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Molecular markers and their applications in fisheries and aquaculture

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ABSTRACT

Genetic variation in a species enhances the capability of organism to adapt to changing environment and is necessary for survival of the species. Genetic variation arises between individuals leading to differentiation at the level of population, species and higher order taxonomic groups. The genetic diversity data has varied application in research on evolution, conservation and management of natural resources and genetic improvement programmes, etc. Development of Molecular genetic markers has powerful ability to detect genetic studies of individuals, populations or species. These molecular markers combined with new statistical developments have revolutionized the analytical power, necessary to explore the genetic diversity. Molecular markers and their statistical analysis revolutionized the analytical power, necessary to explore the genetic diversity. Various molecular markers, protein or DNA (mt-DNA or nuclear DNA such as microsatellites, SNP or RAPD) are now being used in fisheries and aquaculture. These markers provide various scientific observations which have importance in aquaculture practice recently such as: 1) Species Identification 2) Genetic variation and population structure study in natural populations 3) Comparison between wild and hatchery populations 4) Assessment of demographic bottleneck in natural population 5) Propagation assisted rehabilitation programmes. In this review article, we have concentrated on the basics of molecular genetics, overview of commonly used markers and their application along with their limitations (major classes of markers) in fisheries and aquaculture studies.

Keywords: Genetic Diversity; Molecular Markers; Microsatellite; Aquaculture

1. INTRODUCTION

All organisms are subject to mutations because of normal cellular operations or interactions with the environment, leading to genetic variation (polymorphism). Genetic variation in a species enhances the capability of organism to adapt to changing environment and is necessary for survival of the species [1]. In conjunction with other evolutionary forces like selection and genetic drift, genetic variation arises between individuals leading to differentiation at the level of population, species and higher order taxonomic groups. Molecular genetic markers are powerful tools to detect genetic uniqueness of individuals, populations or species [2,3]. These markers have revolutionized the analytical power, necessary to explore the genetic diversity [4]. The conclusion from genetic diversity data has varied application in research on evolution, conservation and management of natural resources and genetic improvement programmes, etc [5-10]

In addition to protein markers, application of DNA markers is finding wide acceptance in population genetics. With DNA markers, it is theoretically possible to observe and exploit genetic variation in the entire genome. Both genomic and mitochondrial DNA is used for varied applications. The commonly used technique are allozyme analysis, types of restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), microsatellite typing, single nucleotide polymorphism (SNP), and expressed sequence tag (EST) markers, etc.

Molecular markers can be classified into type I and type II markers. Type I markers are associated with genes of known function, while type II markers are associated with anonymous genomic regions [11]. Under this classification, allozyme markers are type I markers because the protein they encode has known function. RAPD markers are type II markers because RAPD bands

are amplified from anonymous genomic regions via the polymerase chain reaction (PCR). Microsatellite markers are also type II markers unless they are associated with genes of known function. The significance of type I markers is becoming extremely important for aquaculture genetics. Type I markers serve as a bridge for comparison and transfer of genomic information from a map-rich species into a relatively map-poor species. In general, type II markers such as RAPDs, microsatellites, and AFLPs are considered non-coding and therefore selectively neutral. Such markers have found widespread use in population genetic studies to characterize genetic divergence within and among the populations or species [12]

2. ALLOZYME MARKERS

Analysis of allozyme loci remained one of the most popular approaches in examining population genetics and stock structure questions in fishes [13]. The technique is rapid, relatively inexpensive and provides an independent estimate of level of variation within a population without an extensive morphological and quantitative survey [14]**.** Isohyets are structurally different molecular forms of an enzyme system with qualitatively the same catalytic function encoded by one or more loci [15]. Isohyets, which are encoded by different alleles of the same gene locus, are designated as "allozymes" or "alloenzymes" [16]. Amino acid differences in the polypeptide chain of the different allelic forms of an enzyme reflect changes in the underlying DNA sequence. Depending on the nature of the amino acid changes, the resulting protein products may migrate at different rates (due to charge and size differences) when run through a gel subjected to an electrical field. Differences in the relative frequencies of alleles are used to quantify genetic variation and distinguish among genetic units at the levels of populations, species, and higher taxonomic designations. Disadvantages associated with allozymes include occasional heterozygote deficiencies due to null (enzymatically inactive) alleles and sensitive to the amount as well as quality of tissue samples. In addition, some changes in DNA sequence are masked at the protein level, reducing the level of detectable variation. Some changes in nucleotide sequence do not change the encoded polypeptide (silent substitutions), and some polypeptide changes do not alter the mobility of the protein in an electrophoretic gel (synonymous substitutions). At present 75 isozyme systems representing several hundred genetic loci are known [17]. With the strength as codominant marker, ease of use, and low cost, the allozyme markers are popular in population structure and phylogenetic studies, though has limited role in aquaculture genetics.

