SCIENTIA MARINA

Toward a synthetic eco-ethology of tropical tunas*

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SUMMARY: The aim of this paper is to introduce the study of the eco-ethology of tropical tuna using a synthetic approach (Artificial Life and Artificial Intelligence). Two different models are proposed dealing with tuna schooling behaviour and distribution of tuna schools in the environment. The first model uses a genetic algorithm which is an optimisation technique born from the Darwinian concept of evolution. The aim is to find optimal behaviour (movement and schooling behaviour) for artificial tuna populations living in heterogeneous and dynamic environments. The result are discussed according to knowledge on real schooling behaviour. The second model is based on the ideal free distribution theory for tuna schooling behaviour to describe the possible distribution and migration of animals in a heterogeneous habitat. It is pointed out that simple behavioural sequences can manage an artificial tuna population : tuna schooling evolves depending on both the energetic rate and the biological and physical environment. These models represent examples of possible computational experiments which must be completed with real experiments at sea.

Key words: Tuna fish, genetic algorithm, artificial schooling behaviour.

RESUMEN: HACIA UNA ECO-ETOLOGIA SINTÉTICA DE TÚNIDOS TROPICALES. – Este trabajo analiza la ecoetología de túnidos tropicales mediante la utilización de la vida artificial e inteligencia artificial. Para ello se proponen dos modelos relativos a la formación de cardúmenes en túnidos y su distribución en un hábitat determinado. En el primero, se propone el uso de un algoritmo genético como técnica de optimización generada a partir del concepto darwiniano de la evolución. Su objetivo fundamental es encontrar comportamientos óptimos para poblaciones artificales que viven en un medio heterogéneo y dinámico. En el segundo sin embargo, se propone un modelo para el comportamiento agregatorio de los túnidos basado en el *modelo de distribución libre ideal* que describe la distribución y migración de estas especies sobre un hábitat heterogéneo. Estos evolucionan dependiendo de una función energética fisiológica y su optimización en un hábitat físico-biológico. Los resultados muestran que una secuencia de comportamiento simple puede gestionar una población artificial de túnidos. Es necesario sin embargo implementar los resultados con experimentos reales. Es por ello que estos modelos no aportan nada nuevo sobre la etología de túnidos, pero plantean nuevas cuestiones a los etólogos que podrían culminar en la optimización de nuevos conocimientos.

Palabras clave: Túnidos, algoritmo genético, comportamiento artificial.

INTRODUCTION

Eco-ethology studies the relationship between animal behaviour and the environment. The defini-

tion implies experiments based on observations of animal behaviour related to the dynamics of the environment. In recent years, eco-ethologists have been able to use news tools to study an ecosystem: Artificial Intelligence (AI); or, more specifically, Artificial Life (AL). AI and AL are different disci-

plines but AL takes place at the limit between AI and biology. In fact, AI tries to reproduce an intelligence using the cognitism or the connexionist approach. On the other hand, AL appears to be the science of emergent functions dealing with concepts as autonomy or synthetic lives. In other words, AI refers to the top-down approach (e.g. expert systems with large data bases of knowledge), while AL represents the bottom-up approach, where life or adaptation appears as an emergent function.

AL is seen as a synthetic biology (BOURGINE and BONABEU, 1993). That means that AL exploits the knowledge based on biological studies in order to create synthetic studies. Biology can be seen as the study of life-as-we-know-it and AL however, as life as it could be (LANGTON, 1989). The main objective is to study life from classic biological studies, which leads to real knowledge, and from models which point out some new questions to biologists. The synthetic biology (or in the present case synthetic eco-ethology) corresponds to a global study using experimentations on real fields and computational experiments, which allows a synthetic view of the studied systems. Some work has been developed in this topic, especially about ethology of ants (DENEUBOURG et al., 1991, 1992).

This study proposes some models, or some new approach in order to initiate a synthetic eco-ethology of three species of tropical tuna (yellowfin tuna *Thunnus albacares*, bigeye tuna *Thunnus obesus* and skipjack tuna *Katsuwonus pelamis*). While the ethological study of tuna is complex because the access to environmental information in the open ocean is difficult, the idea is to use AL tools in order to point out some new questions, leading to synthetic views of the ecosystem. By this mean, it is possible to show a second step of synthetic eco-etholgy of these tunas. The third step will be a return from the results of the models, expressed as questions, to real experiments. The process must go on, alternating computational experiments (questions) with biological/ethological results (knowledge).

The aim of this study is to propose two independent models, about schooling behaviour and tuna distribution inside its environment. Each model will present a synthetic view of possible behaviour and new questions. The first model concerns a preliminary study using genetic algorithms in order to show the potential of this optimising technique; the second one deals with a theory from the global foraging hypothesis, trying to point out how it is possible to use it to study tuna behaviour.

