Marine Biodiversity Hub

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Molecular analysis of newly-discovered geographic range of the threatened river shark *Glyphis glyphis* reveals distinct populations

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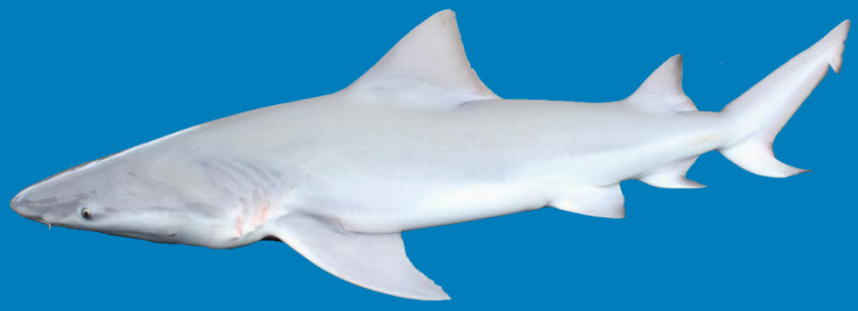

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Important Disclaimer

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EXECUTIVE SUMMARY

The identification of population boundaries is key to determining the appropriate spatial scale for the conservation and management of wildlife. The Speartooth Shark *Glyphis glyphis* is a threatened euryhaline shark of macrotidal rivers and estuaries of northern Australia and southern Papua New Guinea (PNG). The major river drainages (Wenlock River, Alligator Rivers, Adelaide River) comprising the species' known range have been shown to be distinct genetic populations. Recent surveys have revealed a wider range than previously documented with newly-identified populations in the Daly River of the Northern Territory and the Ord River of Western Australia as well as the species' rediscovery in PNG. Using full mitogenome sequencing and DArTseq to genotype single nucleotide polymorphisms (SNPs) we aimed to test the hypothesis that the newly identified rivers (Daly and Ord Rivers), along with the Kikori River in southern PNG, also represent distinct populations given their isolation from known populations. Across the six river systems, the haplotype network showed a non-random distribution of haplotypes. Most of the genetic differentiation was found between rivers (rather than between regions), with highly significant pairwise comparisons between all river systems. The SNP data confirmed the existence of barriers to gene flow with the Ord and Kikori Rivers representing distinct populations. Results from the Daly River also suggest that this is a distinct population, although sample size was small and power limited to infer statistical significance with the nuclear SNP data. Each river system within the range of *G. glyphis* should be treated as a separate management unit.

Keywords: Connectivity, euryhaline, population structure, Speartooth Shark, mitogenomics, DArTseq

1. INTRODUCTION

Sharks, rays, and chimaeras (chondrichthyan fishes) are a diverse group of primarily marine species of increasing conservation concern. A small number of species are adapted to non-marine environments and the combination of their slow life history characteristics and specialised habitat increases their susceptibility to population depletion (Grant *et al.* 2019). The river sharks, genus *Glyphis*, are euryhaline sharks adapted to the interface between marine and freshwater environments. Two species inhabit macrotidal rivers and estuaries of northern Australia and southern Papua New Guinea (PNG) and have been the focus of increased research effort over the last decade (e.g., Bravington *et al.* 2019, Field *et al.* 2013, Feutry *et al.* 2014, 2017, 2020, White *et al.* 2015). In northern Australia, recent surveys have revealed wider ranges for both the Northern River Shark *Glyphis garricki* and the Speartooth Shark *G. glyphis* (Feutry *et al.* 2020, Kyne *et al.* 2021). In PNG, both species were recently 'rediscovered' (White *et al.* 2015).

River sharks are protected within Australia due to their threatened status (Kyne *et al.* 2021). They are a bycatch of commercial fishing operations (Field *et al.* 2013) and there are low levels of legal Indigenous harvest and illegal recreational retention (Kyne and Feutry 2017, Kyne *et al.* 2021). Estimated population sizes for Australia are small (Bravington *et al.* 2019, Patterson *et al.* in prep.) with the most recent assessment of their status highlighting that both species meet Vulnerable by applying the IUCN Red List Categories and Criteria at the national level (Kyne *et al.* 2021). In PNG, these species are not under any specific management and are subject to unregulated artisanal fisheries where they are retained for their fins (Grant *et al.* submitted).