3. MITOCHONDRIAL DNA MARKERS

Mitochondrial DNA (mtDNA) analysis is being increasingly used in recent population and phylogenetic surveys of organisms. Studies of vertebrate species generally have shown that sequence divergence accumulates more rapidly in mitochondrial than in nuclear DNA [18]. This has been attributed to a faster mutation rate in mtDNA that may result from a lack of repair mechanisms during replication [19] and smaller effective population size due to the strict maternal inheritance of the haploid mitochondrial genome [20]. Due to its rapid rate of evolution, mtDNA analysis has proven useful in clarifying relationships among closely related species. Different parts of the mitochondrial genome are known to evolve at different rates [21]. Almost the entire mtDNA molecule is transcribed except for the approximately 1-kb control region (D-loop), where replication and transcription of the molecule is initiated. In general, non-coding segments like the D-loop exhibit elevated levels of variation relative to coding sequences such as the cytochrome b gene [22], presumably due to reduced functional constraints and relaxed selection pressure. The 16S rRNA gene in the mitochondrial genome is one of the slowest evolving genes [21] whereas rapidly evolving regions are control regions [23,24]. Due to non-Mendelian mode of inheritance, the mtDNA molecule is considered as a single locus [2]. In addition, because mtDNA is maternally inherited, the phylogenies and population structures derived from mtDNA data may not reflect complete picture of the nuclear genome if gender-biased migration or selection [20] or introgression [25] exists.

Analyses of mtDNA markers have been used extensively to investigate stock structure in a variety of vertebrates including fishes [26-30], birds [31-34], mammals [35] and reptiles [36-39].

4. RANDOM AMPLIFIED POLYMORPHIC DNA (RAPD) MARKERS

RAPD markers are the amplified products of less functional part of the genome that do not strongly respond to selection on the phenotypic level. Such DNA regions may accumulate more nucleotide mutations with potential to assess inter-population genetic differentiation [40]. The amplification of genomic DNA by PCR with arbitrary nucleotide sequence primers, RAPD can detect high levels of DNA polymorphisms [41,42]. The technique detects coding as well as non-coding DNA sequences, and many of the most informative polymorphic sequences are those derived from repetitive (non-coding) DNA sequences in the genome [43]. Because 90% of the vertebrate nuclear genome is non-coding, it is presumed

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that most of the amplified loci will be selectively neutral. RAPD loci are inherited as Mendelian markers in a dominant fashion and scored as present/absent. RAPDs have all the advantages of a PCR-based marker, with the added benefit that primers are commercially available and do not require prior knowledge of the target DNA sequence or genome organization. Other advantages of RAPDs include the ease with which a large number of loci and individuals can be screened simultaneously. Shortcomings of this type of marker include the difficulty of demonstrating Mendelian inheritance of the loci and the inability to distinguish between homozygotes and heterozygotes. Analysis follows the assumption that populations under study follow Hardy-Weinberg expectations. In addition, the presence of paralogous PCR product (different DNA regions which have the same lengths and thus appear to be a single locus), low reproducibility due to the low annealing temperature used in the PCR amplification, have limited the application of this marker in fisheries science [44].

