THE SEARCH FOR GENETIC DIFFERENTIATION OF TWO SARDINE SPECIES (*SARDINELLA AURITA* AND *S. MADERENSIS*)

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Abstract :

The population genetics of marine fishes has long suffered from the absence of spectacular results which led to a lack of confidence from the fishery managers. The genetic differentiation of two sardine species (*Sardinella aurita* and *S. maderensis*) has been looked at with allozymic data. For *S. aurita* we could not find enough genetic variability to infer genetic structuration. *S. maderensis* showed more variability. We could therefore test the possible differentiation of this species in its distribution area. We found a small but significantly different from zero (*i.e.* from panmixia) value for the WEIR and COCKERHAM (1984) estimator of WRIGHT's Fst index of genetic differentiation (Fst = 0.0085). Genetic differentiation exists for *S. maderensis*. This genetic differentiation means that it is also a dynamic one. We can estimate the number of effective migrants between the different populations. This number (around 30) is probably negligible compared to the effective size of the populations. We need nevertheless estimates of the effective size to better understand the genetic structure of pelagic fishes.

Deficits of heterozygotes inside the samples (Fis values between 0.10 and 0.19) have been observed. This could be due to the existence of different «populations» inside a school, relatedness of individuals sampled, or selection effects. We discuss these points briefly.

Résumé :

La génétique des organismes marins a longtemps souffert du manque de confiance des gestionnaires des pêches par l'absence de résultats spectaculaires. Nous avons analysé la variabilité génétique de deux espèces de sardinelles (Sardinella aurita et S. maderensis) par l'intermédiaire de sa variabilité allozymique. Nous n'avons pas trouvé de variabilité suffisante chez S aurita pour pouvoir conclure sur sa structuration génétique. En revanche S. maderensis s'est révélée plus variable. Nous avons donc pu chercher à mettre en évidence sa différentiation génétique sur son aire de répartition. La valeur de l'indice Fst de WRIGHT estimé selon WEIR et COCKERHAM (1984) s'est révélée faible (Fst = 0.0085) mais significativement différente de zéro (c'est à dire de la panmixie). Une différenciation génétique existe donc pour S. maderensis. Cette différenciation génétique est donc également dynamique. Nous avons en effet pu estimer le nombre de migrants efficaces entre les différentes populations. Ce nombre (autour de 30) est vraisemblablement négligeable devant la taille efficace de la population. Nous avons cependant besoin d'estimation de cette taille efficace pour mieux comprendre la structure des poissons pélagiques.

Des déficits en hétérozygotes ont été observés à l'intérieur des échantillons (valeurs de Fis comprises entre 0.10 et 0.19). cela peut être dû à l'existence de «populations» à l'intérieur des bancs, à un apparentement entre individus ou encore à des phénomènes sélectifs. Nous discutons brièvement ces points.

1. Introduction

The population genetics of fishes and marine organisms in general has not been as well developed as that of other organisms. This relatively small number of studies in marine fish was probably due to a lack of confidence from fishery managers (UTTER, 1991). The first works on fishes tried either to find simple relationships between production traits and one or two genes, or to find markers which would help discriminate different populations (UTTER, 1991). If the first hope has been abandoned the second one is still alive. Nevertheless the latter has lost part of its simplicity: it has indeed been shown that phenotypic differences (size, weight, number of vertebra, etc.) cannot be considered as good markers of genetic differentiation (HEDGECOCK *et al.*, 1989 ; ALLENDORF *et al.*, 1991; UTTER, 1991).

Whatever the genetic markers used to discrimate two or more populations they need to be polymorphic enough to allow differences between these populations to have arisen. If this marker is monomorphic it will be unable to answer any question about population structure.

