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Short communication

Genetic relationships among founders of a silver carp (*Hypophthalmichthys molitrix*) genetic improvement program in Bangladesh

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A B S T R A C T

Silver carp (*Hypophthalmichthys molitrix*) is an important aquaculture species in Bangladesh and globally. Multiple introductions have been made of this exotic species to Bangladesh since 1969. Accordingly, the genetic composition of the species in the country is complex and imperfectly understood. In 2015–16, WorldFish sourced silver carp individuals from 21 Bangladeshi hatcheries as 'candidate founders' of a family-based genetic improvement program. In total, 544 candidate founders were sampled, of which 220 from 17 hatcheries were ultimately spawned as the 'actual founders' of the WorldFish Silver Carp Genetic Improvement Program (WSCGIP) population. The extent of relatedness among candidate founders was unknown when they were sourced from hatcheries. Candidate founders were genotyped using the DArTseq platform – with a total of 15,102 single nucleotide polymorphisms (SNPs) and 13,504 silicoDArT markers obtained – and genetic affinities among hatcheries examined. Based on unsupervised k-means clustering and hatchery-identified origins, each hatchery was assigned to one of six genetic groups to enable the adoption of genetic group models in pedigree-based analyses. Within genetic groups, sibship was assigned using COLONY software, and a pedigree constructed and validated against genomic relationships generated from 2007 SNPs retained after quality control. The mean pedigree-derived additive genetic relationship between actual founders was small (0.0093), indicating that relationships between actual founders are unlikely to have a meaningful impact on future parent selection, mating decisions or rates of inbreeding.

1. Introduction

By weight, silver carp (*Hypophthalmichthys molitrix*) is the second most important cultured finfish species, with a global production of approximately 4.8 Mt. per annum (FAO, 2020). The natural range of this cyprinid species extends from the Amur River (China-Russia border) through several major river systems in the eastern half of China, to the Pearl (southern China) and Red (northern Vietnam) rivers (Lu et al., 2020). The species mainly feeds on phytoplankton and, accordingly, is highly efficient in converting primary production into fish protein (Neori and Nobre, 2012).

In Bangladesh, the species is commonly farmed on a small scale in polyculture (Belton and Azad, 2012), with a total annual production of approximately 0.2 Mt. (DoF, 2017). The first documented introduction of silver carp into Bangladesh occurred in 1969 from Hong Kong to the Freshwater Fisheries Research Station, Chandpur (Rahman, 2005). Additional fish were introduced from Japan to the Chandpur Freshwater Fisheries Research Station in 1970 (Hussain and Mazid, 2001), from India to the Jashore district in 1979 (Rajts, 2008), from Nepal to the Raipur Government Fish Hatchery in 1981 (Rajts, 2008), and from the Yangtze River (by the Network of Aquaculture Centres in Asia; NACA) to government hatcheries in Kotchandpur, Kurigram, Ishwardi and Natore in 1994 (Hussain and Mazid, 2002; Sattar and Das, 2002). More recent introductions have been made from China by the Bangladesh Department of Fisheries (pers. comm. Md. Sirajur Rahman) and multiple undocumented informal introductions are also likely to have occurred. Furthermore, widespread hybridisation with bighead carp (*Aristichthys nobilis*) has been documented (Mia et al., 2005) and in many Bangladeshi hatcheries a single closed population of the species has been maintained for multiple generations – inevitably resulting in the accumulation of relatedness and inbreeding (Meuwissen, 1997). Given this history, the genetic composition of silver carp in Bangladesh is complex and imperfectly understood.

WorldFish sourced silver carp individuals from multiple Bangladeshi hatcheries as 'candidate founders' of a family-based genetic improvement program. Two hundred and twenty of these (i.e. the 'actual

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Table 1
Origins of the WorldFish silver carp genetic improvement program candidate founders.