5. SINGLE NUCLEOTIDE POLYMORPHISM (SNP)

Single nucleotide polymorphism (SNP) describes polymorphisms caused by point mutations that give rise to different alleles containing alternative bases at a given nucleotide position within a locus. SNPs are becoming a focal point in molecular marker development since they represent the most abundant polymorphism in any organism's genome (coding and non-coding regions), adaptable to automation, and reveal hidden polymorphism not detected with other markers and methods [9, 10]. Theoretically, a SNP within a locus can produce as many as two alleles, each containing one of two possible base pairs at the SNP site. Therefore, SNPs have been regarded as bi-allelic. SNP markers are inherited as co-dominant markers. Several approaches have been used for SNP discovery including SSCP analysis [45], heteroduplex analysis, and direct DNA sequencing. DNA sequencing has been the most accurate and most used approach for SNP discovery. SNPs are not without their limitations, however, might provide marginal additional, or even less, utility in some applications (e.g. relatedness) [9].

6. MICROSATELLITE MARKERS

Microsatellites consist of multiple copies of tandemly arranged simple sequence repeats (SSRs) that range in size from 1 to 6 base pairs [e.g., ACA or GATA; 46,47]. Abundant in all species studied to date, microsatellite motifs have been estimated to occur as often as once every 10 kb in fishes [48]. Microsatellites tend to be evenly distributed in the genome on all chromosomes and all regions of the chromosome. However, data from whole genome sequencing has somewhat contradicted this statement. They have been found inside gene coding regions [49], introns, and in the non-gene sequences. Most microsatellite loci are relatively small, ranging from a few to a few hundred repeats. Regardless of specific mechanisms, changes in numbers of repeat units can result in a large number of alleles at each microsatellite locus in a population. Microsatellites have been inherited in a Mendelian fashion as codominant markers. Microsatellites were found to be informative in several species, which showed almost no variation at other markers [50]. However, use of microsatellite markers involves a large amount of up-front investment and effort. Each microsatellite locus has to be identified and its flanking region sequenced to design of PCR primers. Due to polymerase slippage during replication, small size differences between alleles of a given microsatellite locus (as little as 2 bp in a locus comprised of di-nucleotide repeats) are possible. Microsatellites recently have become an extremely popular marker type in a wide variety of genetic investigations.

7. NEW DEVELOPING MARKERS IN FISHERIES AND AQUACULTURE

Various type of DNA markers have been developed, including Allozymes, microsatellites, RAPDs, mt-DNA and SNPs. These markers in fish populations have revealed high levels of genetic variation distributed throughout the fish genome. A recent initiative has been made to accelerate efforts of DNA marker development, genome mapping and species identification. Major progress has been made toward Expressed Sequence Tags (EST) and DNA barcode development in several aquaculture species.

8. EXPRESSED SEQUENCE TAGS (ESTs)

Expressed sequence tags (ESTs) are single-pass sequences generated from random sequencing of cDNA clones [51]. The EST is use to identify genes and analyze their expression by means of expression profiling. It helps for rapid and valuable analysis of genes expressed in specific tissue types, under specific physiological conditions, or during specific developmental stages. ESTs offer the development of cDNA microarrays that allow analysis of differentially expressed genes to be determined in a systematic way [52], in addition to their great value in genome mapping [53]. For genome mapping, ESTs are most useful for linkage mapping and physical mapping in animal genomics such as those of cattle and swine, where radiation hybrid panels are available for mapping non-polymorphic DNA markers [54]. A radiation panel is composed of lines of hybrid

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cells, with each hybrid cell containing small fragments of irradiated chromosomes of the species of interest. Typically, the cells from species of interest are radiated to break chromosomes into small fragments. The radiated cells are unable to survive by themselves. However, the radiated cells can be fused with recipient cells to form hybrid cells retaining a short segment of the radiated chromosome. Characterization of the chromosomal break points within many hybrid cell lines would allow linkage and physical mapping of markers and genes. In spite of its popularity in mammalian genome mapping [55, 56], radiation hybrid panels are not yet available for any aquaculture species. Development of radiation hybrid panels from aquaculture species is not expected in the near future, given the fact that physical mapping using BAC libraries can provide even higher resolution and the fact that BAC libraries are already available from several aquaculture species. Therefore, ESTs are useful for mapping in aquaculture species only if polymorphic ESTs are identified [57]. The value of EST resources and applications of bioinformatics in aquaculture genetics/genomics is inevitable, and it is expected that various EST databases will serve as rich sources of genomic information not only for aquaculture geneticists, but also for aquaculture physiologists, immunologists and biotechnologists.

