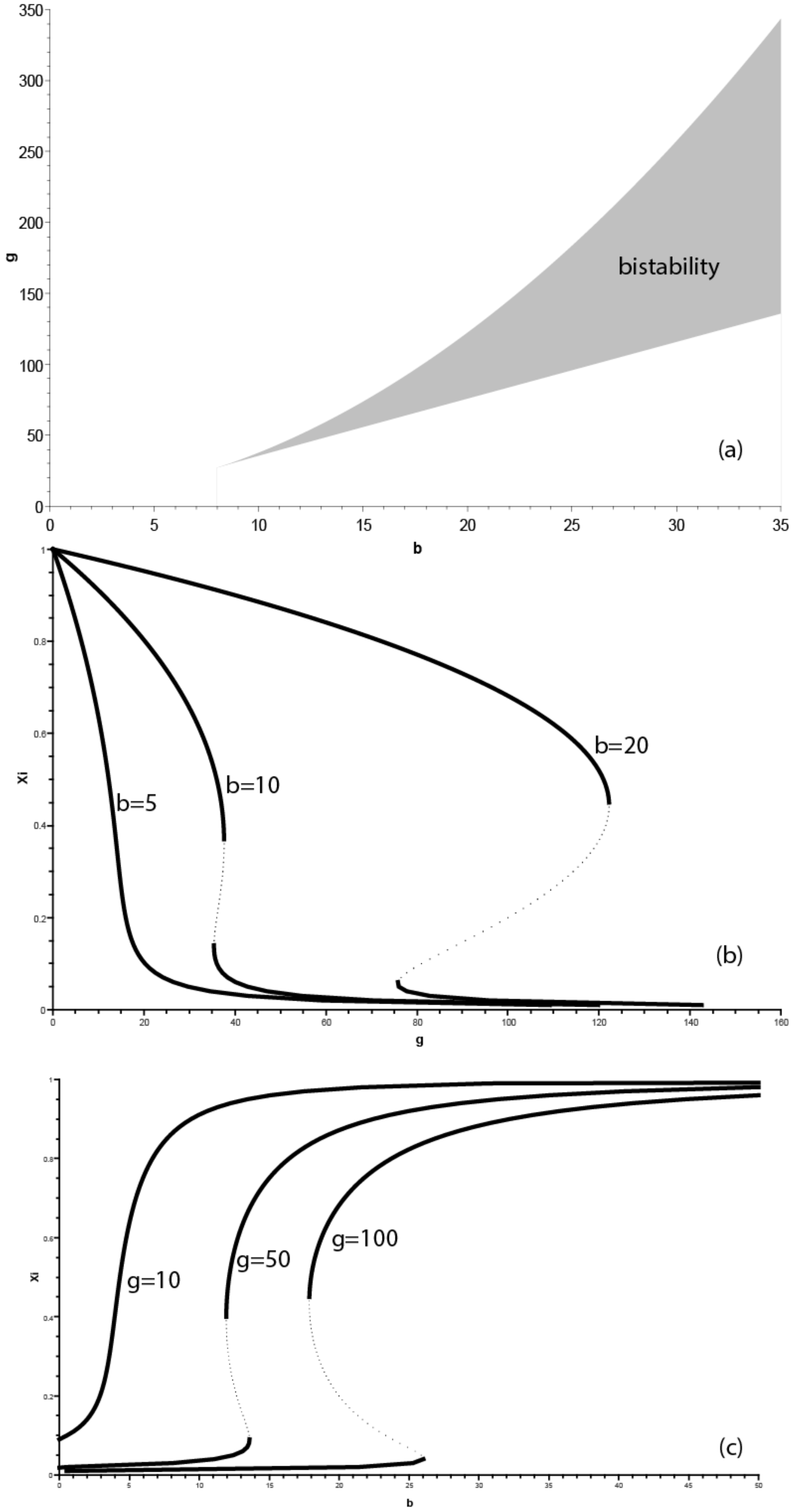

350
300
250
200
150
100
50
0
g
bistability
(a)
0
5
10
15
20
25
30
35
b
b=20
b=10
b=5
xi
(b)
g
g=10
g=50
g=100
xi
(c)
b