Hatchery name	Hatchery Identifier[a]	Sector	Hatchery Location	Hatchery District	Candidate Founders	Actual founders	Hatchery-identified origin	Comment
Sagor Fish Hatchery	Sagor	Private	Chanchra	Jashore	19	14	Jashore	Local Jashore District origin
Mukteshary Fish Hatchery	Mukteshary	Private	Kazipur	Jashore	43	20		
Hoque Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	2		
Kapotakkho Fish Hatchery	Jashore	Private	Chanchra	Jashore	1	1		
MaFatima Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	1		
Matri Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	1		
Modhumoty Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	0		
National Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	1		
Niribili Pally Fish Hatchery	Jashore	Private	Chanchra	Jashore	7	0		
Sonaly Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	0		
Suvro Fish Hatchery	Jashore	Private	Chanchra	Jashore	2	0		
Pari Fish Hatchery	Jashore	Private	Kazipur	Jashore	2	1		
Jashore Fish Hatchery	Jashore	Private	Najirsankarpur	Jashore	4	1		
BRAC Fish And Prawn Hatchery	BRAC	Private	Tebunia	Pabna	63	3	Nepal-NACA[d]	Two sources: 1) imported from Nepal by the Department of Fisheries (DoF) and distributed by the Raipur Government Fish Seed Farm and 2) imported through the NACA from China and distributed by the Parbatipur Govt. Fish Seed Farm
Joyda Aqua Farm	Joyda	BFRI[b]	Trishal	Mymensingh	108	55		
Raipur Government Fish Seed Farm	Raipur	DoF[c]	Raipur	Lakshmipur	26	7		
Akram Fisherman	Akram	Private	Natore	Natore	62	23	NACA[d]	Imported through the NACA from China and distributed by the Parbatipur Govt. Fish Seed Farm
Puthia Govt. Fish Seed Farm	Puthia	DoF[c]	Puthia	Rajshahi	86	41		
Rajshahi Govt. Fish Seed Farm	Rajshahi	DoF[c]	Rajshahi	Rajshahi	51	16		
Parbatipur Govt. Fish Seed Farm	Parbatipur	DoF[c]	Parbatipur	Dinajpur	39	27		
Nimgachi Fish Culture Hatchery	Nimgachi	DoF[c]	Nimgachi	Sirajganj	19	6	Natore	Collected from private hatcheries in the Natore District
Total					544	220		

[a] Data from multiple hatcheries in the Jashore district were combined due to the low number of fish sampled from individual hatcheries.
[b] Bangladesh Fisheries Research Institute (Public).
[c] Bangladesh Department of Fisheries (Public).
[d] Network of Aquaculture Centres in Asia.

founders') were spawned in 2017 to generate base population families. The remaining candidate founders were not sexually mature, not in spawning condition, not able to be spawned due to hatchery capacity constraints or failed to produce viable offspring during the 2017 spawning.

The WorldFish Silver Carp Genetic Improvement Program (WSCGIP) aims to improve growth rate using pedigree-based selection – significant additive genetic variation in growth rate has previously been documented in Bangladeshi silver carp (Gheyas et al., 2009). The first selected generation of WSCGIP silver carp was spawned in 2019. Genetic improvement programs for indigenous Bangladeshi carp species – *Labeo rohita* and *Catla catla* – are also implemented by WorldFish (Hamilton et al., 2019a; Hamilton et al., 2019b).

The objectives of the current study were to increase the accuracy of estimated breeding values (EBVs) and genetic parameters derived from pedigree-based genetic analysis by (1) defining appropriate genetic groups (Quaas, 1988) using single nucleotide polymorphisms (SNPs) DNA markers; and (2) constructing a pedigree accounting for putative sibship (i.e. half-sibling and full-sibling relationships) in the founding population of the WSCGIP population.

2. Methods

In 2015–16, 544 adult silver carp individuals were sourced from 21 Bangladeshi hatcheries as 'candidate founders' of the WSCGIP (Table 1). To avoid the presence of bighead hybrids, only fish exhibiting 'pure' silver carp phenotypes were collected – that is, those with gill rakers fused to form a sponge-like structure, non-overlapping pectoral and pelvic fins, and a long ventral keel (Battonyai et al., 2015; Rajts, 2008). Genotyping of putative silver carp, bighead and hybrid phenotypes was undertaken to validate this approach to selecting silver carp candidate founders (Supplementary material 1).