Optimal foraging behaviour for artificial tuna schools: Preliminary study using a genetic algorithm

Why do animals forage in groups? The classic answer is that this social behaviour increases foraging returns and reduces predation risks (GIRALDEU, 1988). Tunas are well known as predator species, so we can assume that they do not aggregate in large schools. It is possible to build a simple foraging model evolving through genetic algorithm. Then, results can be discussed and evaluated with regard to real schooling behaviour.

The genetic algorithm

Genetic algorithms (GA) were developed by (HOLLAND, 1975). However, the results reported by GOLDBERG (1989) were used to explain the principles of this algorithm. This artificial technique is derived from the Darwin's theory of evolution. It is a search algorithm based on the mechanisms of natural selection and natural genetics. The central theme of research on GA has been robustness and the balance between efficiency and efficacy for survival in different kinds of environments. The goal is to optimise a function or a process in order to reach some optimal point or points.

GA differs from normal search procedures in four ways:
1. GA works with a code of the parameter set, not with the parameters themselves.
2. GA searches a population of points, not a single point.
3. GA uses payoff (objective function) information, not derivatives or other auxiliary knowledge.
4. GA uses probabilistic transition rules, not deterministic rules.

The mechanism of GA is given by (KOZA, 1992): "A population (or what you want) can be genetically bred using the operation of fitness proportionate reproduction and the genetic operation of recombination. The recombination operation combines parts of two chromosome-like fixed length character strings, each selected on the basis of their fitness, to produce new offspring strings".

To explain the mechanism of GA, GOLDBERG (1989) took a simple example : to maximise the function $f(x) = x^2$ on the integer interval [0,31]. The first step of the GA optimisation process is to code the parameter x as a finite-length string. Then GA will work on the code and not directly on the parameters. For example, the string 01000 corresponds

TABLE 1. – Mechanism of a genetic algorithm to maximise the function $f(x) = x^2$ on the integer interval [0,31] from GOLDBERG (1989).

Initial Population (randomly generated)	x Value	$f(x)$ x^2	$f(x)/\Sigma f(x)$	Selection (Roulettewheel)
0 1 1 0 1	13	169	0,14	1
1 1 0 0 0	24	576	0,49	2
0 1 0 0 0	8	64	0,06	0
1 0 0 1 1	19	361	0,31	1
Sum		1 170	1,00	

First generation.

Mating pool after reproduction*	Mate (Randomly selected)	Crossover Site (Randomly selected)	New population	xValue	F(x)
0 1 1 0	1	2	4	0 1 1 0 0	12	144
1 1 0 0	0	1	4	1 1 0 0 1	25	625
1 1	0 0 0	4	2	1 1 0 1 1	27	729
1 0	0 1 1	3	2	1 0 0 0 0	16	256
Sum					1 754

* The cross site is shown by the vertical divider

to x= 8. GA will choose 4 individuals, i.e. 4 strings where each bit is randomly chosen between 0 and 1. A fitness value can be calculated for each string because each one corresponds to one integer (Table 1). Reproduction is a process in which individual strings are copied according to their objective function values (fitness function). This means that strings with a higher value have a higher probability to contribute one or more offspring in the next generation. This operator is an artificial version of natural selection. The easiest way to implement the reproduction operator in algorithmic form is to create a biased roulette wheel where each current string in the population has a roulette wheel slot sized in proportion to its fitness. In this case, summing the fitness over all four strings allows us to obtain a total of 1 170. The percentage of population total fitness is also presented in Table 1. The corresponding weighted roulette wheel for this generation's reproduction is shown in Fig.1. Once a string has been selected for reproduction, an exact replica of the string is made. This string is then entered into a mating pool, a tentative new population, for further genetic operator action.

After reproduction, simple crossover may proceed in two steps. First, members of the newly reproduced strings in the mating pool are mated at ran-dom. Second, each pair of strings undergoes crossing over as follows: an integer position k along the string is selected uniformly at random between 1 and the previous string length l-1 [1,l-1]. Two new strings are created by swapping all characters between positions k+1 and l inclusively (see Table 1).

