

Modeling tuna behaviour near floating objects: from individuals to aggregations

Laurent/Dagorn^{a*}, Erwan/Josse^b, Pascal/Bach^a, Arnaud Bertrand^b

^a Centre IRD de Montpellier, BP 5045, 34032 Montpellier cedex 1, France

^b Centre IRD de Brest, BP 70, 29280 Plouzané cedex, France

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Abstract – A fuzzy logic model of tuna behaviour near Fish Aggregating Devices (FADs) was developed to reproduce individual differences in horizontal movements observed from ultrasonic telemetry experiments. In this model, the behaviour of an individual is based on its surrounding environment (FADs and prey) and on its internal state (stomach fullness), which depends on its recent past actions. Internal sensors are used to determine the motivation of the fish, combined with external sensors, this determines its movements. Sensory information and motivation are modeled using fuzzy sets. A FAD attracts an individual when it is located within the FAD's range of influence. The time spent near a FAD depends on the feeding motivation of the fish and on its surrounding environment. If the fish is not hungry, it stays near the FAD. Otherwise, the fish has to forage in order to eat, and might therefore leave the FAD if no prey is available in its vicinity. By varying the environmental conditions near FADs, the model reproduces the different horizontal movement patterns observed for tunas. The model is then extended to allow multiple individuals to co-exist, each individual modeled through the above behavioural model, without any direct or indirect interactions between them. This way, we study the effects of individual behaviour on tuna aggregation near FADs. We find that the model predicts the temporal dynamics of aggregation around FADs exhibited by tunas. By examining the effects of several FAD network models on the aggregation, we also estimate optimal spatial arrangements of FADs. © 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

tuna / Fish Aggregating Devices / behaviour / model / fuzzy logic

Résumé – Modélisation du comportement des thons autour des objets flottants : des individus aux agrégations. Un modèle de logique floue du comportement des thons autour de dispositifs de concentration de poissons (DCP) est développé pour reproduire les différences individuelles observées dans les mouvements horizontaux à partir d'expériences de télémétrie ultrasonique. Dans ce modèle, le comportement d'un individu est basé sur son environnement local (DCP et proies) et sur son état interne (taux de remplissage de l'estomac), qui dépend de ses actions passées. Des capteurs internes déterminent la motivation du poisson, qui, combinée avec des capteurs externes, détermine ses mouvements. Les informations sensorielles et la motivation sont modélisées avec des ensembles flous. Un individu est toujours attiré par un DCP s'il se trouve dans un certain rayon autour de celui-ci. Le temps passé autour d'un DCP dépend de la motivation alimentaire du poisson et de son environnement local. Si le poisson n'a pas faim, il reste autour du DCP. Sinon, le poisson doit rechercher de la nourriture, et peut ainsi quitter le DCP s'il ne trouve pas de proies aux alentours. En variant les conditions environnementales autour du DCP, ce modèle reproduit les différents mouvements horizontaux observés chez les thons. Le modèle est ensuite étendu pour permettre la coexistence de plusieurs individus, sans aucune interaction directe ou indirecte entre ceux-ci. Ceci permet d'étudier les effets des comportements individuels sur les agrégations de thons autour de DCP. Le modèle prédit avec précision les dynamiques temporelles des agrégations de thons autour de DCP. En simulant différents réseaux de DCP, le modèle permet d'estimer la meilleure organisation spatiale des DCP. © 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

thon / dispositif de concentration de poissons / comportement / modèle / logique floue

*Corresponding author.

E-mail address: Laurent.Dagorn@ird.fr (Laurent Dagorn).



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1. INTRODUCTION

Tropical tuna, *i.e.* mainly skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*), are known to associate with objects floating at the surface of the ocean. These objects can be natural, such as branches, debris, dead animals, or artificial, coming from human pollution, or constructed and released by fishers to increase their chances of finding tuna. These man-made floating objects are named Fish Aggregating Devices (FADs) and some of them are anchored at inshore areas for local tropical fisheries.

Various ultrasonic telemetry experiments have been conducted on tropical tuna near anchored FADs (Cayré and Chabanne, 1986; Holland et al., 1990; Cayré, 1991; Bach et al., 1998; Josse et al., 1998; Marsac and Cayré, 1998; Dagorn et al., 2000b), providing information on horizontal and vertical movements of the fish. The exact influence of FADs on tuna behaviour is not well known. Reviewing the different tracks of tuna, Holland (1996) identified three horizontal patterns:

- fish that leave the FAD and show no tendency to return to it over the duration of the tracking,
- fish that spend the entire duration of the tracking, day and night, within a few hundred meters of the FAD,
- fish that spend the daytime at the FAD site, leave at night and return to the same or to an adjacent FAD the next day.

The reasons for these individual differences are not known (Dagorn et al., 2000b). It is clear that information about the internal state of the fish and their surrounding environment is needed for a better understanding of the motivations for these movements. As fish do not exhibit a unique pattern of horizontal movements near FADs, and as the reasons for the individual differences are not known, we rely on hypotheses to interpret these movements.