Although the ancestry and genetic origins of broodstock held in hatcheries was not in all cases certain, details provided by hatchery managers were used to allocate each hatchery population to one of four 'hatchery-identified origins' – Jashore, Nepal-NACA, NACA and Natore (Table 1). The number of fish sourced from 11 of the 13 hatcheries in the Jashore district was seven or less and, for the purpose of analysis, fish from these hatcheries – Hoque, Kapotakkho, Ma Fatima, Matri, Modhumoty, National, Niribili Pally, Sonaly, Suvro, Pari and Jashore – were assumed to have been sourced from a single hatchery referred to as 'Jashore'.

All candidate founders were fin-clipped – removal of an approximately 2-mm wide sample from the extremities of the dorsal fin – as part of the routine husbandry of the breeding population and archived in the WorldFish tissue sample repository. Prior to fin-clipping, fish were anesthetized with clove oil. Fish were then placed in tanks for monitoring and only released back into ponds once they had satisfactorily recovered from anaesthesia. All candidate founders were managed in accordance with the Guiding Principles of the Animal Care, Welfare and Ethics Policy of the World Fish Centre (WorldFish, 2004). Archived WSCGIP fin-clip samples were subsequently genotyped using the DArTseq platform (Kilian et al., 2012), along with 54 silver carp samples from additional hatcheries that were not available as candidate founders, and SNP and silicoDArT markers identified. Raw data are archived at https://doi.org/10.7910/DVN/EHQAY8. The laboratory procedures and analytical pipelines outlined in Lind et al. (2017) were followed, with the exception that the complexity reduction method involved a

combination of *Pst*I and *Sph*I enzymes (SphI replacing *Hpa*II used in Lind et al. (2017)). Analyses of SNP data were then conducted using R (version 4.0.0 (R Core Team, 2018)) and COLONY (version 2.0.6.4 (Jones and Wang, 2010)). Steps in the analysis were: (1) exclusion of data from non-WSCGIP samples; (2) SNP quality control; (3) assignment of hatcheries to genetic groups; (4) construction of pedigrees, accounting for putative sibship; (5) construction of additive relationship matrices (**A**) within genetic groups from pedigrees; (6) construction of genomic relationship (**G**) matrices; and (7) comparison of **A** matrices with **G** matrices to validate COLONY-derived sibship assignments.

Quality control procedures aimed to retain only high-quality and informative SNPs, in approximate linkage equilibrium, for analysis. This was undertaken by adopting the SNP quality control procedure detailed in Hamilton et al. (2019b). Briefly: (1) SNPs with an observed minor allele frequency (MAF) less than 0.05 or a rate of missing observations greater than 0.05 were excluded; (2) only one randomly-selected SNP was retained from each deoxyribonucleic acid (DNA) fragment; (3) pairwise squared Pearson's correlations (r^2) of genotypic allele counts were calculated, and subsequently a random SNP from the pair with the highest r^2 was iteratively excluded until all pairwise r^2 values were less than 0.2; and (4) SNPs that significantly deviated from Hardy-Weinberg equilibrium were excluded (classical χ^2 test; $P < 0.05$ after Dunn–Šidák correction).

Using SNPs retained after quality control, genetic affinities among source hatcheries were investigated and each hatchery population was assigned to a genetic group. To achieve this, the glPca function of the adegenet package (Version 2.1.1 Jombart and Ahmed, 2011; Jombart and Collins, 2015) was used to undertake principal component analyses (PCA). Subsequently, unsupervised k-means clustering was undertaken (using the find.clusters function of adegenet) and Discriminant Analysis of Principal Components (DAPC, Jombart et al., 2010) was performed for values of k increasing from 2 to 8 (using the dapc function of adegenet).