The mechanisms of reproduction and crossover are simple; they involve random number generation, string copies and some partial exchanges. The mutation operator plays a secondary role in the simple GA. Mutation rates are small and in the simple GA,
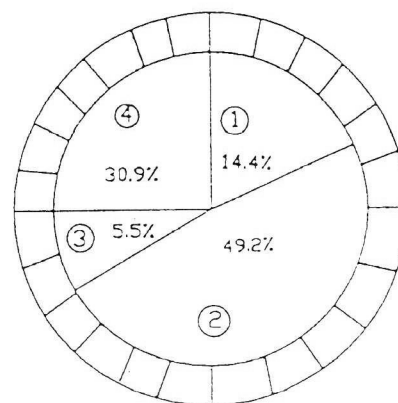

FIG. 1. – Simple reproduction allocates offspring strings using a roulette wheel with slots sized according to fitness. The sample wheel is sized for the problem of table I. From GOLDBERG (1989).

mutation is the occasional random alteration of the value of string position. This simply means changing a 1 to a 0 and vice versa.

Table 1 shows the process from the first to the second generation for our maximisation example of the function $f(x) = x^2$. From generation to generation, it is possible to reach the maximisation of the total fitness.

In the present study, the behaviour of each artificial tuna population with a string structure is coded. For that purpose, a set of random populations is created and each population reaches a result after one run (or generation). Then the best foraging behaviours are selected and submitted to a reproduction process composed of duplications, crossing-overs and mutations, as in real life. From generation to generation, the algorithm creates the best foraging behaviours, according to the optimisation criterion.

The model

Before presenting and building the foraging model that will evolve with the genetic algorithm, it is necessary to determine tuna habitat and tuna behaviour.

The tuna habitat

The habitat is modelled as a square of 50 x 50 nautical miles (nm), but it is also infinite by joining east and west sides and north and south sides. In this environment, four aggregative patches of food are randomly distributed. These patches are small (radius of 3 nm) and every 10 days they disappear and re-appear at a new random location, but always aggregative. In these patches, the prey density is 12 g.m^{-2} and outside these patches, the prey density is 3 g.m^{-2} in the first artificial world and 1.5 g.m^{-2} in the second artificial world created. These "prey density" data were collected from ROGER (1982, 1986).

The tuna behaviour

Inside this habitat, 200 elementary artificial tuna schools are randomly distributed. These schools are the minimum entities of the model. The population formed by these 200 schools has a defined behaviour that means that each school of the same population has the same behaviour. The artificial tuna schools can move, aggregate or scatter. Moving behaviour is defined in terms of velocity and direction and school velocities are selected from 1 to 4 knots. The direction behaviour, or the sinuosity of the scho-

ols, can be a random direction (brownian) or a straight one. A school can aggregate with another one and form one large school or scatter in two parts, reducing the school size. But there is a minimum school size, that is the initialisation size (elementary size).

The previously described behaviours depend on the richness of the area. Thus, schools have one behaviour in the patches rich in food and another in areas poor in food.

Each elementary school has an energetic function which decreases according to displacement. The data are taken from OLSON and BOGGS (1986). Each school gains energy with food intake. All the food is divided according to the number of elementary schools that can compose the school. The functions of the schooling behaviour (energetic function, prospected volume, etc.) are taken from PETIT, (1991) and PETIT and STRETTA (1992). According to energetic and displacement data, these authors defined the prospected volume and the necessary food intake for a tuna school depending on its size. That means that for an energetic function, the cost depends on the velocity and gain depends on both the prospected volume (depending on the school size and its displacement) and the prey density.

The model and the genetic algorithm were developed using object oriented language (C++) and the simulations run on a Sun station under Open Windows.

Evolution of the foraging model by genetic algorithm

The objective is to optimise the energetic function of the 200 schools of an artificial population. The initialisation procedure of the model consists of choosing 20 random populations of the 200 elementary schools. A population is defined by a fixed behaviour and each population lives in the artificial world for 100 days. Each day is divided into 12 hours because we consider that tuna schools spend half a day foraging. The energetical level of all the schools at the first day is 25. After one run (100 days) the population's fitness is calculated by the average energy of all the elementary schools of the population. Depending on the energetic function, the energy is a variable between 0 and 50. When all these 20 populations have lived in the artificial world during 100 days, we classify, for each population, the best behaviours. Then a reproduction[1] between them, using genetic algorithm, leads to 20 new other populations born from the best behaviours of

the first generation. At this time, a second generation is now living in the artificial ocean. At the end of this new generation the best behaviours are classified and the best behaviours are reproduced again. The simulation finishes after 100 generations or when all the 20 populations are optimal (fitness of 50). The final aim is to optimise the best behaviours.

The code of the behaviours is simple. The velocity can evolve from 1 to 4 knots. For the direction the value 1 means a random direction (brownian movement) and the value 0 means a straight direction. For aggregation, 0 equals a scattering of the schools or a stand-by if the schools have the minimum size, and the value 1 means that schools try to aggregate. For this aggregation, schools have to know their neighbours. Neighbours are defined when schools distance is less or equal than an aggregation radius. This parameter (from 0 to 3 in the code) can take respectively the values 1, 2, 5 or 10 nm.