Surveys in suitable habitat across the Northern Territory (NT) and Kimberley region of Western Australia (WA) has revealed occurrence in several turbid macrotidal rivers and estuaries where river sharks had not previously been recorded. For *G. glyphis*, the previously-known range was restricted to the Wenlock River/Ducie River/Port Musgrave system on western Cape York, Queensland (QLD), and various rivers of the Van Diemen Gulf in the NT; an isolated population in the Bizant River on eastern Cape York has not been recorded since 1983 (Pillans *et al.* 2009). While surveying euryhaline elasmobranchs (specifically, *G. garricki* for a population structure study; Feutry *et al.* 2020), 'new' populations of *G. glyphis* were discovered in the Daly River, NT and the Ord River, WA. Furthermore, it

had become apparent that *G. glyphis* persisted in southern PNG (White *et al.* 2015, Grant *et al.* submitted).

Identification of population boundaries is key to determining the spatial scale of units for appropriate conservation and management of wildlife. The development of cheap high throughput sequencing approaches, often referred to as Next Generation Sequencing (NGS), has greatly improved the resolution of genetic methods to infer population structure in non-model species. Restriction site-associated DNA (RAD) sequencing (Baird *et al.* 2008, Miller *et al.* 2007, Sansaloni *et al.* 2011) in particular has changed the landscape of population genetics, making it possible to genotype thousands of single nucleotide polymorphisms (SNPs) in hundreds of individuals. Mitochondrial DNA (mtDNA), which is maternally inherited, provides a unique insight of population historical demography and has been used to delineate management units for a long time (Moritz 1994). It complements nuclear DNA particularly well to study species exhibiting sex-biased reproductive dispersal with philopatric females and dispersive males (Feutry *et al.* 2017). The power of NGS can also be harnessed to gather mtDNA datasets and full mitogenomes, which are more informative than single mtDNA genes/regions (Feutry *et al.* 2014) and are becoming more common in population genetic studies (Ovenden *et al.* 2019).

Using full mitogenome sequencing and DArTseq, a highly efficient RAD protocol, population boundaries have been identified in *G. glyphis* across its previously known Australia range. The major river drainages – Wenlock River, Alligator Rivers (consisting of the East Alligator River, South Alligator River, and West Alligator River), Adelaide River – have been shown to be distinct genetic populations with strong female philopatry (Feutry *et al.* 2014, 2017). Understanding if the newly-discovered populations of *G. glyphis* are genetically distinct is important for defining management units. Here, using the same genetic approaches deployed previously, we aim to test the hypothesis that the newly identified rivers (Daly and Ord Rivers), along with the Kikori River in southern PNG, also represent distinct populations given their isolation from known populations.

2. METHODS

Sampling from the previously known populations (Wenlock River, Alligator Rivers, Adelaide River) is outlined in Feutry *et al.* (2014, 2017). Samples from the Daly River were collected by rod-and-line in Sep. 2014, Oct. 2015, Nov. 2015, Sep. 2019, and Dec. 2019. Samples from the Ord River were collected by rod-and-line in Nov. 2015 and Nov. 2019, or by longline in Sep. 2019. Sampling locations (river systems) are shown in Figure 1. Upon capture, each shark was measured (total length; TL, in mm), sexed (the presence of claspers indicating a male, the absence indicating a female), tagged with a passive integrated transponder (PIT) tag to enable identification of individual sharks in the event of recapture, and had a small piece of the inner posterior margin of a pectoral fin removed for molecular analysis. Samples from Papua New Guinea (PNG) were collected from small-scale fishing operations in Dec. 2018, Oct. 2019, Nov. 2019, Dec. 2019, and Jan 2020 (Grant *et al.* submitted). All PNG samples were collected from the Kikori River or Delta (hereafter referred to as 'Kikori River').