9. DNA BARCODING

The principle of conservation biology is the preservation and management of biodiversity. The two major problems to such an endeavor are the difficulty of developing an assessment of this diversity for prioritization of hotspots of species richness [58] and the identification of lineages particularly worthy, or in need, of preservation [59-64]. Understudied taxa are greatly susceptible to extinction [65], suggesting there is a conservation penalty for our ignorance. Even there are millions of unidentified and unknown species [66]. DNA barcodes, segments of approximately 600 base pairs of the mitochondrial gene cytochrome oxidase I (COI), have been proposed as a fast, efficient, and inexpensive technique to catalogue all biodiversity [67-70]. Barcoding is the use of universal polymerase chain reaction (PCR) primers to amplify and sequence an approximately 600-base-pair fragment of the COI gene. That portion of sequence is then compared using distance-based algorithms with an existing database of "known" sequences from specimens previously identified by taxonomists. DNA barcodes from a small portion of the mitochondrial genome might seem like an effective and rapid way to assess at least some, perhaps minimal, level of biodiversity. And for groups that are already relatively well known, especially birds and mammals, molecular studies based on barcode sized sequences have revealed cryptic DNA lineages and may be helpful [70].

10. APPLICATION OF MOLECULAR MARKERS SPECIES IDENTIFICATION

The inter-specific genetic divergence established through species specific diagnostic molecular markers provides precise knowledge on phylogenetic relationships and also resolve taxonomic ambiguities [71-74]. These markers can be used to detect hybrid and introgressed or backcrossed individuals [75], distinguish early life history stage of morphologically close species [76] both in hatchery and in natural populations.

Species-specific allozyme markers have been identified in many fishes [Tilapia: 72,77,78; Sciaenid: 73; *Anguilla* sp: 79; Mugilidae: 80] Specific diagnostic allozyme loci were used for different species: apache trout (*Oncorhynchus apache*), cutthroat (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) [81] and *Gambusia affinis* and *G. holbrooki* [82]. Allozyme markers have also been used for individual classification in cyprinid species *Zacco pachycephalus and Z. platypus* [83], in cyprinodontid species *V. letourneuxi* and *V. hispanica* [84], in mullets *Mullus barbatus and M. surmuletus* [85] and hake species *Merluccius australis* and *M. hubbsi* [86].

Species-specific diagnostic RAPD fingerprints were generated in several fish species and their taxonomic relationship has been analyzed. The RAPD-PCR technique was employed to identify three endemic morphologically similar Spanish species of *Barbus*: *Barbus bocagei, B. graellsii* and *B. sclateri* that have similar morphologies [87]. RAPD markers were characterized to identify five species of family Cyprinidae: *Chondrostoma lemmingii, Leuciscus pyrenaicus, Barbus bocagei, Barbus comizo*, all endemic in the Iberian Peninsula, and introduced *Alburnus alburnus* [88], for studying genetic relationship and diversities in four species of Indian Major carps (family Cyprinidae): rohu (*Labeo rohita*), kalbasu (*L. calbasu*), catla (*Catla catla*) and mrigal (*Cirrhinus mrigala*) [89], for identification of three eel species, *A. japonica, A. australis* and *A. bicolor* [90] and to estimate the population structure and phylogenetic relationships among the eight species of the genus *Barbus* [88].

Large variation in mtDNA sequences among species can be utilized to produce species-specific markers. Since the structures of mitochondrial RNA genes (tRNA and rRNA) and the functional molecule of the 16S rRNA are highly conserved among the animal taxa that are related even distantly [21], change of even few nucleotides in such a gene between closely related taxa might

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indicate a substantial degree of genetic divergence [2]. Mt-DNA sequences have been used as useful marker for species-specific identification in many fishes [Tuna: 91; Billfish: 92 Snappers: 29, 93; Myctophidae: 94; Grey mullets: 95]. Comparable levels of divergence based on 12S rRNA and 16S rRNA sequences have been reported for several recently diverged fish species [genus *Sternoptyx*: 96; *Cyclothone* sp: 97]. Sequence variation in the control region (D-loop) of the mitochondrial DNA (mtDNA) was examined to assess the genetic distinctiveness of the short-jaw cisco, *Coregonus zenithicus* [98] and revealed high similarity of *C. zenithicus* and the related species *C. artedi*, *C. hoyi*, *C. kiyi*, and *C. clupeaformis*

Identification of *Astyanax altiparanae* (Teleostei, Characidae) in the Iguacu River, Brazil, was done on the basis of mitochondrial DNA and RAPD markers [99]. Two species, *Acipenser baeri*, and *A. stellatus*, was studied using mitochondrial DNA (D-loop, cytochrome b (cyt-b) and ND5/6 genes) sequencing to determine whether traditionally defined subspecies correspond to taxonomic entities and conservation management units [100].

