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COMPUTATIONAL MODELS FOR POPULATION DYNAMICS: TWO CASE STUDIES

Abstract - Individual based models are a widely used tool for the study of population dynamics. They are computational models that allow scientists to explore the mechanisms through which populations evolve from how individuals interact with each other and their environment. Individual based models can embody stochastic aspects in an easy and natural way and are better suited for describing the inherent random character of natural phenomena than classical mathematical models based on differential equations. This is true especially when the size of the population is not large enough to ignore stochastic aspects.

In this paper we show the use of individual based models in two case studies of fish population dynamics to study the advantages/disadvantages of a mixed type of reproduction sexual/asexual in a fluctuating environment and the role of a reproduction system with locality as a cause of persistence of stable polymorphism.

Key words - Computational models, individual based models, population dynamics.

Riassunto - *Modelli computazionali per la dinamica di popolazioni: due casi di studio.* I modelli «individual based» sono usati comunemente per lo studio della dinamica delle popolazioni. Sono modelli computazionali che permettono di studiare l'evoluzione delle popolazioni attraverso i meccanismi con i quali gli individui interagiscono sia tra di loro che con l'ambiente. I modelli «individual based» possono inglobare meccanismi stocastici in modo semplice e naturale. Questo permette loro di descrivere, meglio dei classici modelli matematici deterministici, l'inerente carattere casuale dei fenomeni naturali. Questo è vero, in particolare, quando la consistenza della popolazione non è sufficientemente grande per poter ignorare gli aspetti stocastici.

In questo articolo mostriamo l'uso di modelli «individual based» in due casi di studio relativi alla dinamica di popolazioni di pesci, sia per studiare i vantaggi/svantaggi di un tipo misto di riproduzione, sessuale/asessuale, in un ambiente che cambia, sia per studiare il ruolo di un sistema riproduttivo basato sulla località nel mantenimento del polimorfismo.

Parole chiave - Modelli computazionali, modelli «individual based», dinamica di popolazioni.

INTRODUCTION

Traditionally, population dynamics has been studied by means of mathematical models. In the last few years computational models have been widely used for analyzing biological systems. Computational models are stochastic models in computational science (that usually require extensive computational resources) to study the behaviour of biological system by means of computer simulation. The system under study is often a complex nonlinear system for which analytical solutions are not readily available. Results are obtained by changing the parameters of the model and by studying the differences in the outcomes of the experiments. Theories can be deduced by running multiple stochastic computational experiments.

Among computational stochastic models, individual based ones represent a widely used tool for population dynamics. These computational models allow scientists to explore the mechanisms through which populations evolve from how individuals interact with each other and with their environment. Individual based models are better suited than deterministic non-individual based ones (such as differential equations) for describing the inherent random character of natural phenomena, and can be used in a variety of cases. This is true especially when the size of the population is not large enough to ignore stochastic events and noise. Individual based models can embody such stochastic aspects in an easy and natural way.

In this paper we use individual based computational models for the following two case studies.

Carassius auratus gibelio Bloch 1782, or Crucian carp, is a cyprinid fish from Eurasia which has the ability of reproducing both sexually and asexually. It is an endemic species that colonized almost all continental Europe, starting from Asia and East Europe. The reproduction abilities of Carassius gibelio stimulated this study in which we try to understand the advantages of a mixed type of reproduction. In this paper we describe the dynamics of a population with sexual and asexual reproduction in a periodically fluctuating environment. Tropheus moorii (Boulenger 1898) is a species of cichlid fish that inhabits Lake Tanganyika. There are over forty different morphs of this species distributed throughout the lake. This fish species exhibits colours and patterns ranging from dark green to flame red and yellow. They are found in shallow waters eating algae, which comprise most of their diet. Tropheus eggs are fertilized in the mouth of females. Eggs and fry are then carried by females in their mouth for about one month. In the second case study described in this paper, we try to relate this particular reproductive system of

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genus *Tropheus* with the incredible variety of morphs we find in the species.