The first objective of this paper is to propose a model of individual behaviour that succeeds in representing the individual differences observed in the different tracks of tuna near FADs. One of the major problems in behavioural studies is the change of scales, *i.e.* in our case, from individuals to aggregations. Individual-Based Models (IBMs) have been successfully applied in terrestrial ecology (Huston et al., 1988; Hogeweg and Hesper, 1990), fish ecology (Tyler and Rose, 1994), and more recently to the issue of tropical tuna associated with floating objects in a simulation study of the meeting point hypothesis (Dagorn and Fréon, 1999). IBMs represent appropriate tools to study the consequences of individual behaviour at larger scales. Simulation results will be compared to recent acoustic observations made with acoustics of tuna aggregated around FADs (Josse et al., 2000).

The last objective of this study is to examine the effects of different distances between, and different

spatial distributions of FADs on the number of tuna aggregated near the floating objects. The role of such model as an element of an integrated research program will be discussed.

2. MATERIALS AND METHODS

2.1. Modelling the ocean

The ocean is modeled as a toroidal two-dimensional grid with hexagonal cells. The hexagonal shape of the cells ensures respect for spatial isotropy better than a squared one would. One cell represents 1 nautical mile, *i.e.* 1.8 km. Although tuna live in a three-dimensional environment, only the horizontal movements are considered in this study. Therefore the artificial ocean only requires two dimensions. Prey is distributed in the artificial environment into patches of cells, following a simplified model of spatial distribution and temporal dynamics based on acoustic surveys made in French Polynesia (Bertrand et al., 1999). The nocturnal environment is modeled by the Sound Scattering Layer (SSL), which is composed of small organisms (crustaceans, small fish, cephalopods) migrating vertically at dawn and dusk, and occupying deep waters during daytime and shallow waters during night-time. In contrast to large bigeye tuna in the open ocean (Dagorn et al., 2000a), the fish in the model (mainly juvenile tuna) cannot forage on this layer in deep waters during daytime but can only have access to it during night-time. The SSL occupies the entire grid during night-time, which implies that each cell contains prey. During daytime, two-cell radius patches are randomly distributed over the grid: they represent prey that is accessible during daytime to tuna in their habitat. The density of prey inside a cell remains constant during the lifetime of the patch (daytime or night-time), whatever the consumption by tuna may be. This way, we consider that the consumption by tuna during half a day does not significantly affect the prey density of a patch, considering also that tuna are not the unique predators of this ecosystem.

2.2. Modelling tuna behaviour

Dagorn et al. (2000b) point out that information to interpret the horizontal movements of fish is lacking. In particular, the roles of prey and of the internal state of the fish on tuna movements around FADs were clearly considered major determinants. In the model used here, FADs are considered to be suitable places for tuna, whatever the reason for this may be. The current hypothesis is that a fish is attracted by a FAD (except if the fish is leaving the FAD because of another motivation, see below) and can stay associated with it as long as the association is viable, *i.e.* as long as the fish meets its metabolic requirements. In other words, we consider that as long as the fish is not hungry, or as long as the fish can feed near a FAD, it can stay associated with the floating object. It is widely

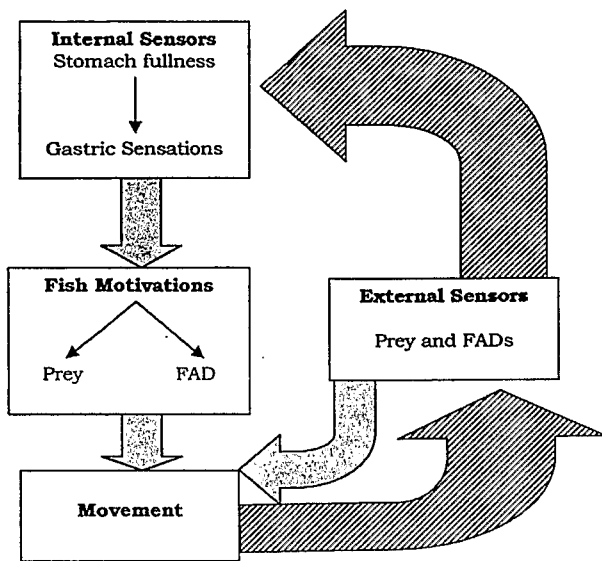


Figure 1. The simplified algorithm for an artificial tuna. The behavioural motivation of the fish is determined from its internal sensors. The movement is determined from the fish's motivation and its external sensors. The consequences of the action reflect on the fish's internal movements.

accepted that the degree of stomach fullness and other physiological parameters are internal factors which determine the feeding motivation (Colgan, 1993). The stretch receptors in the stomach of the fish can make the fish hungry, or satiated. The artificial tuna of the present model therefore have internal sensors to determine their feeding motivation and external sensors to 'know' about their surrounding environment. *Figure 1* represents the simplified algorithm for the behaviour of an artificial tuna in this model.