Sibship was assigned and a pedigree constructed for all candidate founders within genetic groups, using a maximum likelihood approach, with COLONY software (Jones and Wang, 2010) – it was assumed COLONY-derived dummy parents were unrelated. For the COLONY analyses: (1) only SNPs with a MAF greater than 0.2 were retained; (2) individuals from different genetic groups were assumed to be unrelated; and (3) SNPs were assumed to be on separate chromosomes (i.e. unlinked).

In circumstances where large full-sibling groups are present, the maximum likelihood method adopted by COLONY (Almudevar and Anderson, 2012; Wang, 2013, 2017) is prone to erroneously splitting these groups into multiple full- and half-sibling groups (refer to Fig. 3 of Hamilton et al. (2019a) for an example). Accordingly, to validate COLONY-derived sibship assignments, genomic relationships between individuals within genetic groups were computed using the procedure detailed in Hamilton et al. (2019b) using the allele frequencies observed in putatively unrelated individuals (see below). Concisely, the method of VanRaden (2008) was adopted to construct genomic relationship matrices (**G**), based on code from Gondro (page 133 (2015)). This code was modified to replace missing observations in SNP data (representing only 0.58% of all observations) with the observed allele frequency within genetic groups in putatively unrelated individuals. Only data from putatively unrelated individuals was used, to avoid bias in allele frequencies caused by the sampling of excessive close relatives (Wang, 2018). Heatmaps of genomic relationships between individuals were generated after reordering individuals according to clustering of genomic relationships – undertaken by adopting the 'Ward2' algorithm, implemented in the 'hclust' function (Murtagh and Legendre, 2014). Putatively unrelated individuals within each genetic group were then identified by (1) generating the additive relationship matrix (**A**) from the COLONY-derived pedigree using the 'makeA' function of the 'nadiv' package (version 2.16.0.0 (Wolak, 2012)); (2) generating a list of individuals that were unrelated ($a_{ij} = 0$) to other individuals in **A**; (3) excluding indiviudals listed in step 2 from **A**; (4) appending to the list generated in step 2 the individual remaining in **A** with the lowest average relationship with the other individuals; (5) excluding the individual listed in step 4 and its relatives ($a_{ij} > 0$) from **A**; and (6) iteratively repeating steps 4 and 5 until no individuals remained in **A**. Refer to Supplementary Material 2 in Hamilton et al. (2019b) for a worked example.

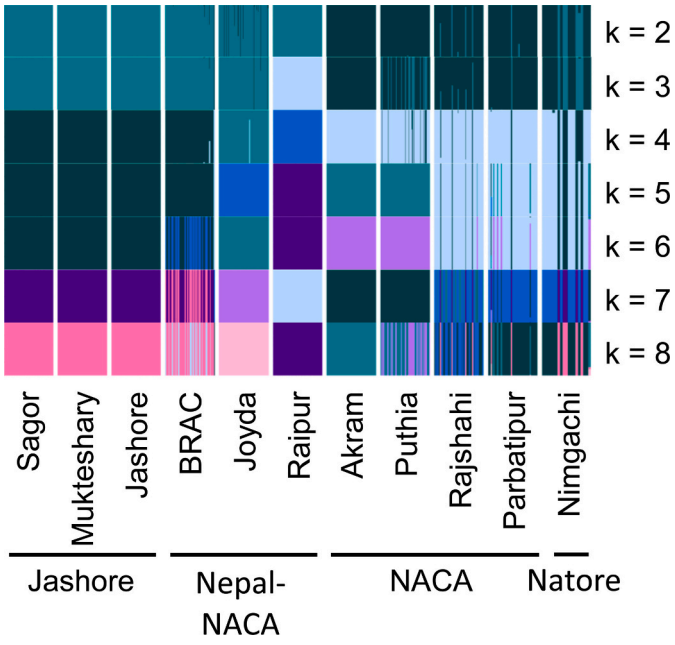

Fig. 1. Unsupervised k-means clustering of individuals sourced from hatcheries performed using Discriminant Analysis of Principal Components (DAPC) for differing number of groups (k). Hatcheries are grouped by hatchery-identified origins – Jashore, Nepal-NACA, NACA, and Natore. Vertical lines represent the cluster membership probability of individuals.