The mixed type of reproduction (sexual/asexual) of *Carassius Auratus Gibelio* block 1782 in a fluctuating environment

During sexual reproduction genes from two individuals are combined in the offspring that receives genetic material from both parents. In diploid populations this includes processes of recombination and segregation of the genetic material. Maintenance of sexual reproduction in most eukaryotes despite evolutionary costs is still matter of discussion. Recombination can break up favourable sets of genes accumulated by selection and asexual populations comprising only females can reproduce two times faster in each generation than sexual populations (producing also males) without the necessity to produce males for ongoing reproduction (Barton & Charlesworth, 1998). Despite its considerable cost, sexual reproduction (Maynard Smith, 1978) is still by far the most frequent mode of reproduction in vertebrates. Asexual reproduction has only been described in less than 0.1% of vertebrate species, which are usually basal from a phylogenetic point of view. Sexual reproduction is source of more genetic variation than asexual reproduction and a high level of genetic variation allows perpetual adaptation to changing environments (Felsestein, 1974).

Genetic variation results from both mutation and recombination. Mutation generates new alleles in both sexual and asexual species, while recombination in vertebrates only occurs in sexual reproduction during meiotic division. Rearrangement of alleles during recombination not only increases genetic variation but also protects against the effects of Muller's ratchet (Muller, 1964) even though accumulation of deleterious mutations has been observed in regions of the genome of organisms with sexual reproduction which do not undergo recombination. In asexual species all new mutations in the whole genome are transmitted directly without change to the next generation, thus facilitating the accumulation of deleterious mutations (Normark & Moran, 2000).

Depending on the evolutionary costs and benefits, nonvertebrate species often coexist in sexual and asexual lineages, either alternating throughout their lifecycle or in spatially or temporally isolated populations. Exclusively unisexual vertebrates are usually closely related to sexually reproducing species (Janko *et al.*, 2007) with many examples demonstrating coexistence of unisexual and bisexual populations (Schlupp *et al.*, 2005; 2010). In most cases various hypotheses have been presented in order to explain the absence of the twofold advantage, many of them based on the discrimination ability and the efficiency of males during mate choice of sexual reproduction.

Depending on the ecological conditions in a habitat, bisexual forms might replace faster reproducing unisexual lineages because of the long-term benefits of increased genetic variation (Waxmann & Peck, 1999). Due to the long-term advantages of sexual reproduction, asexually reproducing species were classically considered as evolutionary dead-ends until the discovery of «ancient asexuals». However, most asexual species indeed represent phylogenetically young groups. Unisexual lineages can evolve by various mechanisms (spontaneous, contagious or infectious origin, hybridization) from ancestral sexual species (Schurko *et al.*, 2008) but as a matter of facts unisexual reproducing species have been described to originate from one or multiple hybridization events involving

bisexual species. Carassius gibelio (Gibel carp or Crucian carp) is a cyprinid fish from Eurasia and it is so far the only vertebrate species described in which asexually and sexually reproducing populations coexist sympatrically (Zhou et al., 2000; Toth et al., 2005; Flajshans et al., 2007; Jia et al., 2008; Gui & Zhou, 2010; Liasko et al., 2010). In natural unisexual populations of Carassius gibelio, the subjects are all females with a triploid genome and reproduce asexually by a mechanism called gynogenesis (sperm-dependent parthenogenesis) (Beukeboom & Vrijenhoek, 1998). During gynogenetic reproduction, offspring are parthenogenetically formed but egg development cannot be completed without sperm. In general, the male DNA is not incorporated into the offspring's genome but triploid gynogenetic females are dependent on sperm donors which usually belong to a closely related species. The heterologous fertilization is required in order to trigger a second meiotic division from which viable zygotes are originated. As suggested by several authors, in this context of heterologous fertilization with fish species phylogenetically closely related, the possibility of exchanges of genetic material cannot be completely excluded.

Although some authors suggest a hybridization event of *Cyprinus carpio* and *Carassius auratus* to explain the origin of asexual Gibel carp, *Carassius gibelio* has also been described as the only known vertebrate species of non-hybrid origin (Schlupp, 2005).

