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Genetic population structure and historic demography of Indian mackerel, *Rastrelliger kanagurta* from Indian peninsular waters

Sandhya Sukumaran*, Wilson Sebastian, A. Gopalakrishnan

Central Marine Fisheries Research Institute, Post Box No: 1603, Ernakulam North P.O., Kochi, Kerala, 682018, India

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ABSTRACT

An attempt was conducted to understand the genetic population structure and historic demography of Indian mackerel, *Rastrelliger kanagurta* from Indian peninsular waters using mitochondrial DNA markers. A total of 241 sequences of mitochondrial control region and 271 sequences of mitochondrial ATPase gene region were amplified and analyzed in Indian mackerels collected from 10 different locations along Indian coast resulting in 123 and 155 haplotypes respectively. In addition, control region sequences representing samples from Thailand downloaded from NCBI were also used for analysis. Significant genetic differentiation (Φ_{ST} value of 0.38; $P < 0.001$) was recorded between samples from mainland India, Portblair and Thailand when both control region and ATPase gene sequences were analyzed. Whilst, Φ_{ST} values were not significant when analyses were carried out between samples collected from mainland India. Oceanographic and environmental barriers between mainland India, Portblair and Thailand contribute to limited larval dispersal and restricted mixing between populations resulting in subtle genetic differentiation. The lack of genetic subdivision between populations from mainland India indicates adequate gene flow and mixing within Indian waters. Bayesian skyline plots revealed a history of population expansion taken place approximately 10000 years ago coinciding with the time after the last glacial maximum or early Holocene. Intensification of monsoon events after the last glacial maximum or early Holocene along the Indian subcontinent contributed to increased productivity in the Tropical Indian Ocean and consequent demographic expansion of mackerel populations historically. Management measures for Indian mackerel populations could be devised regionally so as to conserve intra-specific diversity and biocomplexity of this important resource.

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1. Introduction

Biologically differentiated populations of marine fishes are presumed to confer sustainability and buffering capacity to environmental degradation and hence it is very essential to preserve stock complexity if any (Stephenson, 1999; Ruzzante et al., 2006). Even though many marine fishes showed lack of genetic differentiation, recent studies using advanced markers have provided evidence for low level of differentiation in many marine fishes as these markers are able to resolve signatures of selection and adaptation in response to environmental and habitat fluctuations (Wang et al., 2013; Candy et al., 2015; Brennan et al., 2016). Management strategies should be aimed at conserving such intra-specific genetic diversity as it has profound implications in deciding potential for recruitment and population recovery (Teacher et al., 2013). However, the knowledge regarding spatial and temporal dynamics of coastal pelagic fishes and influence of oceanographic features on their distribution is scanty. Even though gene flow in marine pelagic fishes is thought to be high due to absence of geographical barriers, environmental gradients and oceanographic features prevent mixing and successful larval recruitment (Teacher et al., 2013). In addition to this, natal homing and spawning aggregations also contribute to stock structure (Natoli et al., 2005; Cowen et al., 2006; Svedang et al., 2007). Hence, misdirected management actions without knowledge about the stock structure and complexity of marine fishes may result in inability to recover from environmental impacts and this is more pertinent in view of the climate change related habitat alterations.

Even though many marine pelagic fishes occurring in world oceans, especially Atlantic and Pacific have been well studied and characterized using mitochondrial and nuclear markers (Grant and Bowen, 1998; Cadrin et al., 2013; Da Silva et al., 2015), such stud-

* Corresponding author.
E-mail addresses: sukumaransandhya@yahoo.com, sandhya_sukumaran@yahoo.com (S. Sukumaran), wilsonsebastian10@gmail.com (W. Sebastian), agopalkochi@gmail.com (A. Gopalakrishnan).

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ies are very few among species present in the Indian Ocean. The present authors recently carried out a comprehensive study on Indian oil sardine, *Sardinella longiceps* using mitochondrial DNA markers unveiling information regarding historic demography and genetic stock structure (Sukumaran et al., 2016). Indian mackerel, *Rastrelliger kanagurta* is one of the most important small pelagic fish in Indian waters contributing to 6.6% of the total Indian fishery with annual landings along Indian coast being 0.24million tones (CMFRI, 2015). It is a very important food fish along Indian coast and it contributes to a considerable portion of the income from fishing due to its abundance. South West coast of India contributes a major share of Indian mackerel landings followed by South East coast of India (CMFRI, 2015). It is widely distributed along the Indo-Pacific, mainly along South Africa, Seychelles, India, Indonesia, off Northern Australian up to Melanesia, Micronesia, Samoa, China and Ryukyu islands. It is also present in the eastern Mediterranean Sea having entered through the Suez Canal (Collette and Nauen, 1983). Along the Indian coast, it is distributed around east and west coast of India including Andaman Islands. It is an epi pelagic fish feeding mainly on phyto and zooplankters during juvenile stages and macroplankters during adult stages. It is a migratory, shoaling fish and swims at speeds of 3–4 nautical miles/hour (Devaraj and Martosubroto, 1997). Indian mackerel has a prolonged spawning season along Indian coast beginning by April and extending up to September and length at first maturity is around 20–22.4 cm which is achieved at the end of first year (Devaraj and Martosubroto, 1997). Spawning grounds are not yet located for this species.