If methods of mark-recapture seem to be appropriate to understand how different regions exchange individuals, they suffer a strong bias because they only give information on *movement* of individuals not *on their reproductive*

success. As the definition of a population is implicitly or explicitly a genetic one (OVENDEN, 1990 ; MARCHAL, 1991b ; BINET and MARCHAL, 1992) the information on the movement of individuals is not sufficient. Only genetical studies which are based on a marker that is affected by the history of a species is able to account for that kind of event. Of course genetics could not be a useful tool without the different approaches of other disciplines such as biogeography, ecology, dynamics and sclerochronology (for the latter see PANFILI's project in this volume), etc.

The pattern of variation in genetic markers will be the result of history and therefore of many different forces and events, past and present (see appendix).

Our work followed a classical route in that we decided to first work on enzymatic variability. This genetical tool is indeed the easiest one to develop on a new species and permits to work on a great number of fishes on many different loci. Only three studies on *Sardinella aurita* had been published as we began our work. BARON (1971, 1973) worked on esterases and transferrines of the blood and was not able to see anough variability. WILSON and ALBERDI (1991) addressed a somewhat different problem since they tried to show that both *Sardinella aurita* and *S. brasiliensis* species were the same (*S. aurita*) at least in the eastern Gulf of Mexico. Only one study seems to have ever been published on *S. maderensis (BARON, 1971).*

2. Materials and Methods

The fishes were caught along the African coast during the year 1992 at four different sampling points: Dakar (Senegal : 62 aurita + 95 *maderensis*), Abidjan (Ivory Coast: 113 aurita + 126 *maderensis*), Tema (Ghana: 117 aurita + 115 *maderensis*) and Pointe Noire (Congo: (98 + 92) aurita + 69 *maderensis*). The samples from Ivory coast and Ghana were obtained by pooling individuals of different sampling points off their respective coasts. There were two sampling dates for *S. aurita* off Pointe Noire (98 + 92).

The fishes were either immediately dissected or frozen first at -20°C. Eyes, white muscle and liver were then taken from every individual and stored at -20°C before being thawed and homogenized in order to be used for the electrophoresis. We used strips of filter paper which were dipped in the centrifugated homogenized extract, blotted on filter paper and then applied to the starch gel. The extracts were then refrozen and kept at -20°C for subsequent use. The gels were run between three and seven hours at intensity settings between 50 and 100 mA depending on the buffer system and other practical considerations.

WRIGHT's fixation indices (Fit, Fst and Fis) are basic parameters in the study of population genetic differentiation. The Fit index measures the departure from panmixia in the total species' range sampled. If the population is panmictic it is said to be at the HARDY-WEINBERG equilibrium. This equilibrium can be defined by the expected proportions of both homozygotes and of heterozygotes. This total departure from panmixia can be partitionned in two terms. The first one is the departure at the population level. It is then measured by the Fis index

either as an excess or as a deficit of heterozygotes. The second term measures the differentiation of the total population into subpopulations. It is the Fst index. These indices satisfy the identity :

$$1 - FIT = (1 - FIS)(1 - FST) \qquad \text{(WRIGHT, 1951)}$$

As we are concerned with problems of differentiation between samples we will mostly focus on the Fst index. Its value are between zero and unity. If Fst is equal to zero there is no subdivision at the level observed. If Fst equals unity the different populations are fixed for different alleles. Actually Fst is a standardized variance of the allelic frequencies. It represents the part of the allelic frequency variation which is due to differentiation. Its departure from zero is therefore a measure of the subdivision of the populations.
Fis and Fit both vary between minus one and one.

Different estimators of these indices have been proposed (COCKERHAM, 1969 ; NEI, 1975 ; WEIR and COCKERHAM, 1984) taking or not into account more than two alleles per locus and one or many loci. Even the comparative values of these estimators have been studied (WEIR and COCKERHAM, 1984 ; CHAKRABORTY and LEIMAR, 1987 ; CHAKRABORTY and DANKER-HOPFE, 1991).