In this Section we study the advantages of a mixed type of reproduction in a changing environment following the idea that a species that is able to adapt to environmental fluctuation can easily colonize a new habitat. For this reason, our results provide a reliable explanation of the ability of *Carassius gibelio* to colonize new regions very efficiently.

The Model

The model is based on the comparison of two different populations of fishes competing for the same resources. Each population can reproduce in both a sexual and an asexual mode. Each population is characterized by a percentage of asexual and sexual reproduction. The percentage of asexual reproduction ranges between 0% (completely sexual reproduction) and 100% (all the females reproduce by gynogenesis). In order to study the behaviour of the two populations with respect to the resources they compete for, we assume that they exploit sperm from a third heterologous species and that sperm is not limiting.

We consider diploid individuals whose genotype is represented by L loci, each one with two possible alleles. Because of the diploid assumption a genotype is represented by a sequence of L pairs, where each pair represents the alleles at a locus. In the simulation an individual of the population will be represented only by the sequence of L pairs corresponding to its genotype. We can think of the L loci as the ones which mainly control the fitness of individual for the environment, where each locus corresponds to the fitness for an ecological trait. We consider different strengths of the ecological selection; with a strong selection, individuals with fitness less than 1 suffers from an important disadvantage with respect to fit individual.

We consider that the population has a reproduction season every year. In this season all the females reproduce. Each female has the possibility to reproduce in either sexual or asexual mode with a probability that is proportional to the percentages of sexual/asexual reproduction in her population. If the selected type of reproduction is asexual, the female produces all female offspring with a copy of her genotype. Otherwise a male is randomly chosen, and the offspring are probabilistically composed by half males and half females with genotypes obtained by recombination of the parents' alleles. In this process each locus segregates independently.

The reproductive season is followed by a viability selection in which individuals have a probability of surviving proportional to their fitness.

We consider the young fishes able to reproduce at the age of one year, thus the newly born fishes are able to have offspring in the next reproduction season. We fixed the maximum carrying capacity of the environment to 30,000 individuals.

For allowing the coexistence of sexual and asexual populations we eliminate the twofold advantage of asexual reproduction by increasing the strength of selection for the asexually produced offspring. Such a stronger selection is motivated also by the weaker defences usually offered by the immune systems of asexually reproductive populations against pathogens caused by the limited genetic variation and the high rate of inbreeding. We also assume the stronger selection to incorporate the effects of sexual selection for the males of the third heterologous species since it may disfavour asexual reproduction.

The simulations were performed using Open Watcom C for Windows. The code is available on request.

Results

We performed simulations by considering initial populations with different percentages of asexual reproduction. The percentages start from 0% (meaning totally sexual reproduction) and, by steps of 10, reach 100% (meaning totally asexual reproduction). For each combination of percentages in the two populations we performed 5 simulations, thus, because pairs of different percentages occur twice in this process, for each combination (excluded the ones in which the percentages in the two populations are equal) we performed 10 simulations. The initial consistency is 9,000 individuals for each population. Given the carrying capacity of the environment, the total population rapidly reaches a consistency of, nearly, 30,000 fishes. Every simulation runs for 500 generations. The final result can be of three kinds: a) population 1 survives and population 2 becomes extinct, b) both populations survive, and c) population 1 becomes extinct and population 2 survives. Actually, when the selection is strong, both populations can go towards extinction. These cases are not interesting for our purposes.

A stability period of the environment is considered, that is a period in which the environment does not change. At the end of such a period a fluctuation occurs: the environment changes completely, thus fit individuals become unfit and vice versa. In the simulations we considered three different fluctuating environments, with stability periods of 50, 20 and 10 generations, respectively.

Three different levels of ecological selections are taken into account: strong, medium and weak.

In Figure 1 the results are shown for long stability period and weak selection, while Figure 2 shows the results for short stability periods and strong selection. In both figures population 1 is on the vertical axis while population 2 is on the horizontal axis. In each scheme the percentage of asexual reproduction varies between 0 and 100 by step of 10 and each crossing is coloured in relation with which population survived best: white is where population 1 prevailed, dark where population 2 did, and tones of grey if in the middle.