RESULTS

For both worlds, i.e. 1.5 g.m^{-2} or 3 g.m^{-2} prey densities outside the patches (or in poor areas), the behaviours of the first generations show that some of them are not optimal while another give good results. Now, the genetic algorithm tries to find the optimal behaviours, which are the behaviours that provide the best internal state for our artificial tuna schools. Fig. 2 shows the learning processes of the genetic algorithm and Tables 2 and 3 indicate the behaviours selected at the end of the evolution.

For the first world, apparently less difficult for the artificial schools, optimal populations are found by the third generation. For the second world, the fitness does not increase until the twelfth generation. It is interesting to look at the evolution of these optimal behaviours. We may expect that the robust populations have the optimal behaviour.

First artificial world : 3 g.m^{-2} prey density outside the patches.

At the end of the 100th generation, the best selected behaviours are the following (Table 3):
- inside patches : high velocities, random direction and aggregation to the closest schools;
- outside patches (in poor areas) : high velocities, straight or random direction and no aggregation;
- maximum aggregation radius.

During the evolution, the same behaviours were selected but the aggregation behaviour in patches also includes a scattering of the schools.

Second artificial world: 1.5 g.m^{-2} prey density outside the patches.

The best selected behaviours are (Table 3):
- inside the patches : high velocities, random direction and no aggregation;
- outside patches (in poor areas) : high velocities, straight or random direction and aggregation or no aggregation;
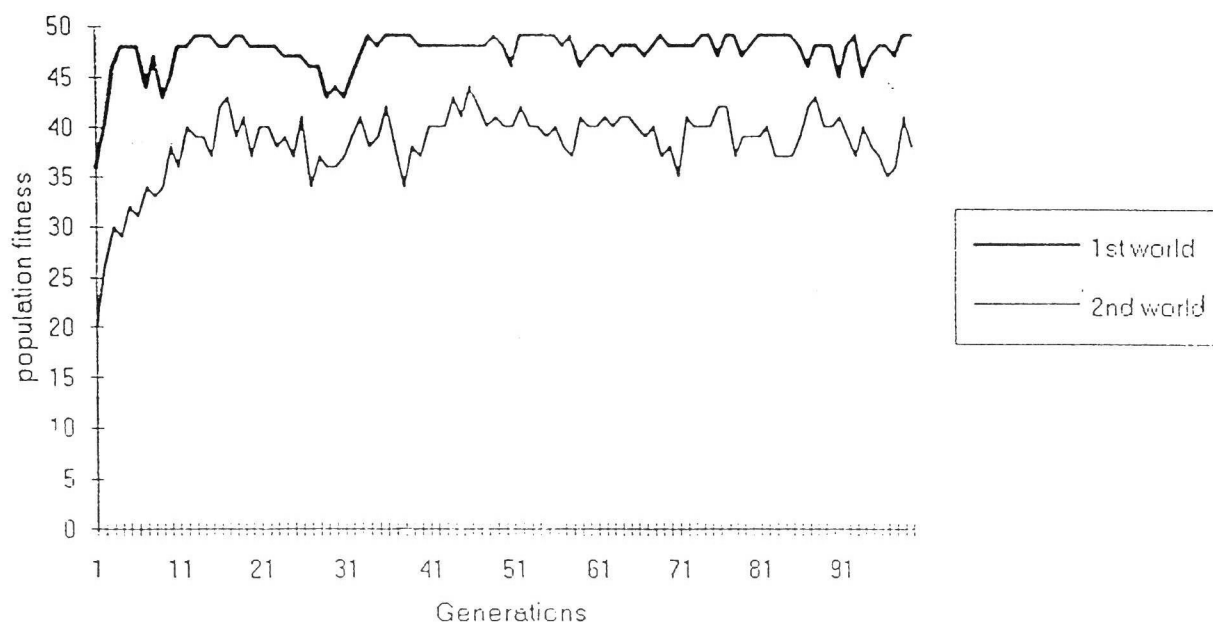- maximum aggregation radius.

FIG. 2. – Fitness evolution from generations to generations.