2.2.1. Feeding and digestion

The temporal evolution of the stomach fullness (St) is modeled as:

If

$$(St(t-1) > 0)$$

then

$$St(t) = St(t-1) + I - E$$

Otherwise:

$$St(t) = 0$$

where t is a time step, and I and E represent the ingested volume and the evacuated volume during one time step, respectively. In the model, $St(t)$ is expressed in percentage and ranges between 0 (empty stomach) and 100 (full stomach), as the internal state of an artificial tuna is determined through the stretch receptors in the stomach.

When the fish does not feed, I equals zero. When it feeds on a cell containing prey, the stomach fullness increases by a constant value (I) that depends on the prey density of the cell. At each time step, the gastric evacuation decreases the stomach fullness with a constant rate E . The rate of digestion will be considered to be constant and independent of the stomach fullness. It is known that the type of prey organism ingested significantly affects the rate at which food passes the fish's stomach (Olson and Boggs, 1986). We consider that the prey organisms of the modeled ocean all belong to the same type. The gastric evacuation rate is calculated as:

$$E = (100/T_d) \times d_{step}$$

where T_d is expressed in hours and d_{step} is the duration (in h) of a time step, i.e. 0.5 h.

2.2.2. Gastric sensation

An artificial tuna does not know its gut fullness (St) with precision, but it "feels" sensations like hunger, satiety, or an intermediate state. Fuzzy sets are a powerful tool for representing sets with fuzzy boundaries like those gastric sensations (Bonarini, 1997).

Given a range of continuous values (such as real numbers, in our case the stomach fullness expressed as a percentage of the maximum total stomach volume), it is possible to define a membership function that gives the degree of membership (μ) to a fuzzy set of any value belonging to the universe of discourse. We define three fuzzy sets, each corresponding to a gastric sensation: *Hunger*, *Intermediate*, *Satiety*. For the considered range of possible values (from 0 to 100 % of the stomach volume), we define a membership function that gives the degree of membership (μ) to one of the three fuzzy sets: μ_{Hunger} , $\mu_{Intermediate}$, $\mu_{Satiety}$. For instance, $\mu_{Satiety}(90)$ represents the probability that a fish with a stomach fullness of 90 % is satiated. *Figure 2* shows that with a fuzzy classification, the value 85 % is always considered as *Intermediate*:

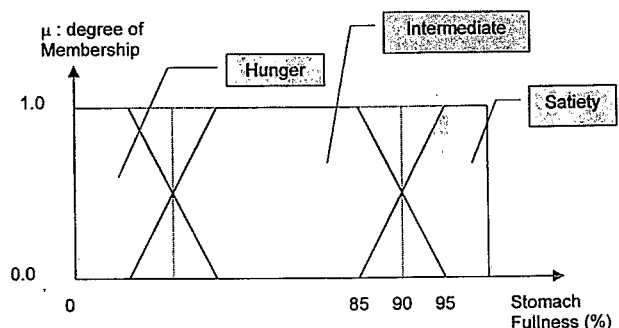


Figure 2. Fuzzy sets and intervals for the classification of values of the variable "stomach fullness" for the determination of gastric sensations. Considering one value of stomach fullness, the degree of membership (μ) determines the probability that the fish is feeling one of the three gastric sensations.

$$\mu_{\text{Intermediate}}(85) = 1$$

The nearby value 90 % is still considered as *Intermediate* with a degree:

$$\mu_{\text{Intermediate}}(90) = 0.5$$

but is also considered as *Satiety* to some extent:

$$\mu_{\text{Satiety}}(90) = 0.5$$

With an interval-based classification, the value 89 % is considered as *Intermediate*, and the close value 91 % is considered as *Satiety*. A fuzzy model, rather than an interval-based model, seems to be more appropriate to represent the gastric sensation (which is called a fuzzy variable).

The membership function needs two threshold values to classify the stomach fullness into one of the three labels (*Hunger*, *Intermediate*, *Satiety*). The threshold distinguishing between *Hunger* and *Intermediate* is set to 10 and the threshold distinguishing between *Intermediate* and *Satiety* is set to 90.

2.2.3. External sensors

An artificial tuna is able to detect prey and FADs within a range detection of one cell, i.e. 1 nautical mile or 1.8 km. From ultrasonic tagging studies on individuals around anchored FADs (Cayré and Chabanne, 1986; Holland et al., 1990; Cayré, 1991) and from models (Hilborn and Medley, 1989; Kleiber and Hampton, 1994), the radius of an area over which a floating object has an effect is estimated at 4 to 7 nautical miles (7–13 km). The value of 5 nautical miles (i.e. 5 cells) was used in most of the simulations, and different values (from 2 to 10 nautical miles, i.e. 2–10 cells) will be tested when different models of FAD networks will be studied. The fish do not know the distance to the FAD but can determine its direction when detecting it. The direction is modeled through a fuzzy variable with six labels (corresponding to the directions of the six neighbor cells), meaning that the fish has only fuzzy information about the direction of the FAD.