Figures 1 and 2 show that when the stability period is shortened and the selection is strengthened populations are advantaged by a higher level of sexual reproduction. Thus, while with a stability period of 50 generations

100	-5	-5	-5	-5	-5	-5	-5	-5	-5	-5	-2
90	5	5	5	5	5	-5	-5	-5	-5	-1	5
80	5	5	5	5	5	3	-3	-5	5	5	5
70	5	5	5	5	5	5	0	0	5	5	5
60	5	5	5	5	5	5	0	1	5	5	5
50	5	5	5	5	5	0	-5	-5	1	5	5
40	5	5	5	5	0	-5	-5	-5	-5	-3	5
30	5	5	5	0	-5	-5	-5	-5	-5	-5	5
20	5	5	0	-5	-5	-5	-5	-5	-5	-5	5
10	5	0	-5	-5	-5	-5	-5	-5	-5	-5	5
0	0	-5	-5	-5	-5	-5	-5	-5	-5	-5	5
	0	10	20	30	40	50	60	70	80	90	100

Fig. 1 - Results for long stability period and weak selection. Population 1 is on the vertical axis while population 2 is on the horizontal axis. In the scheme the percentage of asexual reproduction varies between 0 and 100 by step of 10 for each population, and each crossing is coloured in relation with which population better survived: white is where population 1 prevailed, dark where population 2 did, and tones of gray if in the middle.



Fig. 2 - Results for short stability periods and strong selection. The scheme adopts the notation of Figure 1.

and weak selection (Fig. 1) the greatest advantage is obtained with a percentage of asexual reproduction of 60-70%, when the stability period lowers to 10 and the selection is strong (Fig. 2) the greatest advantage corresponds to percentages of 30-40% of asexuality.

The explanation for this is based on the fact that the percentage of sexual reproduction is necessary to react efficiently to environmental changes, and it must be great enough to allow the population to produce a good percentage of fit genotypes in a time shorter than the length of the stability period. Intuitively, adaptation by sexual reproduction takes more time with longer genotypes and it is faster with a stronger ecological selection.

Further considerations must be done for what concerns the percentage of fit individuals in the population. To this aim we considered a single population without any fit genotype, and we ran some simulation for 100 generations. For each simulation we recorded the dynamics of fit genotypes.

Figures 3 and 4 show these adaptation phases of a completely sexual population, a population with 50% of asexual reproduction of and a population with 80% of asexual reproduction, respectively. Figure 3 shows the adaptation phase in presence of weak selection, while Figure 4 refers to strong selection. In each figure, the black line corresponds to the fit individuals of the completely sexual population; the dark grey line corresponds to the fit individuals of the population with a percentage of asexual reproduction of 50%, and light gray line to the population with 80% of asexual reproduction.

The figures show an interesting behaviour. The way in which the percentage of 100% of fit genotypes is reached differs greatly with the differences in percentages of asexuality. Essentially there are two phases in the



Fig. 3 - Adaptation phase, in presence of weak selection, of a completely sexual population, a population with 50% of asexual reproduction of and a population with 80% of asexual reproduction, respectively. The black line corresponds to the fit individuals of the completely sexual population, the dark grey line corresponds to the fit individuals of the population with a percentage of asexual reproduction of 50%, and light gray line to the population with 80% of asexual reproduction.



Fig. 4 - Adaptation phase, in presence of strong selection, of a completely sexual population, a population with 50% of asexual reproduction of and a population with 80% of asexual reproduction, respectively. The figure adopts the notation of Figure 3.

adaptation process. A first phase in which fit genotypes must be created (*generation phase*). A second phase in which fit genotypes must be multiplied (*amplification phase*). With complete sexuality the generation phase is very quick, while the amplification phase is slow. When the percentage of asexual reproduction grows, the generation phase slows down but the amplification phase becomes faster. Recall that all the populations have an initial composition of all unfit genotypes. Figures 3 and 4 show that adaptation is faster in presence of a stronger selection.