11. GENETIC VARIATION AND POPULATION STRUCTURE STUDY IN NATURAL POPULATIONS

Molecular markers provide direct assessment of pattern and distribution of genetic variation [5] thus helping in answering, "if the population is single unit or composed of subunits". Several evolutionary forces affect the amount and distribution of genetic variation among populations and thereby population differentiation [101]. Geographic distance and physical barriers enhance reproductive isolation by limiting the migration and increase genetic differentiation between populations [102]. Impact of migration and gene flow on genetic differentiation also depends upon effective size of receiving population and number of migrants. Increased computational power and mathematical models have enhanced the scope of conclusions that can be drawn out of genotype data generated through molecular markers. Some of the possibilities are assignment of migrants [103], determination of genetic bottlenecks [104], effective breeding population estimates [105] besides genetic variation and differentiation estimations [106-108]. These markers have been extensively employed across various taxonomic groups [mosquito: 109**;** turtle: 39; amphibians: 7; panda: 110; five vertebrate classes including fish, amphibian, reptiles, birds and mammals: 6]. Experiments on fish populations have significantly contributed towards development of science of population genetics, models and analytical softwares.

Population genetic structure has been investigated using allozyme markers in many fish species [*Oncorhynchus gorbuscha*: 111; *Tenualosa ilisha*: 112 and Lal *et al*., 113; *Pagrus auratus:* 114].

Fifteen random primers were used to analyze the genome DNA of Jian carp (*Cyprinus carpio* var jian) by the RAPD technique [115]. Study on cold tolerant traits for common carp *Cyprinus carpio* was conducted by Chang *et al*. [116] and nine RAPD-PCR markers associated with cold tolerance of common carp were identified. The genetic diversity has been studied using RAPD markers in *Carassius auratus* [117], *Epinephelus merra* population [118] and *Solea solea* [119].

Genetic variation have been assessed with Allozyme and RAPD markers on *Mullus surmuletus* L., [120] and three species of Pimelodidae catfish [121].

Population structure has been examined using microsatellite markers of sockeye salmon [122], Chinook salmon [123] and Arctic charr populations [124]. Genetic variation have been assessed using microsatellite genetic markers to identify the population structure of brook charr, *Salvelinus fontinalis* [125] and 14 populations of northern pike (*Esox lucius*) in the North Central United States and in six populations from Quebec, Alaska, Siberia, and Finland [126].

Based on five microsatellite loci, the genetic structure of endangered fish species *Anaecypris hispanica* was studied in eight distinct populations in the Portuguese Guadiana drainage to determine levels of genetic variation within and among populations and suggested implications for conservation of the species [127].

Combination of allozyme and microsatellites was used to investigate genetic divergence in *Salmo trutta* [128] and *Salmo salar* [129].

Alarcon *et al*. [130] represents population genetic analysis of gilthead sea bream (*Sparus aurata*) and Kanda [131], Kanda and Allendorf [132] examine population genetic structure of bull trout *Salvelinus confluentus* using a combination of allozyme, microsatellite and mtDNA variation.

Genetic variability of *Salmo trutta* [133] and Sparus aurata [130] was evaluated on the basis of Allozyme, Microsatellites and RAPD markers.

Patterns of population subdivision and the relationship between gene flow and geographical distance in the tropical estuarine fish *Lates calcarifer* (Centropomidae) were investigated using mtDNA control region sequences [134].

Allozymes and mtDNA sequences were assessed to evaluate the genetic variability in small marine fish *Pomatoschistus microps* [135], brown trout [136] and *Macquaria novemaculeata* [137].