The data on allele frequencies were analysed using the GENETIX program developed by the «Groupe de Génétique des Populations» in Montpellier (France). The method of WEIR and COCKERHAM (1984) was used to calculate the F-statistics for several alleles at a locus to estimate the level of population differentiation at polymorphic loci. We used then the averaged value over the different loci as proposed by WEIR and COCKERHAM (1984) to have a single estimate of the structure of the species on the sampled area.

To estimate the departure of the Fst value from zero (*i.e.* from panmixia), the GENETIX program is generating permutations of the alleles of each locus creating this way a panmictic urn which represents what should happen if the individuals were reproducing randomly and not like more or less independant populations. For each permutation the Fst (and Fis and Fit) value is calculated. After a great number of permutations a distribution of the Fst is obtained. The actual value is then compared to the distribution. The percentage of values of the distribution higher than the actual is obtained. It is then possible to see whether or not the actual value is statistically different from zero. The number of permutations depends on the size of the data file. It was enough to perform 3000 permutations for our data. Other sets of replicates were done and never differed from the initial results.

3. Results

Sardinella aurita

Among the 15 loci that we could read and interpret correctly only two were variable. We could not therefore use most of them to answer the question of genetic structuration.

The reader should be aware that this does not mean at all that the species can be regarded as a single panmictic unit. It only means that another genetical tool should be used to solve the problem.

WILSON and ALBERDI (1991) also found a very low degree of genetic variability (at the same time they noticed problems to read some of the loci studied). Their study was based on 36 to 41 loci but could not find significant allelic differences between samples of the Gulf of Mexico and the sample of Brazil.

Sardinella maderensis

We found five variable and interpretable loci for *S. maderensis*: ACP, SDH, FDP1, FDP2 and 6PGDH.

At the African level

The Fst value is 0.0085. This value indicates a very low degree of subdivision. But the permutations generated by GENETIX showed that although low this value of Fst was significantly different from zero. We present in fig.1 the distribution of the values calculated after each permutation. We can see that the value of our original data set is in the extreme side of the distribution. This means that there is a population subdivision along the African coast for *S. maderensis*. We present one distribution for which 1000 permutations were used. We also used simulations increasing the number of permutations up to 5000. We made replicates for any given number of permutations and never had more than 1.6 % of the values superior to our real value.

As Fst is 0.0085 this differentiation seems quite small and we shall discuss it further.

At the Ivory Coast- Ghana level

The same analysis gave a value of -0.0007 for Fst. We must first notice that this negative value is inherent to the parametric model proposed by COCKERHAM (1969). See COCKERHAM (1969, 1973) and CHAKRABORTY and DANKER-HOPFE (1991) for further discussion. When such a value is obtained it means that its expectation is zero.

The permutation analysis indicated that this value is not significantly different from zero. There is *a priori* no reason to think that the ivorio-ghanean stock of *S. maderensis* is composed of two (or more) reproductive units. Only further analyses could help us answer this question.

At the population level: the large Fis values

As we are much more concerned with genetic subdivision, the following results will be presented rapidly.

The Fis measures the departure from panmixia inside each sample. There is one value for each sample although it is possible to have an averaged value over the samples. The WEIR and COCKERHAM (1984) estimator gives such an averaged value. If its value is significantly different from zero it means that inside the sample the individuals are not the result of a panmixia. Positive values correspond to deficit of heterozygotes while negative values are caused by excess of heterozygotes.

All Fis values were positive and varied between 0.10 and 0.19 (values obtained for all population pairs). They were clearly different from zero as no Fis value obtained by the permutations was larger than the actual.

4. Discussion

Sardinella aurita

If we could not yet answer the question of subdivision of that species along the African coast, we must point a few things of importance.

First of all these results do not mean that there is no subdivision. We just are unable so far to answer this question for *this* species with *this* set of genetic markers. We need another genetic approach which will provide more variability.