From the simulations we performed we can infer the following considerations explaining the adaptability of species with a dual (sexual/asexual) reproduction system. First of all we see that a population with complete sexual reproduction produces different genotypes very quickly. This is due to recombination and segregation with their maximal expression in pure sexuality. The occurrence of new genotypes is delayed by introducing a percentage of asexual reproduction. However the amplification phase is faster in presence of asexuality, thus the mixed type of reproduction gives a big advantage in a fluctuating environment. The optimal percentage of asexual reproduction depends on the strength of the selection and on the length of the stability period of the environment (as shown in Figures 1 and 2).

We can conclude that, under the hypothesis of the model, the reproduction strategy of *Carassius gibelio* is very efficient and, this could be the reason of the ability of the species in colonizing new water bodies.

Relationships between polymorphism and reproduction strategy in *Tropheus Moorii*

Tropheus moorii is a small mouth brooder cichlid fish from Lake Tanganyika with more than forty colour morphs. The fishes of this species live in shallow water, in rocky reefs eating algae. Either females or males have a territory in which they live permanently. A female chooses a partner among the males which are «near» to her territory. After the choice the female reaches the territory of the male and spends from 4 to 21 days there before spawning (affiliation time). After spawning, the brooding female leaves the male territory for another territory and, after about 35 days, she frees the offspring composed by 4-8 young fishes. The fry is dispersed in very shallow water for avoiding predators. During the brooding period the female cannot eat freely (because of the eggs and the fry in her mouth), thus, after the reproduction she recover in her territory for nearly one month (Yanagisawa & Sato, 1990; Yanagisawa & Nishida, 1991; Šchürch & Taborsky, 2005; Egger et al., 2006; Sefc, 2009).

In this Section we study the role of the locality of the reproduction system of *Tropheus* in the maintenance of stable polymorphisms as it happens in Lake Tanganyika.

The Model

We use an individual based model to describe the reproduction strategy in *Tropheus moorii* and run simulations to study its effect on the population dynamics. Each fish of the reef is represented by its genotype and its breeding condition. The simulation proceeds day by day by considering each individuals and by applying to it suitable behavioural rules (with the right probability). The territories in the reef are represented by a grid (with 150×150 entries); each entry in the grid can be occupied by an individual.

For the representation of genotypes we consider diploid individuals whose colour morph is coded by L loci, each one with two possible alleles. Because of the diploid assumption we have 2^{2L} possible genotypes. We consider the 2^{2L} different genotypes groped in three phenotypes: the *zero phenotype*, the *one phenotype*, and the *hybrid phenotype*. For assigning a genotype to its phenotype we consider the distribution of the alleles in the genotype itself. We consider all the different phenotypes as having the same fitness, thus individuals with different phenotypes have the same survival probability. The surviving probability is such that the percentage of the occupied territories in the reef is about 70%. We assume a higher probability of death for the individuals in their first year of life.

The population of fishes follows the reproduction system of Tropheus. The reproduction system we consider is characterized by a strong locality. A female chooses a male in a small area around her territory, this area (actually a square) has a size which depends on the density of the reef. We consider assortative mating: A female chooses among available males depending on their phenotype. A female prefers males exhibiting the same phenotypes: as the phenotypes diverge her preference decreases. Thus a female of phenotype zero prefers hybrid males with a medium strength, and prefers a male of phenotype one with still less strength. Assortative mating in *Tropheus* has been reported by several authors (Salzburger et al., 2006; Maderbacher, 2008; Egger et al., 2009). After spawning, the female moves into a new territory close to the one of the male. We performed simulations by varying the strength of the female preferences.