3. Results and discussion

In total, 15,102 SNPs and 13,504 silicoDArT markers were identified (Supplementary material 2; https://doi.org/10.7910/DVN/EHQAY8). However, many SNPs had a low MAF and large numbers of SNPs were not expressed in individual hatcheries – between 2705, for Parbotipur, and 10,121, for Raipur (Supplementary material 3). Of the 15,102 SNPs, 14,827 remained once the 54 samples that were not available as candidate founders were removed, 5815 remained after removal of those with more than 0.05 missing values and a MAF lower than 0.05, 5562 remained after removal of all but one SNP per fragment, 2627 remained after applying the constraint that all pairwise estimates of $r^2 \leq 0.2$, and ultimately 2007 remained after removal of those that were not in putative HWE.

Unsupervised k-means clustering (Fig. 1) revealed clusters of hatcheries in partial agreement with hatchery-identified origins (Table 1). At k = 2, a clear distinction between hatchery-identified origins of 1) Jashore and Nepal-NACA, and 2) NACA and Natore was evident – although 32% of Natore origin (i.e. Nimgachi hatchery) individuals clustered with Jashore and Nepal-NACA, and 27% of individuals from Joyda Hatchery clustered with NACA and Natore. At k = 3, Raipur formed a separate cluster. At k = 4, Sagor, Mukteshary, Jashore and Bangladesh Rehabilitation Assistance Committee (BRAC) hatcheries clustered together, Joyda and Raipur each formed their own cluster and hatchery-identified origins NACA and Natore remained as the fourth. At k = 5, the Akram and Puthia hatcheries formed a distinct cluster, separate from Rajshahi, Parbatipur and Nimgachi. At k = 6, 44% of individuals in the BRAC populations clustered separately from Sagor,