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12. COMPARISON OF GENETIC VARIATION BETWEEN WILD AND HATCHERY POPULATIONS

Molecular markers also find application in aquaculture to assess loss of genetic variation in hatcheries through, comparison of variation estimates between hatchery stocks and wild counterparts. The information is useful obtained in monitoring farmed stocks against inbreeding loss and to plan genetic up gradation programmes. A major aspect such studies address is concerned with the assessment of farm escapes into the natural population and introgression of wild genome.

Brook trout *Salvelinus fontinalis* from ustocked waters, naturalized lakes, and hatcheries in New York and Pennsylvania were analyzed electrophoretically for allozyme expression [138]. All wild-unstocked samples were highly differentiated populations and significantly different from each other and from hatchery samples.

Genetic diversity was investigated using microsatellites between farmed and wild populations of Atlantic salmon [139]. Farmed salmon showed less genetic variability than natural source population in terms of allelic diversity.

Variation in allozymes and three microsatellite loci was assessed in populations of wild and cultured stocks of *Sparus aurata* [140] and *Sparius auratus* [130]. The microsatellite heterozygosity values were high in wild, but lower in the cultured samples.

13. ASSESSMENT OF DEMOGRAPHIC BOTTLENECK IN NATURAL POPULATION

Demographic bottlenecks occur when populations experience severe, temporary reduction in size. Because bottlenecks may influence the distribution of genetic variation within and among populations, the genetic effects of reductions in population size have been studied extensively by evolutionary biologist [141,142].

It may often be necessary to perform genetic analyses of temporal replicates to estimate the significance of spatial variation independently from that of temporal variation in order to ensure the reliability of estimates of a defined population structure. Such estimates provide understanding about changes in genetic variation, effective population size and other historical bottlenecks and can be extrapolated to define evolutionary trends of species. Today various models are available that can resolve bottlenecks or effective population size changes through use of heterozygosity excess, linkage disequilibrium etc. However, estimates through temporal changes are considered more accurate. Analysis of temporal changes is limited due to lack of historical data as well as samples. Therefore, such studies are limited and mostly use archived samples, wherever available. In vertebrates, a limited number of studies have specifically assessed the temporal changes in genetic variation for more than one generation.

Microsatellite DNA markers have been used to assess bottlenecks in many fish species. A microsatellite analysis of DNA was performed, from archived scales to compare the population structure among four sympatric landlocked populations of Atlantic salmon [143], Atlantic salmon [144], European hake [145] and steelhead from [146].

Larson *et al*. [147] recommended close monitoring of negative effects on sea otter population based on the conclusion from mtDNA, D-loop, microsatellite variability comparison between prefur trade and present population. Prefur trade DNA samples were obtained from excavated bones.

14. PROPOGATION ASSISTED REHABILITATION PROGRAMMES

Habitat alterations and over harvesting have contributed to the decline or disappearance of numerous natural populations. In addition, reinforcement programs of wild populations based on releases of hatchery reared fish of non-native origin compromise the conservation of remnant native trout resources. Effect of these programmes through releases in natural populations has been studies in many fishes through molecular markers.

Beaudou *et al*. [148] found through allozyme polymorphism that brown trout (*Salmo trutta* L.) in the Abatesco river basin on the eastern coast of Corsica restoration was mainly due to the populations of the tributaries, which had been less disturbed by the spate. This study has shown that the wild population was primarily restored by the surviving individuals, particularly those from the tributaries that escaped the spate.

To assess the levels of gene introgression from cultured to wild brown trout populations, four officially stocked locations and four non-stocked locations were sampled for one to three consecutive years and compared to the hatchery strain used for stocking. Allozyme analysis for 25 loci included providing allelic markers distinguishing hatchery stocks and native populations [133]. Different levels of hybridization and introgression with hatchery individuals were detected in stocked drainages as well as in protected locations.

The foregoing review incorporates the wide spectrum of information that the molecular markers provide. The literature indicates that different markers have been employed depending upon the question to be answered. The importance of the research on molecular markers improved due to enhanced computational power, large data

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available that has enabled researchers to derive various mathematical estimators. Such innovations provide insight concerning the population bottleneck, migration patterns besides the genetic structure in natural populations.

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