Fig.2

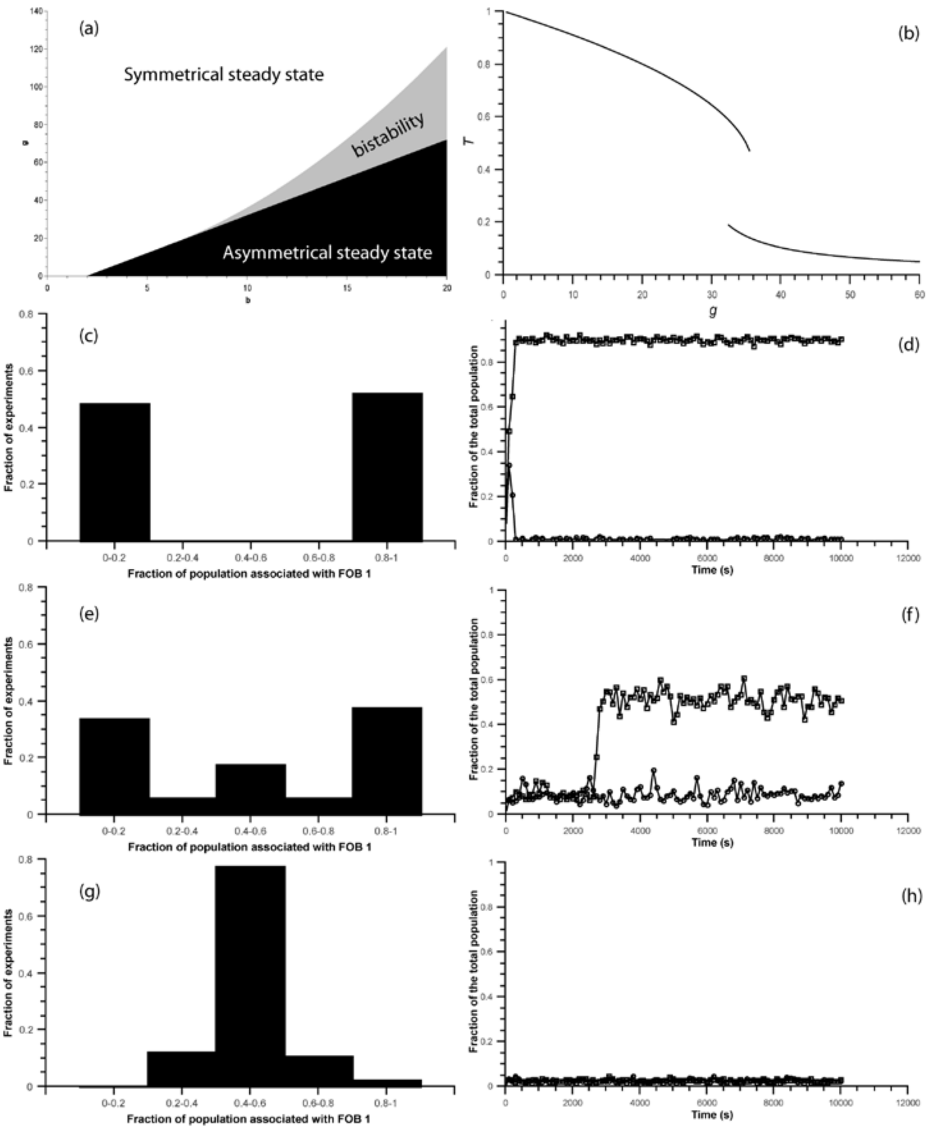