TABLE 2. – Behavior parameters generated Patch density: 12 g.m^{-2} Desert density : 3 g.m^{-2}

Generation 1

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	4	1	0	2	1	1	48
2	2	2	0	1	3	0	0	50
3	0	2	0	1	3	1	0	49
4	2	1	0	1	3	1	1	24
5	2	2	0	0	4	1	1	31
6	2	4	1	1	1	1	0	12
7	2	3	0	1	2	0	0	46
8	0	3	0	1	4	0	0	50
9	2	1	0	0	2	0	0	48
10	2	4	1	0	4	0	1	19
11	2	2	1	0	1	0	0	21
12	3	1	0	1	1	0	1	20
13	0	2	1	1	2	0	0	48
14	0	1	1	1	1	0	0	15
15	3	3	0	1	4	0	1	23
16	1	1	0	1	2	1	0	48
17	1	3	0	0	4	1	1	28
18	3	3	1	0	3	1	0	50
19	0	3	0	1	2	0	1	31
20	1	1	0	0	3	1	1	32

Generation 50

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	4	1	0	4	0	0	50
2	1	4	1	0	4	0	0	50
3	3	4	1	1	4	1	0	50
4	3	4	1	1	4	1	0	50
5	3	4	1	0	4	0	0	50
6	3	4	1	0	4	1	0	50
7	2	4	1	0	4	0	0	50
8	3	4	1	1	4	1	0	50
9	3	4	1	1	4	1	0	50
10	3	4	1	1	4	1	0	50
11	3	4	1	1	4	1	0	50
12	3	4	1	1	4	1	0	50
13	3	3	1	1	4	1	0	50
14	3	4	1	1	4	1	0	50
15	3	4	1	1	2	1	0	47
16	3	3	0	1	3	0	0	50
17	3	3	1	0	4	0	0	50
18	3	4	1	0	4	1	0	50
19	3	4	1	1	4	1	0	50
20	3	4	1	1	4	1	0	50

Generation 100

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	4	1	1	4	0	0	50
2	3	3	1	1	4	1	1	24
3	2	4	1	1	3	0	0	50
4	3	4	1	1	4	1	0	50
5	3	4	1	1	3	1	0	50
6	3	2	1	1	4	0	0	49
7	3	4	1	1	4	0	0	50
8	3	4	1	1	3	1	0	50
9	3	4	1	1	4	0	0	50
10	3	4	1	1	4	0	0	50
11	1	2	1	1	4	0	0	49
12	3	2	1	1	3	0	0	49
13	3	3	1	1	3	0	0	50
14	3	4	1	1	4	1	0	50
15	3	3	1	1	4	1	0	50
16	3	4	1	1	4	1	0	50
17	2	4	1	1	4	1	0	50
18	3	4	1	1	4	1	0	50
19	3	3	1	1	3	0	0	49
20	3	2	1	1	3	0	0	49

TABLE 3. – Behavior parameters generated Patch density : 12 g.m^{-2} Desert density : 1.5 g.m^{-2}

Generation 1

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	2	0	1	1	0	0	0
2	1	2	1	1	1	0	1	20
3	1	1	1	1	4	0	0	24
4	2	4	1	1	4	0	0	23
5	0	4	1	1	4	0	0	31
6	3	3	0	0	4	0	1	40
7	2	4	0	1	2	1	1	24
8	2	1	0	0	4	1	1	29
9	1	4	1	0	3	1	1	38
10	1	3	0	0	1	1	1	20
11	3	2	1	1	1	0	1	24
12	1	1	1	0	4	0	0	40
13	3	4	1	1	1	0	1	24
14	0	3	0	0	2	1	0	0
15	1	3	1	0	2	1	0	4
16	3	3	0	1	2	0	0	0
17	2	3	0	1	3	0	0	8
18	2	3	1	1	2	1	1	23
19	3	3	0	1	2	0	0	0
20	0	3	0	1	4	1	0	30

Generation 50

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	4	1	0	4	0	1	32
2	3	4	1	0	4	1	1	32
3	3	4	1	0	2	0	1	28
4	3	4	1	0	4	0	1	29
5	3	4	1	0	2	0	1	26
6	3	3	1	0	4	1	1	46
7	3	4	1	0	4	0	1	48
8	3	4	1	0	4	0	1	48
9	3	4	1	0	4	0	1	44
10	3	4	1	0	3	0	1	45
11	3	4	1	0	4	0	1	39
12	3	4	1	0	4	0	1	45
13	3	4	1	0	4	1	1	49
14	3	4	1	0	4	0	0	35
15	3	4	1	0	4	1	1	49
16	3	3	1	0	4	1	0	41
17	3	4	1	0	4	1	1	34
18	3	4	1	0	4	1	1	49
19	3	4	1	0	4	1	1	41
20	3	4	1	0	3	1	1	49