2.2.4. Behavioural motivation

A set of fuzzy rules is defined to determine the motivation of the fish. A fuzzy rule is an “if-then”-rule, mapping fuzzy variables to other variables (Bonarini, 1997). In this fuzzy control, gastric sensation is the antecedent and classifies the input from internal sensors. The variable in the consequent is the motivation, which can take two labels: *Prey* and *FAD*, corresponding to the search for prey or FADs. The rules mapping the gastric sensation to the motivation are illustrated in Figure 3. When the gastric sensation is *Hunger*, then the motivation is always *Prey*. When the gastric sensation is *Satiety*, then the motivation is always *FAD*. When the gastric sensation is *Intermediate*, the motivation depends on the recent history of the gastric sensation; it corresponds to the motivation established

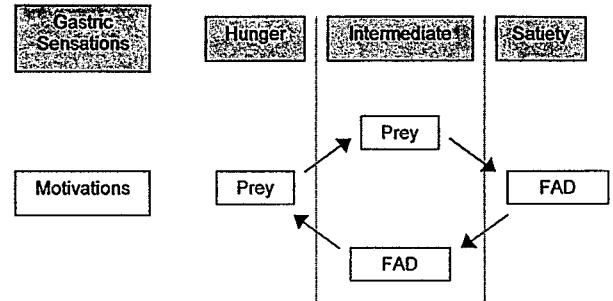


Figure 3. Determination of the fish motivations from its gastric sensation. If the fish is in the *Intermediate* state, the motivation depends on the previous gastric sensation. If the fish was *Hungry*, the fish's motivation is still to look for prey. If the fish was *Satiated*, the fish's motivation is still to look for FADs.

after the previous gastric sensation. If the previous sensation was *Hunger*, and if the fish is in an *Intermediate* state because it fed, then the motivation remains *Prey*. In contrast, if the fish was satiated, and if digestion brought it to an *Intermediate* state, the motivation remains *FAD*.

2.2.5. Movement

Another set of fuzzy rules connects motivation to action. If the individual's motivation is *Prey*, the fish forages. The fish examines the five nearest cells (it does not have access to the cell directly behind it) and it randomly chooses the cells that contain prey (Figure 4). The fish then moves towards a rich cell and feeds. If no rich cell is detected, the fish adopts a random movement. These random movements correspond to an extensive search mode adapted to patchy environments with a low sinuosity, i.e. a low probability of changing directions (Benhamou, 1992). The probability to keep the same direction is 0.5; the probability to change the direction by -60° or $+60^\circ$ is 0.2; the probability to change the direction by -120° or $+120^\circ$ is 0.05, and the fish can not change its direction by 180° in one time step. If the fish detects a FAD while having a *Prey* motivation, and if it does not detect a rich cell, the fish moves towards the FAD (Figure 5).

If the motivation is *FAD*, the richness of the cells around it does not affect its movement. The fish randomly moves according to an extensive search mode, similar to when it looks for prey, to find FADs (see above). When a FAD is detected, the fish moves towards it to stay on the cell containing the FAD. If the gastric sensation is *Satiety*, the fish does not feed, even when located on a rich cell. Otherwise, the fish can feed if the cell contains prey.

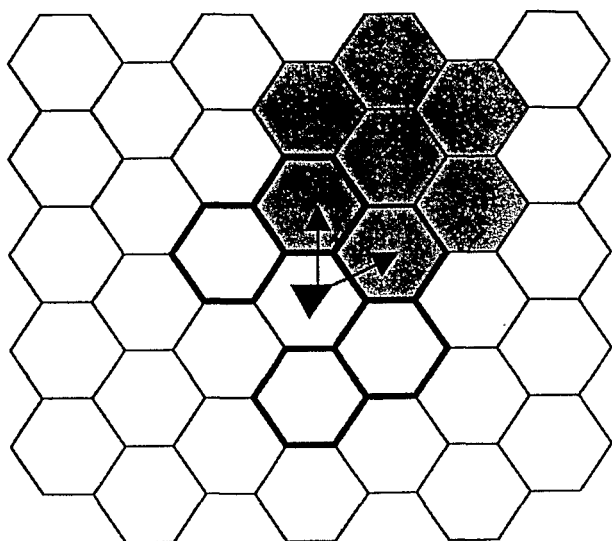


Figure 4. Movements of a fish after detecting prey in its surrounding environment. The black triangle represents the fish. Grey cells contain prey, white cells do not contain any prey. The fish randomly chooses between the rich cells.

3. RESULTS

3.1. Individual behaviour

One FAD was put in the middle of a 10×50 -cell grid and the biological environment was modeled using the model described previously (SSL for nighttime and 2-nautical miles (3.6 km) radius prey patch during daytime). Simulations were performed for a