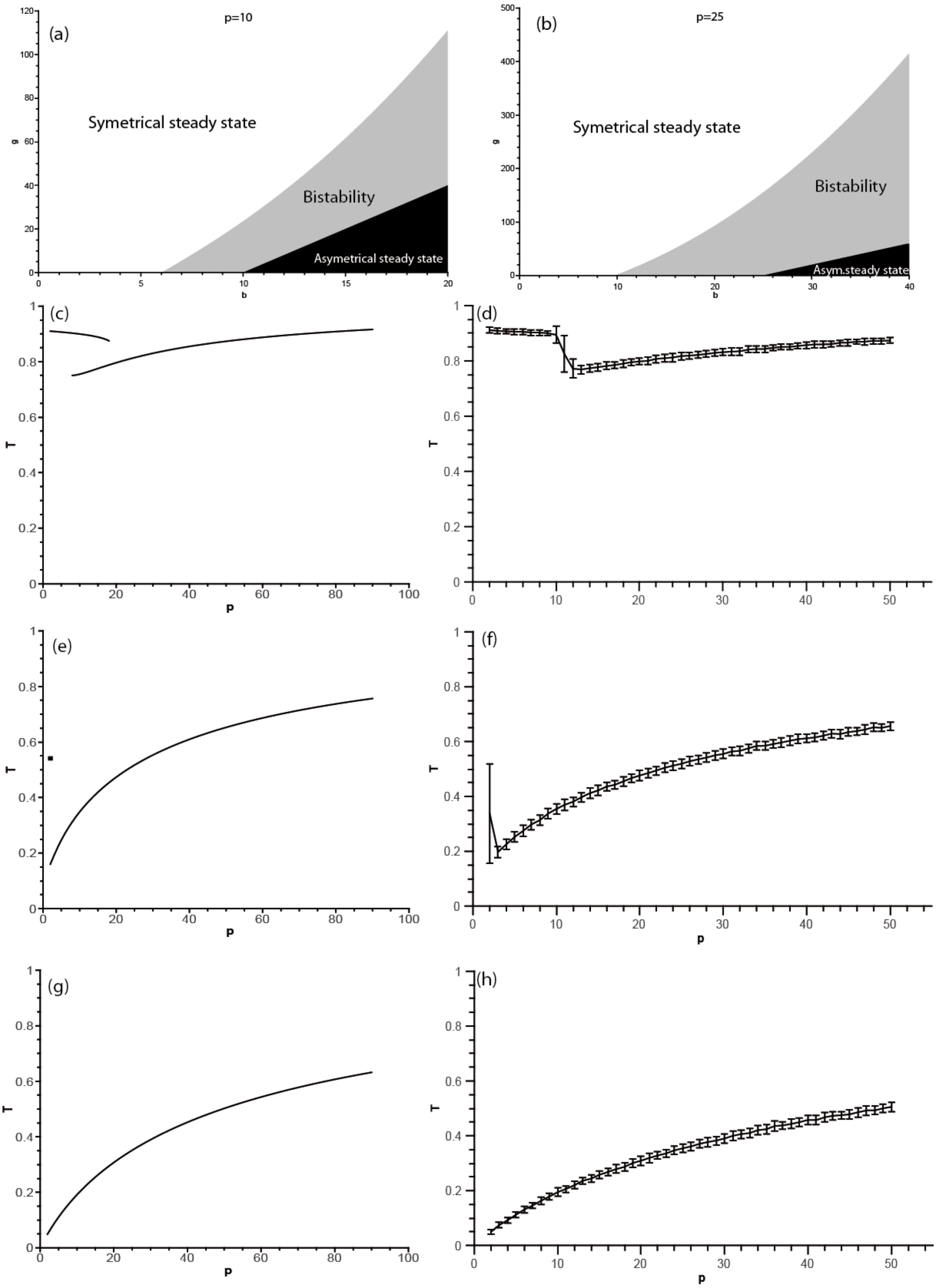