Second the lack of genetic variability that has been observed confirms the results of WILSON and ALBERDI (1991) as we already noticed earlier. This result raises a problem which cannot be neglected in the study of pelagic fishes as it gives information about the possible history and reproductive behaviour of that kind of fishes. How can indeed such a species show so little genetic variability if it composed of so many individuals? The loss of genetic variability is all the more probable that a species is composed of few individuals and therefore subject to genetic drift. Rare alleles are then lost randomly because of the small number of individuals reproducing. There seems to be a contradiction: on one side you have many individuals and on the other side you have little genetic variability at loci which are neutral. Therefore we shall introduce here an idea that should help understand that phenomenon.

In population genetics there is a concept which tries to take account for the real number of individuals which reproduce. It is the effective size. This effective size (*Ne*) is of course smaller than the total number of individuals. It takes into account the unequal numbers of males and females, the variance in the reproductive success, overlapping generations, etc. The problem is of course to estimate the effective size of the population. It can be approached by temporal changes in allele frequencies (WAPLES, 1989) but necessitates a few generations to provide good estimates of *Ne*. Whatever the accuracy of this method to quantify *Ne,* our results indicate clearly that the effective size of *S. aurita* is much smaller than expected by the catches data.

A few hypotheses can be advanced to explain it. This low degree of genetic variability can be due to bottleneck effects which can have occured about 18 000 years ago. The sea was about 100 meter below its current level. This implies that there was a dramatic reduction of the continental shelf. As *S. aurita* seems to be dependant on this environment it could have suffered a strong reduction of its distribution. If this dependance can be proved (which has not yet been done) there seems to have been two possible refugia, one at the Bissago islands where the continental shelf is very large and the other off Angola. The study of scale deposition by core sampling could be of great help to know the past distribution of *S. aurita* along the african coast (see the interesting study of SHACKELTON (1986) on scale deposition of pilchard and anchovy off Namibia). Nevertheless anoxic conditions are necessary for the conservation of the scales (SOUTAR and ISAACS, 1974 ; SHACKELTON, 1986). It seems difficult , if possible, to find that conditions in the west African coast.

The lack of variability can also be caused by regular variations in the populations of *S. aurita.* It is indeed well known that this species is dependant on upwelling systems and sensitive to environmental variations (CURY and FONTANA, 1988 ; PEZENNEC et al., 1993). It exhibits much variability in the catches in very small time scales (a few years). Again data from core samples could be of interest to study the past (and long-term) variability of this species.

Another factor that can be responsible for a small effective size in pelagic fish species is the variance in the reproductive success. A female of *S. aurita* (and of *S. maderensis*) is able to hatch between 50 000 and 200 000 eggs per year (CONAND, 1977). Thereby a few number of females can give rise to a population (at least a great number of individuals) if the environment conditions were good for the larvae produced. This variance can be even greater because the environment is variable and can induce strong mortality variability.

Sardinella maderensis

At the African level

Though this species shows more variability than *S. aurita,* we cannot generalize this result as we worked on a small number of loci. Nevertheless this variability was large enough to show that along the African coast the species cannot be considered as a single population. This result is not a minor one as we know that the triggerfish (*Balistes carolinensis*) populations have invaded very large areas in a few years (CAVERIVIERE, 1991 ; MARCHAL, 1991a ; PEZENNEC *et al.*, 1993). Indeed the ability of some fish populations to invade quickly large areas can lead to a genetic uniformity on that area. Our observation of different levels of genetic variability of the two sardine species is nevertheless consistent with the catches of the two species. The fact that *S. aurita* is economically much more important (the catches are significantly higher) does not mean that its effective size (*Ne*) is larger. Indeed the effective size along the

time is not the arithmetical mean of the population effective size say each year but its harmonic mean. The lowest level of *Ne* reached during time plays the major role as it is responsible for the loss of genetic variability. If a species reaches a very high level after a crash the variability will not be increased by this way as new alleles will not be created so fast. *S. aurita* appears to collapse much more than *S. maderensis* and frequently has population sizes less than that of *S. maderensis*. This indicates a (presumably) larger effective size for the latter species.