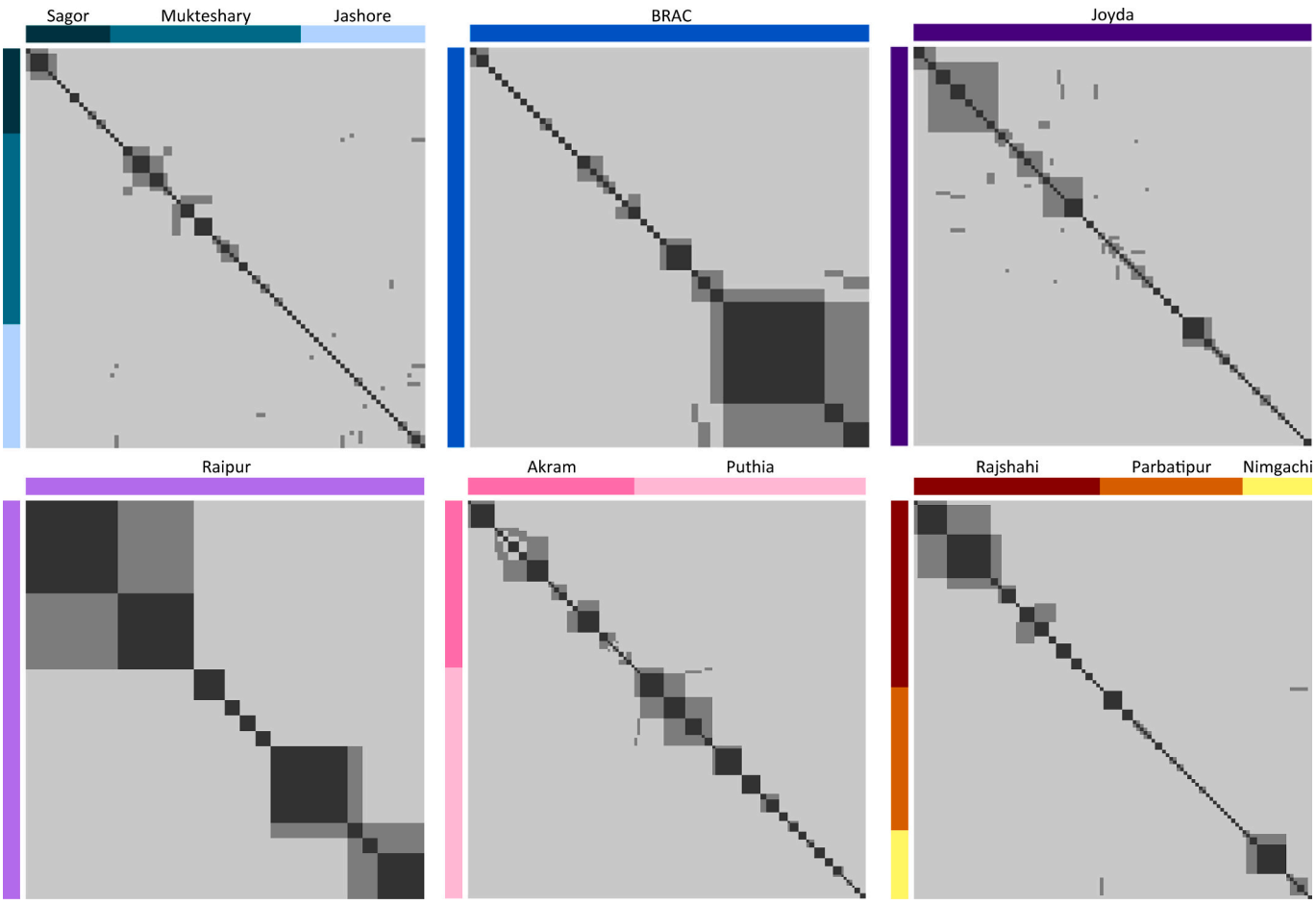

Fig. 2. Heatmaps of COLONY-derived additive relationship matrix (**A**) for all individuals sampled from six genetic groups: a) Sagor-Mukteshary-Jashore; b) BRAC; c) Joyda; d) Raipur; e) Akram-Puthia; and e) Rajshahi-Parbatipur-Nimgachi. Black represents a full sibling relationship (i.e. 0.50), dark grey represents a half sibling relationship (i.e. 0.25) and light grey represents no relationship (i.e. 0.00).

Mukteshary and Jashore – alluding to the possibility of multiple origins as an explanation for the inconsistency between the hatchery-identified origin of the BRAC population and clustering at k = 5. At k = 7 and k = 8, individuals within the Rajshahi and Puthia hatcheries, respectively, also formed distinct clusters. The notion of multiple origins and incomplete admixture in some hatchery populations was supported by the fact that the Bayesian Information Criterion (BIC) reached its minimum value of 2776 at k = 8 (compared with 2818 at k = 1), albeit only marginally less than 2780 at k = 6 (Fig. 1; Supplementary material 4).

Based on unsupervised k-means clustering (Fig. 1) and hatchery-identified origins (Table 1), six genetic groups were defined (Fig. 2): (1) Sagor-Mukteshary-Jashore (90 individuals), (2) BRAC (63 individuals), (3) Joyda (108 individuals), (4) Raipur (26 individuals), (5) Akram-Puthia (148 individuals), and (6) Rajshahi-Parbatipur-Nimgachi (109 individuals). The BRAC hatchery was defined as a separate genetic group – given its partial divergence at k = 6 using k-means clustering (Fig. 1), its hatchery-identified origin and the relatively large number (i.e. 63) of sampled individuals (Table 1). Furthermore, in preliminary analyses where BRAC was grouped with Sagor-Mukteshary-Jashore (i.e. k = 5), COLONY produced spurious results in which most individuals from the Sagor, Mukteshary and Jashore hatcheries were assigned to a single full-sibling family. Despite the relatively small number of individuals sampled from Raipur, it was also defined as a separate genetic group in analyses given its divergence from other hatcheries at k = 3 (Fig. 1).