(a)
Symmetrical steady state
bistability
Asymmetrical steady state
(b)
T
g
(c)
(d)
(e)
(f)
(g)
(h)
Fraction of experiments
Fraction of population associated with FOB 1
0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1
Fraction of the total population
Time (s)

Fig.3



(a)
p=10
Symetrical steady state
Bistability
Asymetrical steady state
g
b
(b)
p=25
Symetrical steady state
Bistability
Asym.steady state
g
b
(c)
(d)
(e)
(f)
(g)
(h)
T
p

Fig.4

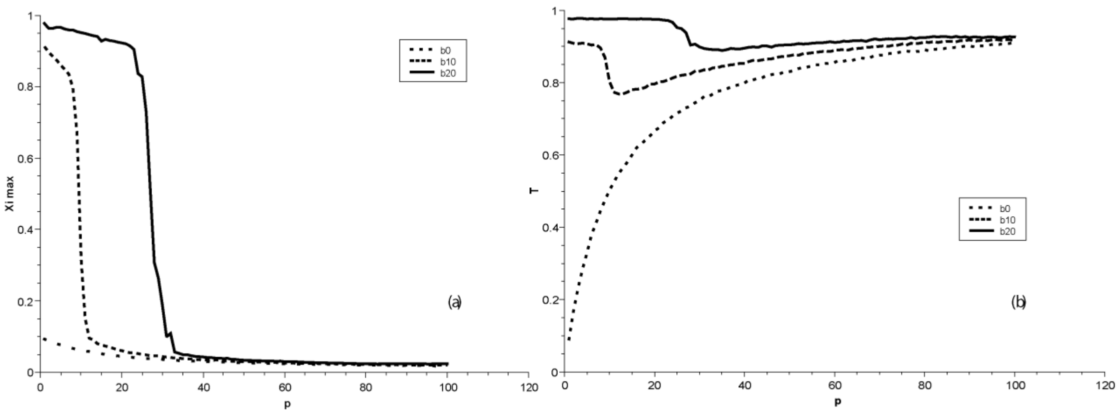


Fig.5

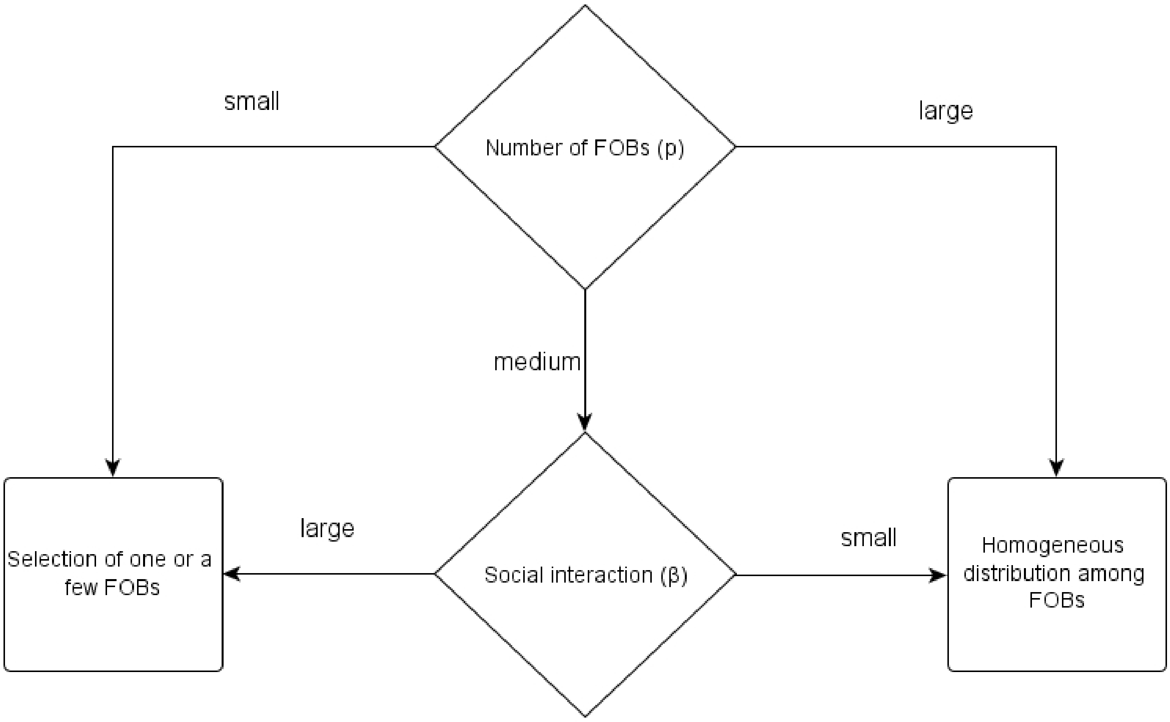

Number of FOBs (ρ)
small
large
medium
Social interaction (β)
large
small
Selection of one or a few FOBs
Homogeneous distribution among FOBs