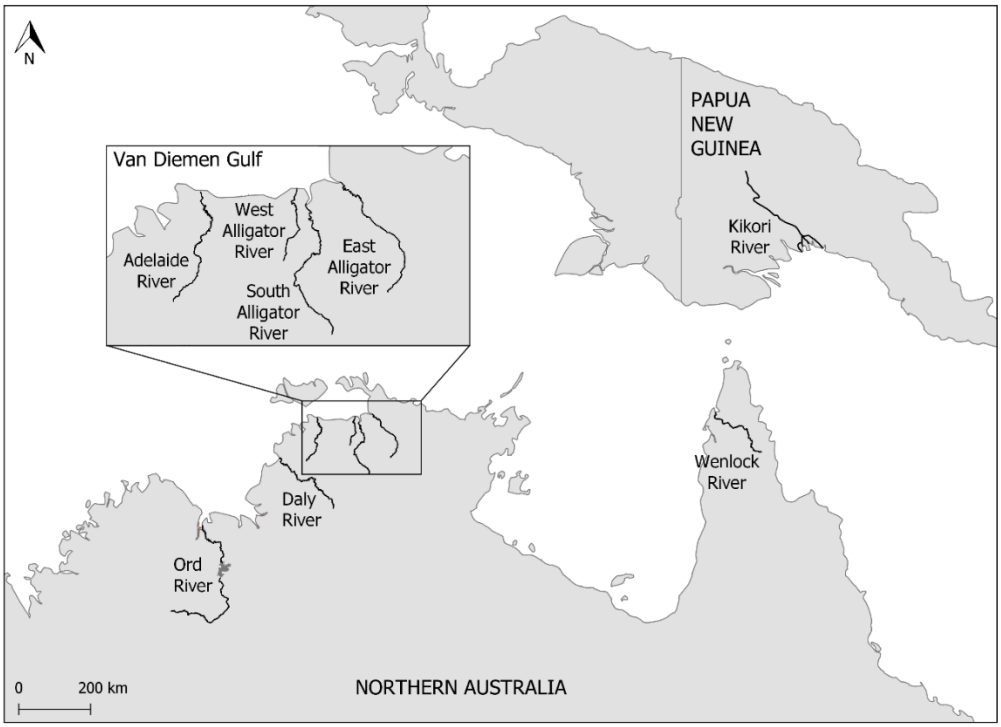

Figure 1: Sampling locations (river systems) for *Glyphis glyphis* across northern Australia and southern Papua New Guinea. Sampling in Van Diemen Gulf and the Wenlock River was undertaken for Feutry *et al.* (2014, 2017) and sampling in the Ord, Daly, and Kikori Rivers for the current study.

Mitogenome sequencing and SNP genotyping followed the approach previously described by Feutry *et al.* (2014, 2017) except for the following. Quarter reactions were used to prepare the Nextera XT libraries in order to reduce cost of the mitogenome sequencing. We used only the forward reads for the assembly as the sequencing of the reverse reads was unsuccessful during the Miseq run. This did not affect the quality of the assembly as there was still high sequencing coverage for all individuals. To further reduce costs of this study, only one complexity reduction method was deployed for the DArTseq genotyping. The R package pegas v. 0.12 was used to calculate the haplotype network and carry out an AMOVA with 10,000 permutations after calculating genetic distance with apex v. 1.0.3. Two different grouping levels were investigated with the AMOVA, first at the regional level, comprised of Joseph Bonaparte Gulf (Ord and Daly Rivers), Van Diemen Gulf (Alligator rivers and Adelaide River), Gulf of Carpentaria (Wenlock River), and PNG (Kikori River), then at the river system level. Pairwise Φ_{ST} were calculated for all river systems using haplotype v. 1.1.2, based on the same genetic distances as for the AMOVA and also with 10,000 permutations.

Population structure was also investigated with the nuclear SNP data. First, Pairwise F_{ST} values between river systems were calculated with 1,000 bootstraps in R using StAMPP v. 1.6.1. Second, Discriminant Analysis of Principal Component (DAPC), as implemented in adegenet 2.1.2, with river systems as putative groups and the alpha-score method to avoid over-fitting, was used to further investigate population structure.

3. RESULTS

Daly River specimens (n=9) ranged between 860–1125 mm TL and comprised two females and 7 males. Ord River specimens (n=32) ranged between 460–1290 mm TL and comprised 24 females and eight males. Kikori River specimens (n=33) ranged between 593–1220 mm TL (size available for n=20) with sex information available for 21 specimens (six females and 15 males) (Table 1). All individuals for which size was available were considered to be immature as they were well below the size-at-maturity (>1900 mm TL; Kyne *et al.* unpubl. data).

Table 1: *Glyphis glyphis* sample details. NT, Northern Territory; WA, Western Australia; AUS, Australia; PNG, Papua New Guinea. Size and sex information were available for only 20 and 21 Kikori River specimens, respectively.

River system	n	Size range (mm total length)	Sex
Daly River, NT, AUS	9	860–1125	2F:7M
Ord River, WA, AUS	32	460–1290	24F:8M
Kikori River, PNG	33	593–1220	6F:15M

The haplotype network for all samples combined shows non-random distribution of haplotypes across the six river systems (Figure 2), which was confirmed by the AMOVA and pairwise Φ_{ST} values. The AMOVA indicated that most of the genetic differentiation was found between rivers (rather than between regions) and pairwise Φ_{ST} were highly significant (*p* value <0.0001) between all river systems, ranging from 0.1074 (Wenlock River vs Kikori River) to 0.9490 (Daly River vs Alligator rivers) (Table 2).