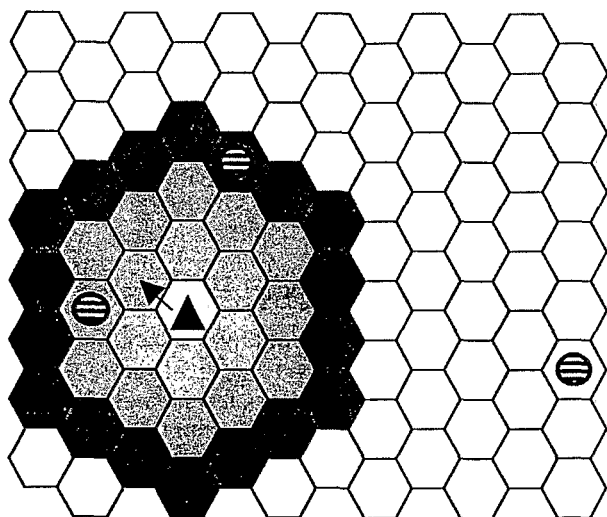


Figure 5. Movements of an artificial tuna in the presence of FADs. The black triangle represents the fish. Black circles correspond to FADs. The grey cells represent the range within which an artificial tuna can detect a FAD. In the present case, the range is three cells.

complete evacuation of a full stomach in 5 h. (see Brill, 1996) and a radius of detection of FADs of 5 nautical miles (9 km).

Figure 6 represents simulation results showing the three patterns of horizontal movements as they were identified by Holland (1996) from ultrasonic telemetry experiments on tropical tuna at FADs around the world. These movements were produced by the same artificial tuna, i.e. a unique algorithm for the behavioural rules. The different patterns were obtained due to a different spatial distribution of the prey patches, and as a consequence, different fish motivations. In *figure 6a*, no prey was located under the FAD with which the fish was associated. The fish lost energy and when its stomach was empty, its motivation changed from *FAD* to *Prey*. The artificial fish then left the FAD to look for food. Since no prey was located in the vicinity of the FAD, the fish did not return to the FAD and had to forage away from the FAD to fill its stomach.

Figure 6b shows that a prey patch was located in the very close vicinity of the FAD. In this simulation, the fish could stay associated with the FAD, or could make very small-range movements around the FAD in order to feed. The association could then last for a long time.

Figure 6c shows that the fish had to leave the FAD to feed. However, in contrast to *figure 6a*, the fish found a prey patch and could return to the FAD when it detected it again, which was dependent on its detection range.

3.2. Temporal dynamics of the aggregations

A total of 1 000 individuals, all with the same behaviour, are randomly distributed throughout the artificial ocean which in size and biological environment is similar to the one used in the previous section. The individuals show no direct or indirect interactions, as they cannot communicate and they do not modify their habitat. The stomach fullness of each individual at the start of a simulation is a random integer value between 0 and 100; individuals do not start under identical internal conditions. The number of fish under the FAD is recorded for each time step of 0.5 h. Yellowfin and skipjack tuna evacuate food from the stomach faster than most other fishes studied (Olson and Boggs, 1986; Brill, 1996). Small tuna reach 100 % gastric evacuation in approximately 5–12 h (Brill, 1996). Therefore, different lengths of time for a complete gastric evacuation were tested: 5, 10, and 12 h, to test values in agreement with our knowledge of the biology of tuna (Brill et al., 1996). Out of the range of biological values, gastric evacuation times of 3 h and 15 h were tested. *Figure 7* shows the temporal evolution of the sizes of the aggregations over a 48-h period, chosen once the system has stabilized (after some 'days' of simulation). In *figure 7*, the sizes of the aggregations are relative to the maximum biomass reached during the 48-h period of each simulation. This allows us to compare the patterns between the different simulations. When fish have a complete gastric evacuation duration of 15 h, the size of the aggregation under