Generation 100

population	aggregation radius	patches velocity	patches direction	patches aggregation	poor area velocity	poor area direction	poor area aggregation	fitness
1	3	4	1	0	4	1	0	41
2	3	4	1	0	4	1	1	45
3	3	4	1	0	3	1	0	25
4	3	4	1	0	4	0	1	46
5	3	4	1	0	4	1	1	36
6	3	4	1	0	4	1	1	39
7	2	4	1	0	4	1	1	43
8	3	4	1	0	4	1	1	34
9	3	4	1	0	4	0	1	42
10	3	4	1	0	4	1	0	41
11	2	4	1	0	4	1	1	37
12	3	4	1	0	4	1	1	49
13	1	4	1	0	4	1	0	42
14	3	3	1	0	3	1	1	48
15	3	4	1	0	2	1	0	5
16	3	4	1	0	4	1	0	41
17	3	4	1	0	4	1	1	49
18	3	4	1	0	4	1	1	42
19	3	4	1	0	4	1	1	41
20	3	2	1	0	4	0	1	30

The behaviours are the same for the two artificial worlds except for aggregative behaviour inside patches. When outside patches (in poor areas) prey density is very low, the schools do not aggregate, while they can aggregate when the prey density is higher.

The optimal behaviours reached by the genetic algorithm appear to be logical. The high velocities allow, to the schools, a prospection of large volume of waters. According to the cost function which depends on velocity, it seems that schools must accept high costs in order to gain high benefits. The high velocities in the poor areas provide the schools with the opportunity to quickly find food patches. The optimal search behaviour for a forager in a patchy environment was studied by BENHAMOU and BOVET (1991). These authors found that in poor areas, the animal has to accelerate and to reduce its sinuosity, while in rich areas, it has to reduce its velocity and increase its sinuosity.

We find approximately the same results, except for the velocity inside the patches. Reducing its velocity allows a forager to pay more attention to the search of prey. In the artificial world created behind, the main issue, for the foragers, is to prospect rich areas. While the distribution of prey is not considered, then the reduction of the speed is not necessary. To adopt high velocity inside patches, as it is suggested by the model, is the best adaptation to harvest large quantities of food. For the direction, inside the patches, the forager uses a random direction that corresponds to the best behaviour to stay inside. On the other hand, in poor areas, we should expect that the best behaviour would be a straight direction. The genetic algorithm model points out two kinds of behaviour for direction, the random and the straight one, by giving an equal fitness for them. It is possible to consider here that the random direction can give good results for searching behaviour due to (i) the aggregative distribution of the patches, and (ii) the high temporal dynamic of the patches. Leaving a patch and adopting a random search can be efficient for the forager looking for a patch. By this way, it can find the previous patch or a close one.

The aggregative behaviour shows that inside patches, behaviour depends on the prey density outside the patches in the poor area. This result is surprising, but it is logical. In poor areas with a very low prey density (second artificial world), the schools can aggregate because they gain more food. The share is high while the behaviour gives the lowest energy loss. When the prey density of the poor areas is higher, the best behaviour is not to share the food, so the schools have to reduce their size. Reaching patches,

the aggregative behaviour depends on the loss during the search in the poor areas. In the second artificial world, the schools have lost a lot of energy and they have to scatter in order to avoid the sharing of food. In the first artificial world, as the schools have lost less energy, they do not have to scatter in the patches. Why this behaviour? When schools scatter, they lose contact. When they have to aggregate in order to harvest more, then, it is difficult to do so due to the dispersion. Avoiding the scattering in the patches allows a good behaviour in the poor areas.

This discussion shows that these results give some indications to the understanding of tuna schooling behaviour. The notion of risk is not included in these artificial worlds but these results depend on the foraging model and on costs and gains functions. The schools can increase their prospected volume by increasing their velocity or by increasing the school size. In the present model, a higher prospected volume always gives a higher harvesting of food. The prospected volume allows the schools the possibility to find more prey and the own search behaviour also allows it. The increase in the school size, increases the prospected volume but does not help schools to find more patches. The schooling behaviour may be the result of a kind of compromise between finding more food, without a too high share. The two possibilities are an increase in the velocity and an increase in the size. We do not consider the two possibilities in our search behaviour.

The results of genetic algorithms are always attractive. From generation to generation, the evolution of the behaviour is observed and at the end, the artificial tuna schools live with an optimal behaviour. For this problem, it is possible that other methods could have been efficient. But the aim of this work is to use genetic algorithms to find optimal behaviours. The problem is that many variables and functions act on the schooling behaviour. The genetic algorithm represents a powerful tool to study complex behaviours with different solutions.

Ideal free distribution theory as a basis for a tuna schooling behaviour model.