In fact the Fst value, small but significantly different from zero, means that the differentiation is not very important from a genetical point of view. This can be due to continuous exchange of individuals (migration) between the populations. This can also be the result of a recent separation: the allelic frequencies would not have had time enough to diverge by genetic drift. All the more that the effective size might not be very small.

The fishery managers are concerned with populations of fishes over very short periods of time. The studies of population genetics on marine fish have been rarely able to prove the existence of differentiation even on large areas while it has been observed for freshwater species (GYLLENSTEN, 1985). This kind of result has been largely considered as a failure of population geneticists. WYATT *et al.* (1991) consider indeed that the existence of these units of reproduction is a fact but that the lack of variability and the possible time scale inferred has been too short. Thereby JORSTAD *et al.* (1991) have been calling for other genetic tools.

Fishery managers should not forget that the period of time examined by the geneticist is larger than a few years. But this implies that when a geneticist shows that there is population subdivision this result is likely to be valid. Moreover under a few hypotheses the Fst value can be relied to an estimate of the number of effective migrants (*M*) between the populations : $Fst = 1/(1 + 4M)$. (CROW and KIMURA, 1970)

Our value of Fst is 0.0085 therefore *M* is about 30. Our results mean therefore that, as a result of their history since they separated, the current population differentiation is equivalent to that they would have if they had exchanged about 30 individuals every generation. These migrants are effective migrants. The populations could exchange thousands of individuals but only 30 could reproduce successfully. This result is of a great importance as it underlines the difference between the dynamic as opposed to the genetic evolution. The value of *M* is only approximative and cannot of course be used as an absolute value as long as we do not have ideas of the effective size of *S. maderensis*. Nevertheless this value is certainly negligible as compared to *Ne*. We have thereby two answers at two different levels. The populations have genetically diverged. This first point is necessary to stress the second one. As these populations have significantly diverged we can estimate the value of *M* which shows that from a dynamical point of view the exchange of migrants is small. Otherwise we would not find any significant Fst at all.

At the Ivory Coast-Ghana level

No subdivision has been proved to exist. But the use of another marker could be of interest as we know that even at such a large scale as the African distribution (between Dakar and Pointe Noire) the differentiation is not very marked. The existence of different populations cannot be denied by our results. The use of another genetic tool is of importance. If the mitochondrial DNA proves to be variable it could be very useful for understanding the population subdivision of this fishery and therefore its managing.

At the population level : the large Fis values

First, we must stress the fact that the individuals sampled are members of a school as they have been bought to fishermen on the beach (most of the time and when not they were taken from a case of a boat). We can therefore suppose that they belong either to one school or to the pooling of a few schools.

According to SHUSTER (submitted and pers. comm.) if the Fis values are more than as twice large as Fst values «*(and certainly if these values differ by more than an order of magnitude) the scale of subdivision may be smaller than is currently recognized in the analysis*». This could mean that inside each sample the individuals belong to different populations. Suppose that two populations have for one gene the same alleles at different frequencies. Then, if they are mixed, although each population is panmictic the resultant population will present a deficit of heterozygotes. This is the WAHLUND effect. But to allow such a departure the populations should have had large allelic differences. This would imply that the individuals of each population have been produced by a small number of individuals. In such a case we have to understand how a few individuals produce schools or parts of schools. But if the analysis of SHUSTER is of much interest it is a theoretical approach in which his basic populations are by definition panmictic. Therefore the departures from the panmixia can only be caused by subdivision and of course by the scale at which the subdivision is observed. This approach does not take into account the possible inbreeding structures that can exist.

On the other hand, this kind of deficit can be caused by the existence of inbreeding in the population. If individuals of a school are say brothers and sisters then this will generate large values of Fis as homozygotes will be produced more likely than heterozygotes. Just because individuals have the same alleles with a greater probability. How can then related individuals breed together so that these Fis values are produced? And how can schools have such a duration that these results could be observed? FREON (1985) showed indeed that individuals of the same fry cannot stay in one school because of the great disparity in their growth.