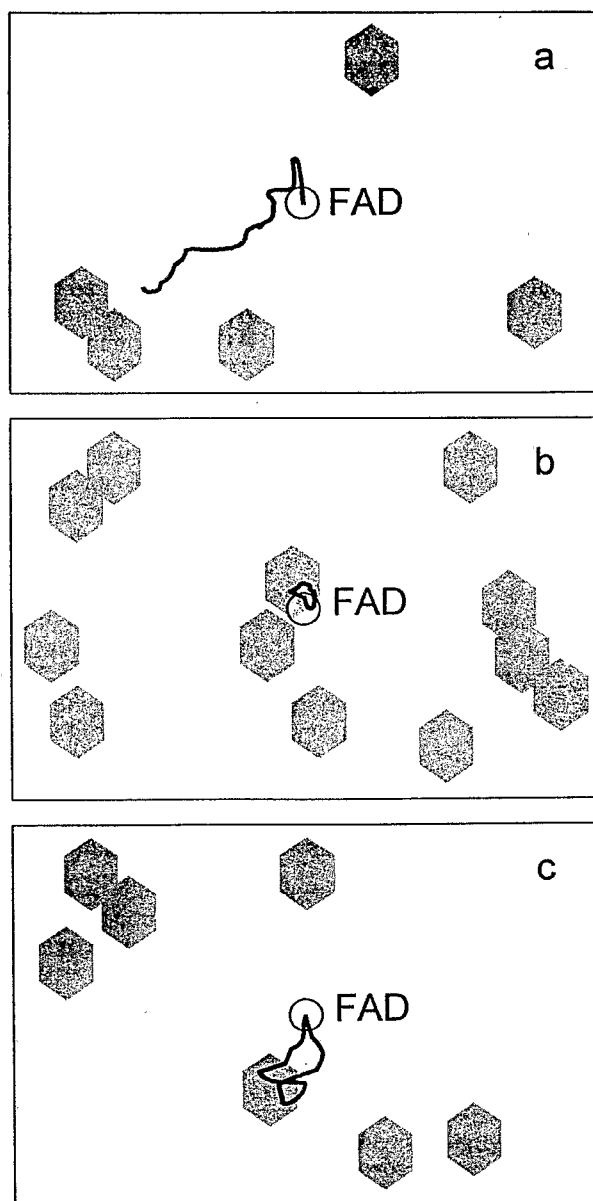


Figure 6. Different patterns of horizontal movements obtained from the same individual, in different environments: (a) no prey patch in the vicinity of the FAD, the fish leaves the FAD when it is hungry and does not return to it; (b) a prey patch and the FAD are located at the same site, the fish does not leave the FAD; (c) a prey patch is located in the vicinity of the FAD, the fish leaves the FAD to forage, find the prey patch, then comes back to the FAD. There is no spatial memory.

the FAD is quite constant over a 24-h cycle and very different from patterns obtained with other digestion rates. With a duration of a complete gastric evacuation equal or lower than 12 h, we observe a common pattern where fish start to aggregate under the FAD around 20h30 or 21h00 in a very fast aggregating process until midnight. Then the aggregation rate slows down. The time at which the maximum biomass is obtained varies

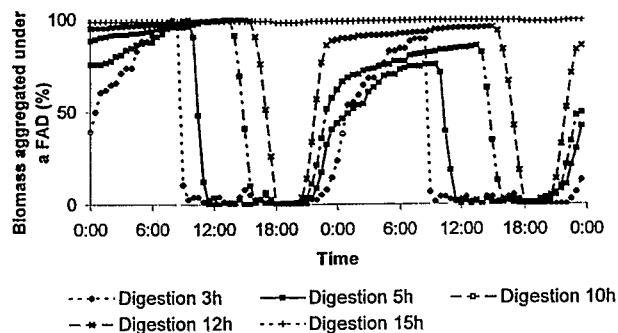


Figure 7. Simulation results: the temporal evolution of the number of tuna aggregated under a FAD during a period of 48 h, from simulations with different duration of complete gastric evacuation. The number of fish in the artificial environment is 1 000.

from 08h30 (for a digestion of 3 h) to 15h30 (for a digestion of 12 h). After these peak times, the size of the aggregation drops down drastically. Fish with fast digestion rates leave the FAD sooner than fish with lower digestion rates.

3.3. Effects of distance between FADs and network structure on the number of fish aggregated by FADs

Seven FADs are put in a 200×200 toroidal grid and 5 000 individuals, all with a 5-h duration of complete gastric evacuation, are randomly distributed in the artificial ocean. The biological environment is similar to the one used in the previous simulations. Two different networks are tested. The first one has the form of a star, with a FAD in the center and the six other FADs around it (*figure 8a*). The second network has all seven FADs in a line (*figure 8b*). Different distances between FADs have been tested (from 4 to 28 nautical miles, i.e. 7.4 to 52 km, arithmetic progression of 4 nautical miles, i.e. 7.4 km) as well as different ranges of detection of FADs (from 0 to 10 nautical miles, i.e. 3.6–18 km, arithmetic progression of 2 nautical miles, i.e. 3.6 km).

The objective of these simulations is to determine the maximum number of fish aggregated under each FAD each day. Runs lasted 14 400 steps (i.e. 300 days) and *figure 9* shows the mean values of the maximum number of fish aggregated under each FAD each day in each network.

First, the type of network did not affect the number of fish aggregated by the FADs of the network. For all the different ranges of influences tested, and whatever the type of network was, the maximum number of fish per day is obtained when the attraction areas of FADs do not overlap. It appears however, that values such as 12 or 16 nautical miles (22.3–29.8 km) always produce big aggregations, despite any overlapping of the FADs' influence. Greater distances between FADs do not modify the number of fish aggregated by the network.

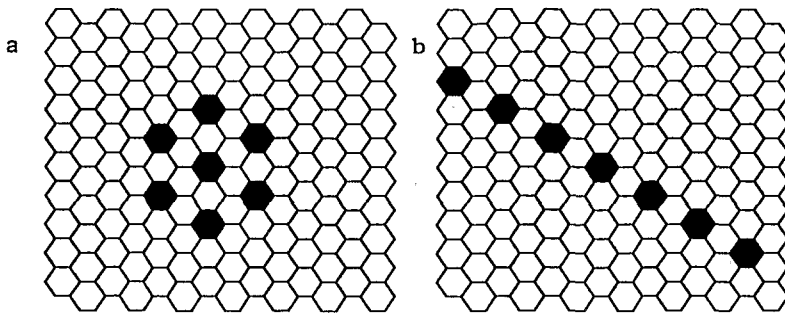


Figure 8. The two different types of networks of FADs tested in the simulations: (a) star and (b) line.