Results

We first study the outcome of a situation in which two different populations came into contact in the same territory (Fig. 5). This could have happened during one of the frequent fluctuation of the water level in Lake Tanganyika (Sturmbauer, 2001). The two populations, of the same size, are mixed randomly in the reef: the first population is composed by individuals with phenotype zero while the second population with phenotype one. The results on the rows of Figure 5 correspond to increasing values of the female preferences. The columns show situations corresponding to: the initial configuration, the situations after 10, 150, 300, 500 and 1000 years. The light grey dots represent individuals of the zero phenotype, the black dots individuals of the one phenotype, and the dark grey dots individuals of hybrid phenotype. We can observe that with a small female selectiveness only one phenotype survives. This is due to the quite high randomness of mating, which is responsible for a random drift of the population. When the selectiveness increases the two populations (and possibly the hybrid one) distribute in the reef by separating the areas in which they live. They are, in this way, able to maintain a stable polymorphism in the reef. We hypothesize that the outcomes of Figure 5, in which the two (or three) populations aggregate on different areas in the reef, are due to the locality of the reproduction system of Tropheus. To investigate this hypothesis we remove locality by allowing females to choose males in a larger area. We maintain the structure of the areas in which a female chooses a mate, moves for brooding, and the fry is released, but we increase dramatically the radius of the area itself. This means that, with a population density of 70%, a female is able to range in a area of radius 15. This does not mean that



Fig. 5 - Results for two different populations, with females' local choice, which live in the same territory. The two populations, of the same size, are mixed randomly in the reef: the first population is composed by individuals with phenotype *zero* while the second population with phenotype *one*. The rows correspond to increasing values of the female preferences. The columns show situations corresponding to: the initial configuration, the situations after 10, 150, 300, 500 and 1000 years. The light grey dots represent individuals of the *zero* phenotype, the black dots individuals of the *one* phenotype, and the dark grey dots individuals of hybrid phenotype.

the female is able to evaluate all the available males in the big area. The model is such that the number of possible choices is exactly the one a female should have in a small area (as presented in the previous subsection): the males are evaluated randomly in the big area in a quantity which does not exceed this number. Thus the number of attempts for mating is the same as in the previous subsection, but the female can swim freely in the reef.

The results are shown in Figure 6. In this case, also with strong female preference, the populations cannot exploit different areas of the reef. The possibility of freely swimming in the reef allows the females to choose preferred males even if they are not in the neighbourhood, but this behaviour prevents the formation of compact zones in which individuals of the same phenotype occur. The populations of different phenotypes are exposed to stronger fluctuations. These size fluctuations can take a population under the threshold for its survival. By using the three phenotypes and the given female preferences, hybrid individuals have a mating advantage. They are preferred by hybrid females and they can rely on a medium preference by the other females. The males of non-hybrid phenotypes are preferred by females with the same phenotype, they have a medium preference by hybrid females, and they have a very low preference by females of the opposite phenotype. Thus, if the population is composed by the three phenotypes in the same percentages, hybrid males mate more than the others, and the population evolves towards a unique hybrid population.

If the female selectiveness is high, hybrid individuals are not produced (or produced in small quantity), thus the population maintains the original phenotypes. In the case in which the selectiveness of females is low, hybrid individuals are produced in a significant quantity, and, eventually they replace the initial populations.

We can conclude that the reproductive system of *Tropheus*, with its locality, favours the maintenance of



Fig. 6 - Results for two different populations, without females' local choice, which live in the same territory. The figure adopts the notation of Figure 5.

polymorphism when associated with assortative mating in which females prefer male of their phenotype. This could explain the great number of different colour morphs as well as the fact that, in some cases, different morphs live in the same reef in the lake.

CONCLUSION

In this paper we have shown two examples of application of individual based modelling and simulation to case studies of fish populations. In the first case study, inspired by *Carassius gibelio* populations, we have investigated the advantages of a mixed (sexual and asexual) type of reproduction in a fluctuating environment. In the second case study, inspired by *Tropheus morii* populations in Lake Tanganika, we have investigated the role of the locality of the reproduction system of *Tropheus* in the maintenance of stable polymorphisms. In both case studies, the use of individual based models has allowed the population dynamics to emerge from the description of how individuals interact with each other and with the environment. In addition, individual based models allowed stochastic aspects of population dynamics to be taken into account.

Validation of hypotheses on both the investigated phenomena has been supported by simulation results.

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