Another view is that selection could induce these effects. This argument has already been advanced for marine invertebrates for which large Fis values have been observed particularly in the first stages of the life cycle. But as the age of colonies is growing these deficits of heterozygotes disappear. As our samples

were not composed of larvae or young individuals or different age classes there is no reason to adopt this view. Although it cannot be eliminated. As noted CHAKRABORTY and LEIMAR (1987) a good strategy is to «*try to interpret electrophoretic data without invoking selection so long as no information to the contrary is available.*»

That means, because of our sampling method, that individuals of a school could either be composed of individuals of different small populations or of related individuals. Whatever the truth both hypotheses lead to the idea that the effective size can be much smaller than expected for exploited populations. They also lead to the problem of homing that is known to exist in many freshwater species and other marine organisms. But the reproduction of related individuals necessitates a very precise homing, in time and space. It seems difficult to imagine it unless schools persist for a long time. These individuals would then reproduce together. The mixing with other schools could be negligible. It is nevertheless far from being proved.

The existence of a large variance in the reproductive success could be meaningful in the genetic structure of the species. This would indeed result in the reduction of the effective size causing also large deficits in heterozygotes.

6. Conclusion and Perspectives

We have been able to show the existence of a differentiation for *S. maderensis* but could not answer for *S. aurita*. We need therefore more polymorphic markers for this second species as we also need a larger sampling scale. We recently obtained individuals of *S. aurita* from Mediterrannea, Venezuela, and Gulf of Mexico. Comparing individuals from both parts of the Atlantic could be of interest to see whether this lack of genetic variation is due to bottleneck effects or not. It could also help understand from which continent, Africa or America the species colonized the other one.

As mitochondrial DNA (mt-DNA) is very sensitive to bottleneck effects (BERMINGHAM and AVISE, 1986 ; HALLERMAN and BECKMANN, 1988 ; BERNATCHEZ et al., 1989) it could help us in our goal. We have just begun to sequence the cytochrome-B gene of the mt-DNA molecule. Although very few individuals have been sequenced, this part of the mt-DNA does not seem to be very variable. It appears to be necessary to look for a more variable region. Therefore we shall sequence the control region which is a non coding region supposed to be more variable. It has been proved for mammals that the mt-DNA molecular rate of evolution is two to ten times larger than that of the nuclear coding DNA (AVISE, 1986 ; BROWN, 1985 ; BOURSOT et BONHOMME, 1986). But BILLINGTON and HEBERT (1991) noticed that the evolution rate was two or three times slower than that of mammals for salmonids and ten times slower in the genus *Alosa*. Results have to be obtained for both sardine species.

We need more biological data to confirm our results. Tagging data could help us understand the movement of individuals as compared to our effective

migrants. Sclerochronology, and particularly studies on the chemical composition of the otoliths, could also be of great help to understand the growth and the movements of fishes in the fished areas (PANFILI in the present volume and pers. comm.). Core sampling could also provide very interesting results on the ancient distribution and variability of these species over great periods of time. A better understanding of the reproduction behaviour of pelagic fishes in general and of sardines in particular is absolutely needed. We have indeed shown that homing behaviour, variance in the reproductive success and relatedness of individuals both reproducing and inside a school are fundamental great importance in the genetic structure of the species. School formation and duration is directly linked to these reproductive behaviours as what is fished is a school or a group of schools.

Genetic studies are of much importance as they have proved their strength to indicate differentiation and their ability to raise questions in other fields that might have been neglected. It has also shown its ability to work in collaboration with other fields of the fishery management. Population genetics is able to answer questions that no other field can. It needs to be developed in the fishery management.

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APPENDIX

In this appendix we shall try to recall the basis of population genetics on which our work is based. Population genetics is interested in the evolution of the allele frequencies of a locus. It is therefore a branch of the Theory of Evolution. We will be interested in populations of individuals of the same species.