Fig.6

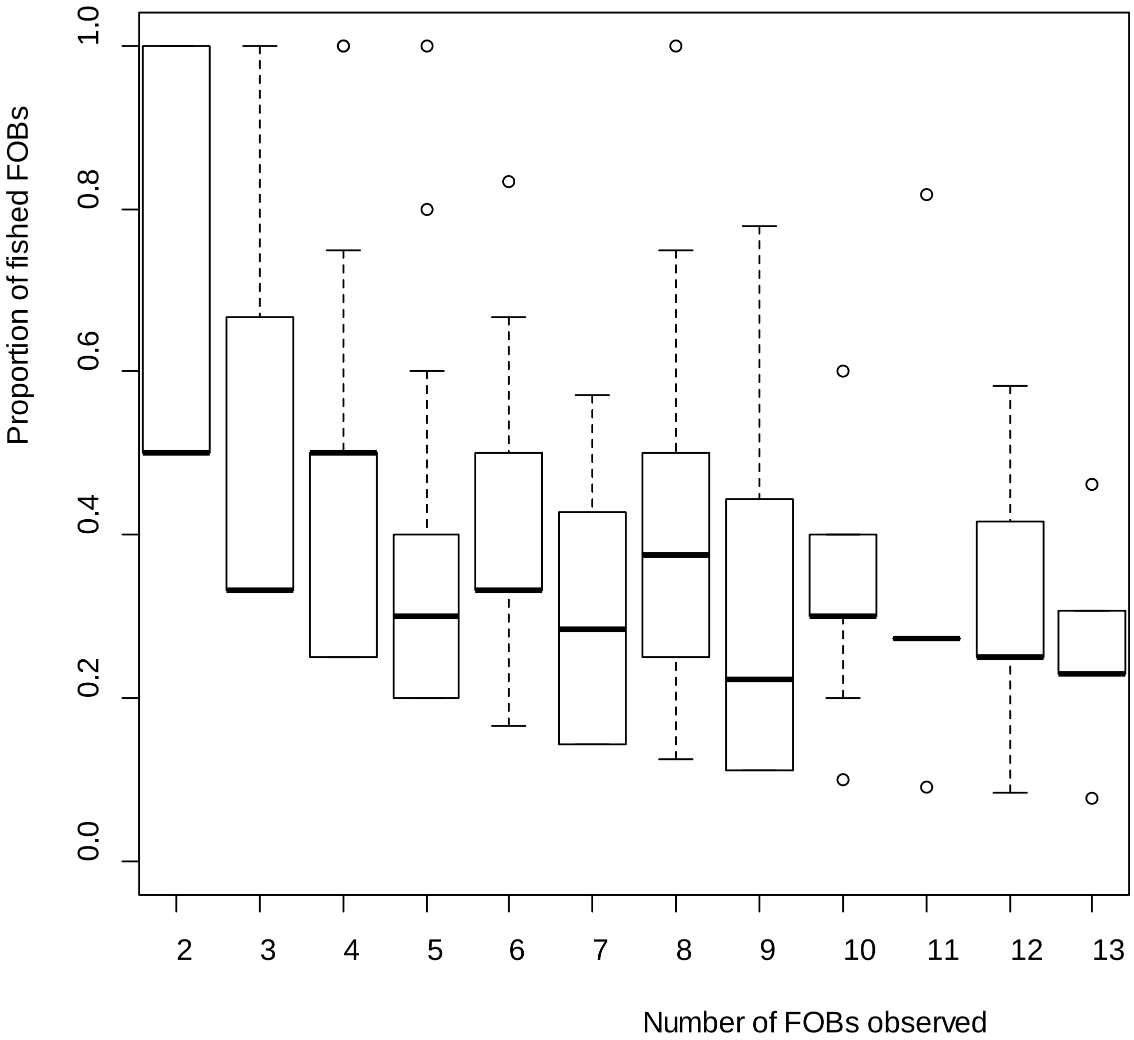

Proportion of fished FOBs
0.0
0.2
0.4
0.6
0.8
1.0
2
3
4
5
6
7
8
9
10
11
12
13
Number of FOBs observed

Fig.7