For COLONY analyses within genetic groups, 969, 1022, 1005, 647, 1095 and 1086 SNP were retained (MAF > 0.2) for Sagor-Mukteshary-Jashore, BRAC, Joyda, Raipur, Akram-Puthia and Rajshahi-Parbatipur-Nimgachi, respectively. Candidate founders with no putative parents in common were subsequently identified in all genetic groups – Sagor-Mukteshary-Jashore (49 individuals; 54%), BRAC (24 individuals; 38%), Joyda (37 individuals; 34%), Raipur (7 individuals; 27%), Akram-Puthia (29 individuals; 20%), and Rajshahi-Parbatipur-Nimgachi (42 individuals; 39%).

The **G** matrices, generated using observed allele frequencies in candidate founders with no putative parents in common, revealed no obvious blocks of related individuals between hatcheries within genetic groups (part b of figures in Supplementary material 5), a distribution of genomic relationships between individuals with a peak close to zero (part e of figures in Supplementary material 5), and a pattern of relationships closely aligned with **A** matrices (parts b and c of figures in Supplementary material 5). That is, there was no evidence that COLONY falsely split large full-sibship groups, indicating that the COLONY-derived pedigrees could be adopted to account for sibship among actual founders in WSCGIP genetic analyses. This was the case for Raipur, even though only seven individuals with no putative parents in common were identified. However, there were a small number of aberrant relationships in the COLONY assignments, where individuals sourced from different hatcheries were identified as siblings (Fig. 2a and f). It is uncertain if these anomalous relationships were the result of errors in sibship assignment, labelling or fish management. Furthermore, in some genetic groups there was evidence of distant relationships not fully explained by sibship assignment. For example, in the case of Joyda, histograms of genomic relationships between individuals