4. DISCUSSION

The model developed in this study is based on simple rules to govern the behaviour of individuals. These rules, combined with a plausible model of the prey environment derived from acoustic surveys, allow us to reproduce the different patterns observed during ultrasonic telemetry experiments (Holland, 1996; Dagorn et al., 2000b). The single and simple model constitutes a reliable model for tropical tuna behaviour near floating objects. The use of fuzzy sets allowed the development of models of fish behaviour more realistic.

Simulations involving numbers of individuals with no direct or indirect interactions and that follow the

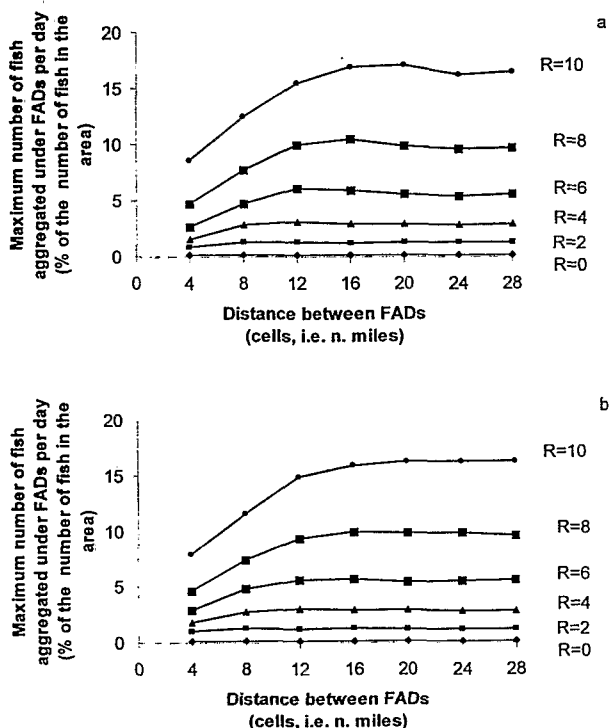


Figure 9. Maximum number of fish aggregated under each FADs, each day, for each network: (a) star and (b) line. Different radii of attraction by a FAD (R), were tested.

same rules can be compared with in situ acoustic observations of tuna associated with anchored FADs (Josse et al., 2000). Two-hour acoustic surveys were conducted around FADs in order to estimate the number of fish aggregated under them. It should be noted that we assume that the number of fish observed during each survey is constant over the 2-h period of each survey. It was not possible to continuously record the aggregation sizes over 24 h, so we only have discrete values at some periods of the 24-h cycle. The comparison of the simulations with real observations made with echo sounders in French Polynesia shows some clear similarities. *Figure 10a* compares two series of survey made around a FAD anchored north of the Marquesas Islands with simulations of fish having a complete gastric evacuation in 5 h, which was the simulation that reproduced best the observed peak time of aggregation. *Figure 10b* shows a series of acoustic survey made around a FAD located close to the island of Tahiti, compared with simulations with fish having a complete gastric evacuation in 12 h, which produced a similar peak time. First, the speeds of the aggregation/disintegration processes in the simulations and in the real data were similar. This similarity suggests that the aggregation/disintegration processes may be triggered by a single stimulus. In the present model, this is due to the dynamics of the prey, in particular the accessibility of nocturnal prey, and similar digestion rates of fish in the area. Second, the three series of acoustic survey have shown three different peak times: 07h30, 10h30, and 16h50. The differences between these peak times (two in the morning and one in the afternoon) may result from the presence of different sizes of fish in the aggregations. The two series of survey that have shown peak times in the morning comprised small fish (yellowfin and bigeye tuna of 50 cm fork length), while the aggregation with the maximum biomass in the afternoon was composed of larger fish (yellowfin and bigeye tuna between 60 and 100 cm fork length). These differences in fish size may correspond to differences in digestion rate, as suggested by the model. Nevertheless, we also notice clear differences between simulated and real data. The most important one is the time at which fish start to aggregate (in particular in *figure 10a*). This can be due to the fact that possibly the modelled environ-

ment does not exactly reproduce some important features of the real prey environment. Therefore particular attention should be paid to the observation of prey and to their accessibility to tuna. Differences in the time span required to empty a full stomach might represent different biological abilities of the fish, or different types of prey with different spatial organizations, since it is also known that the type of prey affects digestion. In the absence of communication between individuals, the model shows that the cycle is imposed by the prey environment. Even if fish have different internal states, exploiting the same prey patch leads to homogeneity of the fish's conditions, hence homogeneity of fish's motivations and actions, and high speeds for aggregation or disintegration processes. We only rely on three series of acoustic survey, a data set that is not sufficient to draw convincing conclusions and to really test the hypotheses incorporated in the model. Moreover, tuna are known to school, which may also affect the aggregation process. Combining the present model with a model for schooling behaviour (Stocker, 1999) would be a good way to examine the role of schooling on the aggregation of tuna near floating objects.