The concept of "density-dependent selection habitat" refers to the differential use of habitats depending on overall population density. This theory is the base of behavioural models such as the Fretwell-Lucas theory (MAC.CALL, 1990). In the 70's, FRETWELL and LUCAS proposed the term "ideal free distribution" to describe the distribution of ani-

mals in heterogeneous habitats (MILINSKI and PARKER, 1991). Only three hypothesis are necessary for this model:
1. An heterogeneous and not homogeneous habitat.
2. Inside a patch of food the fitness value of a competitor decreases with increasing number of individuals that exploits the patch.
3. The individuals are "free" to move to alternative patches without any constraint or restriction.

First of all, the competitors should have identical competitive abilities but this hypothesis would have been given up. The main result of this model is that "ideally", each individual goes to the place where its gain would be the highest. So it is expected that the number of competitors, in each resource patch, is directly proportional to the input rate to the patch. This is the input matching rule (MILINSKI and PARKER, 1991).

Applying the ideal free distribution model (IFDM) to fish schooling behaviour may appear attractive. However, PITCHER, (1986) considers that the hypothesis of this model is not realistic because there are constraints to a fish, and the third assumption above can not be verified. Moreover, he considers that the social behaviour of a school is not considered in this theory. At first, PITCHER's objections appear logical. This will be discussed below and then a model will be proposed for tuna schooling behaviour based on the ideal free distribution.

The ideal free distribution predictions

All the following explanations about the IFDM are selected from the MILINSKI and PARKER (1991) paper. When all competitors are equal, the model predicts that group size depends on the profitability of each patch. Profitability can be explained as the synthetic parameter combining density of preys with the number of predators present. When the competitors have various abilities, the tendency is to have the "truncated phenotype distribution". It is necessary to have individuals from the same species but with various sizes, inside habitats where the patches profitabilities depend on the individual size. In some patches, the competitive weight of the largest competitors is not too different from the smallest competitors. That means that the largest competitors do not have advantages over the small ones. In other patches, the biggest competitors perform much better than smaller ones. The model predicts that the largest competitors should be found in patches where the effects of sizes are most critical. The smallest competitors occur in the first kind of patches,

where the effects of the size are least important. The medium-sized competitors occur in the intermediate patches.

Using these results, it is expected to have a truncated phenotype distribution according to the age classes. The youngest individuals go to the patches where the size effect is the lowest. The oldest individuals however, go to the patches where the size effect is the most important.

The IDFM can also explain the trophic migrations of the animals. When an habitat becomes poorer, it is expected to have some foragers leaving the place while other stay in. MILINSKI and PARKER (1991) exposed the migrations of many birds that travel a long distance to spend the winter in more suitable place. The number of birds that must stay at home is given by the input matching rule. We can expect to find migrants and non migrants with equal fitness distributed by the IFDM. From all these remarks, it is necessary to test the output of this model in order to understand tuna behaviour.

It is possible to apply the ideal free distribution model to tuna schooling behaviour?

In this paper, schools are considered as entities that can aggregate to other ones to form larger schools. The IFDM however, was designed for individuals and did not consider social behaviour (PITCHER, 1986). If the hypothesis that the elementary entities are schools is considered, it is possible to keep the social behaviour of fish inside the model. Schooling brings many advantages to fish : (i) a higher prospected volume; (ii) a share of the information that makes fish in large schools find food faster (PITCHER et al., 1982); (iii) hunting co-operation (PARTRIDGE et al., 1983); and (iv) increasing of the individual feeding rate. For the last point, the social facilitation seems to increase the feeding rate by a higher intra-group competition forcing individuals to feed more, and allows a best sharing of vigilance (STREET et al., 1984). The assumption of the school as an elementary object allows modelling of the schooling behaviour, including the advantages of the social behaviour described above.

While a fish loses energy during swimming, the assumption of "free" movements between patches can not be verified. PITCHER (1986) reviewed the experiments fitted on the ideal free distribution theory applied to fish schooling behaviour. Some experiments have fitted the IFD (GODIN and KEENLEYSIDE, 1984; MILINSKI, 1979 cited by PITCHER, 1986). Other papers have reported large

differences between fishes, and this model cannot be exactly applied to fish in schools. PITCHER (1986) for example, specified that fishes are not free of constraint and the predictions of the theory are not good. However, the same author advanced that theory claiming it can give good estimates for some particular ecological problem. The problem is to know if the assumption of "free moving" can be approximated.

Tunas have a behavioural thermoregulation or a high physiological activity and they have an energy-expensive foraging strategy to search over large, and often, oligotrophic areas for food (Au, 1986). As a consequence, to find a rich area with food patches represents success for the schools. In poor areas the costs can be expected to be the first problem for tuna schools to search rich areas and to harvest the largest quantity of food. When schools find a rich area, the aim is to optimally exploit these patches as soon as possible. In this case, the movements between patches or even between school prey into a patch, can have very low influence on the behaviour. The costs are probably negligible if they are compared with the gains, the assumption of "free" movement is verified and the schools can follow the IFDM in order to optimise their food intake.