An allele is one of the two forms that a gene can take. We also use the term locus in allusion to its physical location. An individual has, for each gene he possesses, one allele from his father and the other from his mother. If the two alleles are the same the individual is said homozygote and if they are different he is heterozygote.

The evolution through time of the allelic frequencies in a population is the result of many different phenomena. New alleles can appear by **mutation** or **migration** from another population. They can be subject to **selection**

(or counterselection). They can be lost **randomly**. This event which is all the more frequent that the population size is small is called **genetic drift**. Strong collapses («bottlenecks») of a population can be responsible for a loss of genetic variability.

We should point here that if for most of the people the idea if evolution is closely linked to that of selection, we will be much more concerned with **neutral genes**.(*i.e.* non subject to selection). Motoo KIMURA who developed The Neutral Theory of Molecular Evolution (1983) insisted on the fact that he was interested in genes for which the evolution through time was much more due to random effects than to selection. He did not deny the strong force of selection on the evolution of life but showed that most of the variation observed at the molecular level (*i.e.* the genetic polymorphism we are looking for) is neutral or quasi-neutral.

If we can suppose that the loci we are studying are neutral the evolution of the allelic frequencies in different populations will be the result of two different forces which act in opposit directions. The mutations will create new alleles in each population and thereby differentiation while migration between the populations will permit the «private» alleles to be shared, homogenizing the frequencies through the species' area. The result on the genetic structure of the populations will depend on the relative effects of these homogenizing and differenciating forces and of the time since their separation. These relative effects will of course depend on biological parameters (migration capacity, effective size, reproduction behaviour, sex ratio, variance of the reproductive success), physical parameters (barriers to migration, more or less heterogeneous environment) and biogeographic history of the species (transgressions, glaciations or droughts responsible for possible bottlenecks).

While a selected locus could be of no use to understand the structuration of a species (unless the actual effects of the selection are understood) it appears here that because of its neutrality a locus will be a good witness of the functioning of a species in its environment. Indeed suppose that we have a gene for which one allele is selected for in an environment and counterselected in another. Then we will see that there is a strong variation in the allelic frequencies of this gene. But this will be of no use to understand wether or not these populations are isolated. Even if these population exchange a great part of their population each generation the environment will filter the individuals and give the same view. The noise of selection will darken the migration events.

The only problem will be to use the information given by the genetic data as they are the result of the history of a species and not only of its current behaviour.

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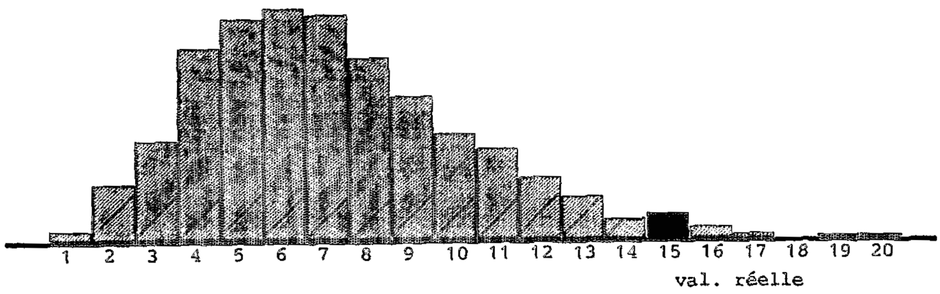

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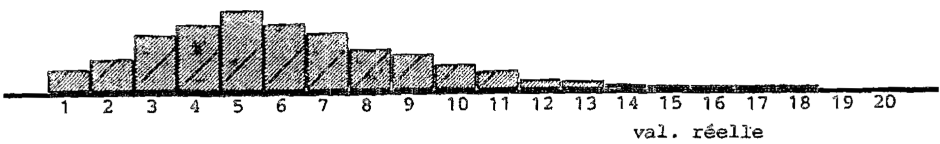

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