In spite of the importance of Indian mackerel, very few genetic studies have been carried out in populations from Indian peninsular waters. Allozymes, morphometric ratios and RAPD markers (Menezes and Qasim, 1993; Menezes et al., 1993; Jayasankar et al., 2003) were used to detect population sub-structuring if any in Indian mackerel populations and all these studies indicated panmixia among mackerel populations from Indian peninsular waters. Substantial divergence of mackerel populations from Andaman waters was recorded in allozyme study by Menezes et al. (1993). A recent investigation using microsatellite markers was carried out by collecting mackerel populations from Bay of Bengal Large Marine Ecosystem in which the present authors also participated (BOBLME Report, 2015) and preliminary analysis indicated sub-structuring on a geographic scale. However none of the studies have been conducted using mitochondrial DNA markers in mackerel populations from Indian peninsular waters and hence the present study was undertaken. The maternal inheritance pattern and non-recombining nature of Mitochondrial DNA has made it a valuable tool for inferring historic patterns (Castro et al., 1998) and hence these markers were used in the present study to deduce valuable information regarding historical demography along with genetic stock structure for this important resource.

2. Material and methods

2.1. Sample collection, DNA extraction and amplification of the two mitochondrial fragments

The Indian mackerel samples were collected during 2013, 2014 and 2015 from 10 different locations from gill netters and ring seiners (a mini purse seine) operated near the coast; 2 locations along NW coast of India; Gujarat (20°43′N;70°22′E) and Mumbai (19°6′N;72°55′E), 3 locations along SW coast of India; Mangalore (12°43′N;74°47′E), Calicut (11°4′N;75°39′E) and Trivandrum (8°26′N;76°55′E), 3 locations along SE coast of India; Tuticorin (8°42′N;78°8′E), Nagapatnam (10°42′N;79°49′E) and Kakinada (16°59′N;82°14′E), one location along NE coast of India; Paradeep (20°18′N;86°36′E) and one location along the coast of Andaman islands; PortBlair (11°37′N;92°44′E) (Fig. 1). Genetic analyses were conducted on 269 samples altogether; 241 sequences generated in the present study and 28 sequences downloaded from NCBI (28 sequences from Thailand, KJ734562-734589) using mitochondrial control region and 271 samples (271 sequences generated in the present study) using mitochondrial ATPase 6/8 gene markers.

Skeletal muscle tissue was used for DNA extraction using a standard phenol/chloroform extraction protocol and ethanol precipitation. The partial control region and ATPase 6/8 gene sequences were amplified using universal primers (Page et al., 2004; Cheng et al., 2012). PCR reactions were carried out in 25 μl reaction mixture containing 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$, 200 μM of each dNTP, 0.2 μM of oligonucleotide, 1 unit of Taq DNA polymerase and 50 ng of template DNA using a Biorad T100 thermocycler (Biorad, USA) programmed for an initial denaturation at 94 °C for 4 min followed by 35 and 33 cycles of denaturation (for control region and ATPase 6/8 genes respectively) at 94 °C for 30S, annealing at 48 °C and 42 °C (for control region ATPase 6/8 genes respectively) for 30S, extension at 72 °C for 55S and 40S (for control region ATPase 6/8 genes respectively) and a final extension at 72 °C for 7 min. PCR products were purified by using Qiagen PCR purification kit and sequenced with both primers using the BigDye Terminator Sequencing Ready Reaction v3.0 kit (Applied Biosystems) following instructions of the manufacturer. Sequencing was carried out on an ABI 3730 automated sequencer. An 844 bp region of the control region and 832 bp region of ATPase 6/8 gene of *Rastrelliger kanagurta* was amplified in all the sampled individuals for phylogenetic and population genetic analysis. Sequences of all individuals were submitted to GenBank and assigned Accession Nos. (KT931707-KT931947) (KU297998 – KU298268).

2.2. Population genetic statistics

Even though both control region and ATPase genes are from the same mitochondrial DNA, we did not concatenate the sequences due to differential evolutionary rates exhibited by different regions of mitochondrial DNA (Hauser et al., 2001). The sequence alignments were optimized for 844 bp of control region and 832 bp of ATPase using Clustal W in MEGA 6.06. The phylogeny was reconstructed using Geneious R7 (Biomatters Ltd., New Zealand) using the neighbor joining method with 1000 bootstraps (Felsenstein, 1985) and a bootstrap consensus tree was constructed. A Bayesian phylogenetic tree was also constructed using the Mr.Bayes plug-in in Geneious R7. The best evolutionary model for the sequences was selected using the Akaike information criterion implemented in MEGA 6.06. Population genetic analyses were carried out in Arlequin Version 3.5.1.2 (Schneider et al., 2000) and DnaSP 4.0 (Rozas et al., 2003). Population specific parameters like number of polymorphic sites (S), nucleotide diversity (π, Nei, 1987), haplotype diversity (H_d, Nei, 1987), average number of pair-wise nucleotide differences (K, Tajima, 1983), percentage of private haplotypes, total number of synonymous and non-synonymous mutations (ATPase region) and Transition/Transversion ratios were assessed for each population.

Analysis of population genetic structure was carried out using the F-statistics, Φ_{ST} (Excoffier et al., 1992) using 20,000 permutations to estimate significance (calculated with Arlequin Version 3.5.1.2, Schneider et al., 2000). The proportion of variance distributed among samples was determined using the hierarchical analysis of molecular variance procedure (AMOVA) in Arlequin Version 3.5.1.2. The sequence divergence values were estimated using the algorithm of Tamura and Nei (1993) for control region sequences and ATPase gene sequences (HKY is not available in Arlequin). Sequential Bonferroni correction was applied to adjust P values during multiple comparisons (Rice, 1989). A network of haplotypes was constructed in PopART version 1.7 (http://popart.

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