The kind of model described here depends on hypotheses about behavioural mechanisms, or about biological threshold values. The simulations show some patterns that depend on these hypotheses as well on the environment where the 'artificial' tuna behave. When a model reproduces patterns observed in the wild, then we may assume that the hypotheses (concerning the behavioural mechanisms or the threshold values) are likely to be real ones, which can provide a framework for some new field observations. But when such models do not reproduce patterns, it is sometimes possible to reject certain hypotheses used to develop the model and which is of key importance.

The model has a double objective. The first objective of this kind of model is to be an element of an integrated research program where modellers and biologists work in very close collaboration to improve the understanding of tuna behaviour near floating objects. A second objective can be addressed when some apparent similarities between real data and the model are found. Because these models are based on behavioural mechanisms, they may be used to predict the effects of particular environmental conditions, or of changes in the habitat of these fish, on their behaviour. The previous results of simulations of individual behaviour ensure the realism of the present model and allow us to test the effects of different types of networks and differently spaced FADs, with respect to FADs having different ranges of influences. Several authors estimated the attraction area of FADs to be 4 to 7 nautical miles (7–13 km) (Cayré and Chabanne, 1986; Hilborn and Medley, 1989; Holland et al., 1990; Cayré, 1991; Kleiber and Hampton, 1994). It is noteworthy that whatever the range of influence of FADs was (from 2 to 10 nautical miles, i.e. 3.6–18 km), deploying FADs with inter-FAD distances equal to or

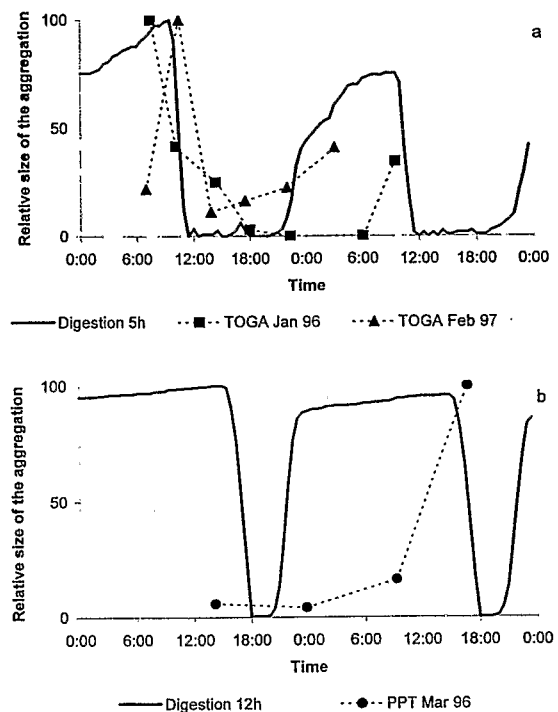


Figure 10. Temporal evolution of the aggregated biomass in a 48-hour period from acoustic and simulated data. Acoustic estimations of the number of fish aggregated under FADs were made through 2-h acoustic surveys in French Polynesia (Josse et al., 2000). For each 2-h survey, the estimated number of fish is reported by a point at the time corresponding to the middle of each survey (start of the survey + 1 h). (a) Acoustic surveys made in the Marquesas Archipelago around an anchored FAD (called TOGA FAD) in January 1996 (TOGA Jan 96) and February 1997 (TOGA Feb 97), compared with simulations with a duration for complete gastric evacuation of 5 h (*digestion 5 h*). (b) Acoustic survey made around a FAD anchored near Papeete (called PPT FAD) in March 1996 (PPT Mar 96), compared with simulations with a duration for complete gastric evacuation of 12 h (*digestion 12 h*).

greater than 12 nautical miles (22.3 km) yielded high numbers of fish aggregated by the network of FADs. This value corresponds to the 11 nautical miles (20.5 km) proposed by Holland et al. (1990) and Cayré (1991) as the minimizing dilution of fish resources between adjacent FADs. In the absence of exact values of the range of influence of FADs, which may vary according to local conditions, it appears that this estimation, i.e. 12 nautical miles or 22.3 km, represents a good compromise. Values above 12 nautical miles do not strongly affect the maximum number of fish aggregated by day by the network of FADs.

An important advantage of models of this type is that they use mechanisms well known by biologists, and they are based on parameters that biologists are accustomed to measure. For instance, the model used here is mainly based on the role of prey, stomach fullness, and rates of digestion on the movements of fish. The main idea of this study is that prey and stomach fullness after tuna have fed on prey, control

the dynamics of the association of tuna with floating objects, whatever the reason for such an association may be. The model uses biological data that are practical to measure. Using an echo sounder, as in Josse et al. (2000), it is possible to estimate the sizes of aggregations over a 24-h period. The target-strength values provide information about the size and species of the individuals in the aggregations. It is also possible from physiological studies to estimate the rate of digestion of the fish in the aggregation. Combined with simultaneous acoustic observation of the prey environment, it is also possible to estimate the distribution of prey around FADs. We consider that an important goal of such models is to indicate how these different 'static' biological observations can be linked in a dynamic framework, in order to improve our understanding of this striking phenomenon. Simple models can advance the understanding of a system by resolving the minimal set of assumptions under which one can duplicate the features that are observed in the wild.

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