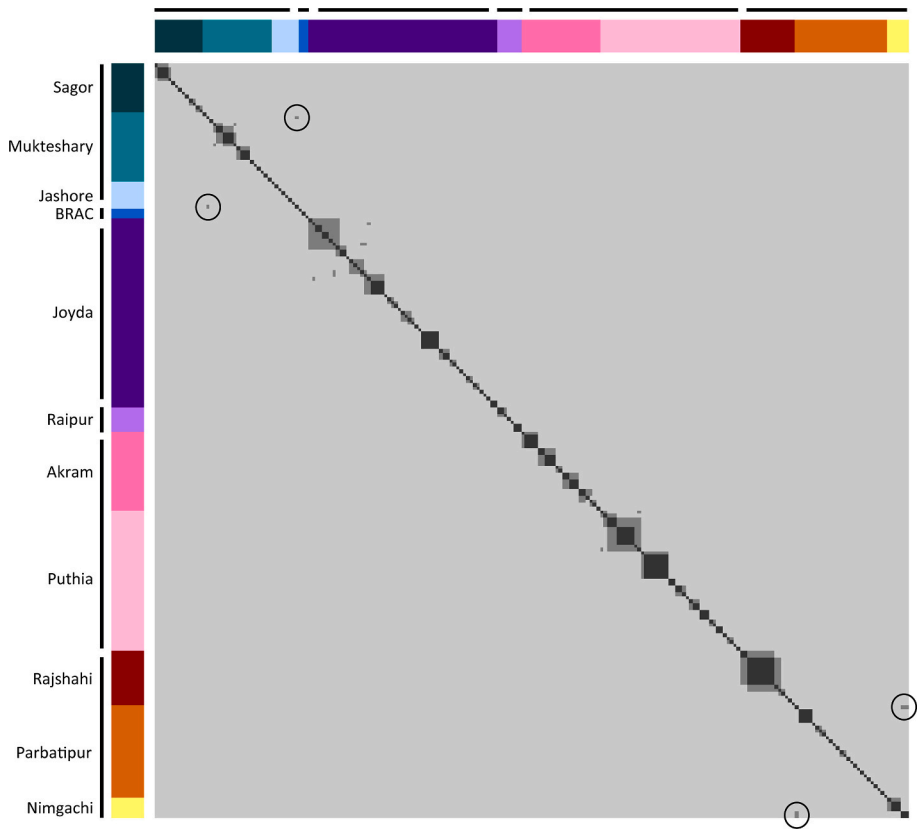

Fig. 3. Heatmap of COLONY-derived additive relationship matrix (**A**) for 220 founders of the WorldFish Silver Carp Genetic Improvement Program population. Black represents a full sibling relationship (i.e. 0.50), dark grey represents a half sibling relationship (i.e. 0.25) and light grey represents no relationship (i.e. 0.00). Circles identify aberrant COLONY-derived half-sibling relationships between individuals sourced from different hatcheries. Bold black lines indicate genetic groups.

exhibited positive skew, indicating the presence of genomic relationships between 0 and 0.25 (Supplementary material 5 – Figs. S5.3e and S5.3f). This was not unexpected, given that closed populations have been maintained for multiple generations in most Bangladeshi hatcheries – inevitably resulting in the accumulation of some degree of relatedness between individuals (Meuwissen, 1997) that cannot be fully explained by a pedigree accounting for sibship only. Indeed, historically, poor performance of hatchery-produced carp seed in Bangladesh has been attributed, in part, to inbreeding caused by mating between relatives in closed hatchery populations (Hussain and Mazid, 2005; Rajts, 2008). However, the COLONY-derived pedigree explained the majority of genomic relatedness among WSCGIP candidate founders (part f of figures in Supplementary material 5).

It is conceivable that genomic selection will be adopted within the WSCGIP in the future, to enable selection of traits that – unlike growth rate – are difficult or expensive to measure directly on selection candidates. However, our SNP panel was not developed for this purpose, would require substantial financial resources if it was to be applied across generations and – with the implementation of the, arguably stringent, SNP quality control procedures detailed herein – yielded a relatively small number of SNP in the context of what is required for accurate genomic selection (Nguyen et al., 2018; Wang, 2016).

Putative sibship observed among the 544 candidate founders was also evident in the subset of 220 actual founders that were spawned in 2017 as the parents of the WSCGIP base population (Fig. 3). The mean COLONY-derived additive genetic relationship between actual founders was 0.0093 (0.0048 for off-diagonals). An increase in average relationship of this magnitude in each generation would equate to a future increase in inbreeding (ΔF) of 0.0039 per generation (Meuwissen, 1997; Wright, 1922) and an effective population size (Ne) of 107, where Ne = 1 / (2ΔF) (Meuwissen and Woolliams, 1994). Accordingly, additive genetic relationships between actual founders of the WSCGIP population are unlikely to have a meaningful impact on future parent selection, mating decisions or rates of inbreeding.

4. Conclusion

Each of 21 Bangladeshi hatcheries, from which candidate founders of the WSCGIP breeding population were sourced, were assigned to one of six genetic groups. Using SNP data, a putative pedigree was constructed for each genetic group using a maximum likelihood approach with COLONY software (Jones and Wang, 2010) and validated against genomic relationships generated using the method of VanRaden (2008). This pedigree and genetic group models will be used in future WSCGIP genetic analyses to: (1) increase genetic gains from pedigree-based selection by improving the accuracy of genetic parameters and breeding values; and (2) maintain genetic variation – while minimising long- and short-term inbreeding – by informing parent selection and mate allocation decisions (Meuwissen, 1997; Quaas, 1988; Visscher et al., 2002).

Authors' contributions

Matthew Hamilton: Conceptualization, Formal analysis, Methodology, Writing - Original Draft, Visualization. Wagdy Mekkawy: Conceptualization, Data Curation, Writing - Review & Editing, Supervision. Benoy K Barman: Conceptualization, Data Curation, Writing - Review & Editing, Supervision. Md. Badrul Alam: Conceptualization, Data Curation, Writing - Review & Editing, Supervision. Manjurul Karim: Conceptualization, Writing - Review & Editing, Supervision. John AH Benzie: Conceptualization, Methodology, Writing - Review & Editing,

Supervision, Funding acquisition.

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Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2021.736715.

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