Each patch can be defined by the density and the distribution of the prey. PETIT (1991) and PETIT and STRETTA (1992) found a relation between the maximum tuna school size and the prey density. Over this size, the fish within the school would not share too much food and the energetic balance of the fish would become negative. This could be considered as a normal regulation of the school density generated by the energy balance of individuals. However, the high prospective abilities of tuna schools would allow some of them to go away to search another prey patch. The basin model of MACCALL (1990) explained that habitat regulates population density. He defined the suitability (profitability in this work), of certain area, described as a continuous geographic suitability topography which the appearance of an irregular basin, whose shape may also vary over time. For instance and according to the ideal free distribution, population will fill the basin as a geophysics fluid under the influence of gravity.

A simple model for tuna schools foraging with an ideal free distribution behaviour

We have built a model in order to examine the organisation of a tuna population composed of schools with simple behaviours. It was programmed in an oriented object language (C++) which allows us to create independent schools, the dynamic environment and the relations between all these actors. As SAARENMAA et al. (1988) reported, the oriented-object approach gives the advantage to simulate heterogeneous environments and to reproduce animal behaviours.

To mimic schools behaviours using the ideal free distribution theory we have to define the artificial environment and the artificial tuna schools.

The artificial environment

The habitat of the schools appears on the screen as a toroidal square of 400 x 400 nautical miles. At random location, a source of enrichment area appears and generates four aggregative food patches. The food patches are similar but they evolve throughout the time. Their prey densities and distributions evolve to mimic the evolution of food chain in the oceans.

The artificial tuna schools

On the first day, 100 elementary schools appear at a random locations in the habitat. The behaviour of these schools is relatively simple:

The schools look for food patches, adopting a high speed and a low sinuosity in poor areas. Reaching a favourable source area, the schools reduce the velocity and increase the sinuosity until the prey patch is detected. Then they attack the prey within the patch. Here, the optimal search behaviour used in various models of animals movements is adopted (BENHAMOU and BOVET, 1991).

During one day (the time step), the schools sample the small patch and then a reorganisation of the schooling structure occurs in order to have optimal exploitation determined by an optimal tuna school biomass on each prey patch. When tuna school biomass is higher than optimal, they distribute themselves according to the ideal distribution, but the surplus leaves the patch to sample the environment. In other words, there is no over-exploitation of a patch.

In poor areas, two possibilities to the school behaviourist are allowed. We hypothesise that schools adopt high velocities to find rich areas. During this search, they do not aggregate if they find other tuna schools, and they can (i) keep their structure considering that the velocity is not high and fish can keep on their relations within the school; or (ii) scatter, when swimming speed increases and the school is divided into two smaller schools.

DISCUSSION

In this work, artificial behaviour has not been evaluated to test if it was optimal or not. It was built as an optimal exploitation of food in a patchy environment. This model has limitations, but we can consider that the difference with real behaviours remains in the time delay of the transitions.

What are the contributions of such a model? First, it is observed that simple behavioural sequences can manage an artificial tuna population. With these simple rules, an emergent function is pointed out. This means that an organisation of the population depends on decisions of particular entities (schools). Without flux of information between schools, schools evolve depending only on their own energetic rate in relation to their biological and physical environment. Second, it will be very useful to run simulations including real estimates of prey density and distribution on a real ocean. It would be possible to compare the distribution of the simulated schools, their sizes and the time delays with real fishing observations, but, there is a lack of pelagic fish ethology observations in real oceans. Here, the purpose of these simulations is to initiate discussions, because the iteration of the simple and the elementary generates the surprise and the difference (QUEAU, 1986). This model is a first step in the contribution of an artificial life approach to pelagic fish ethology.

Conclusions

This is a preliminary study and the aim is not to find new ideas concerning tuna schooling behaviour or its distribution. The main objective is to show the advantages of such a synthetic approach. With ethological models the researchers have new tools to study biological systems. Historically, modeler and ethologist were often separated, generating some lack of understanding because there was no exchange of knowledge. Artificial life tries to build a synthetic ethology including both ethology and computational experiments.

The objective of the models proposed is not to build models for models but to show how simulations can help eco-ethologists to study their systems. The models do not constitute a real advance in the knowledge of tuna behaviour. They only represent a part of a synthetic work which can be the source of new information after the implementation with real data. The results described in this paper do not exactly show all the power of the simulation because se of the importance of the dynamic, which can only be seen on the screen of a computer. The main objective was to show the importance of mixing models and real experiments, toward a synthetic eco-ethology of tropical tunas.

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