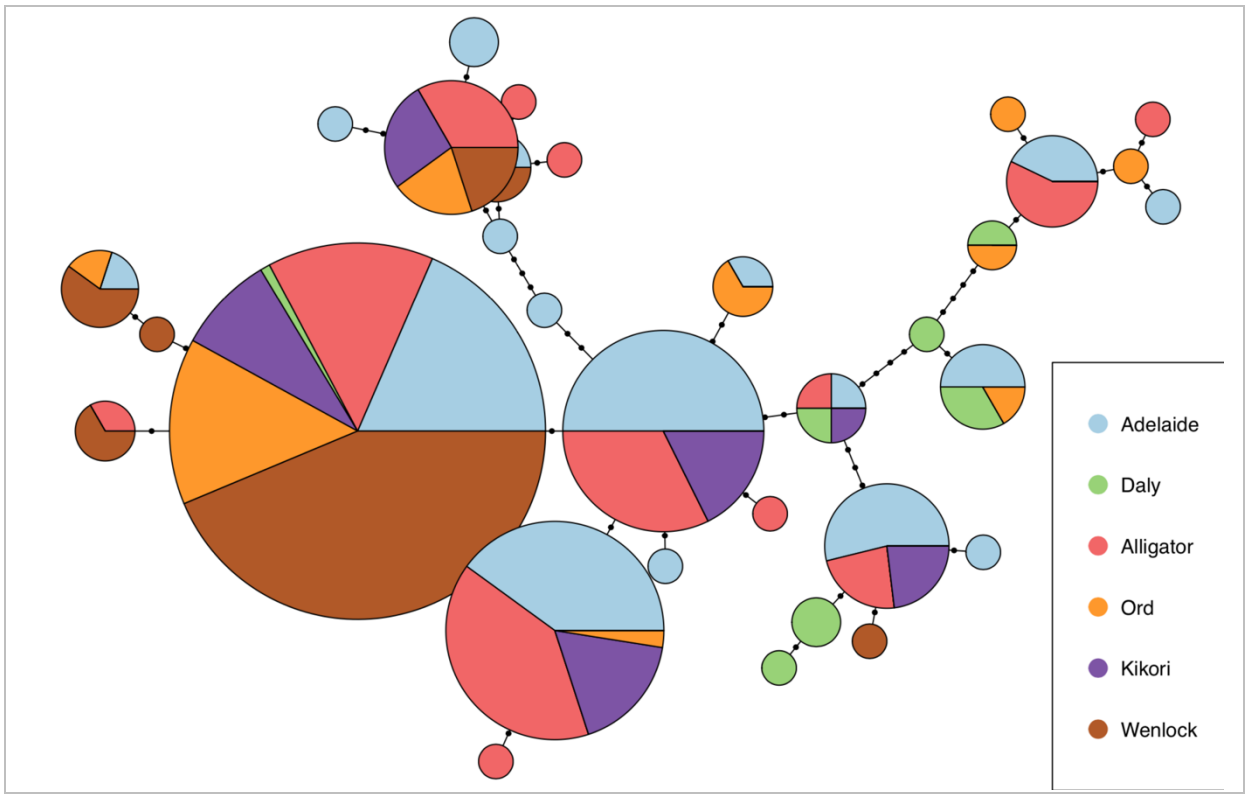

Figure 2: *Glyphis glyphis* haplotype network. Size of the pie charts is proportional to the square root of the number of individuals habouring that haplotype. Black dots on the lines connecting the pie charts indicates mutations.

Table 2: Pairwise Φ_{ST} values (above) and associated *p* values (below) between all sampled locations (river systems) for *Glyphis glyphis*.

	Adelaide	Alligators	Wenlock	Daly	Ord	Kikori
Adelaide	-	0.1706	0.3448	0.9373	0.5953	0.6353
Alligators	0	-	0.4073	0.9490	0.6010	0.7594
Wenlock	0	0	-	0.6427	0.2803	0.1074
Daly	0	0	0	-	0.4861	0.8923
Ord	0	0	0	0	-	0.4191
Kikori	0	0	>0.0001	0	0	-

Pairwise F_{ST} on the SNP data ranged from 0.0011 (Adelaide River vs Alligators rivers) to 0.0078 (Ord River vs Wenlock River) with *p* values <0.01, except for comparisons involving the Daly River, for which *p* values were comprised between 0.038 and 0.086 (Table 3). DAPC patterns of probability membership within each river system are fairly distinct, thereby confirming the existence of barriers to gene flow (Figure 3).

Table 3: Pairwise F_{ST} values (above) and associated *p* values (below) between all sampled locations (river systems) for *Glyphis glyphis*.

	Adelaide	Alligators	Wenlock	Daly	Ord	Kikori
Adelaide	-	0.0011	0.0044	0.0016	0.0014	0.0034
Alligators	0.006	-	0.0049	0.0022	0.0036	0.0061
Wenlock	0	0	-	0.0065	0.0078	0.0042
Daly	0.086	0.075	0	-	0.0025	0.0022
Ord	0	0	0	0.038	-	0.0050
Kikori	0	0	0	0.068	0	-

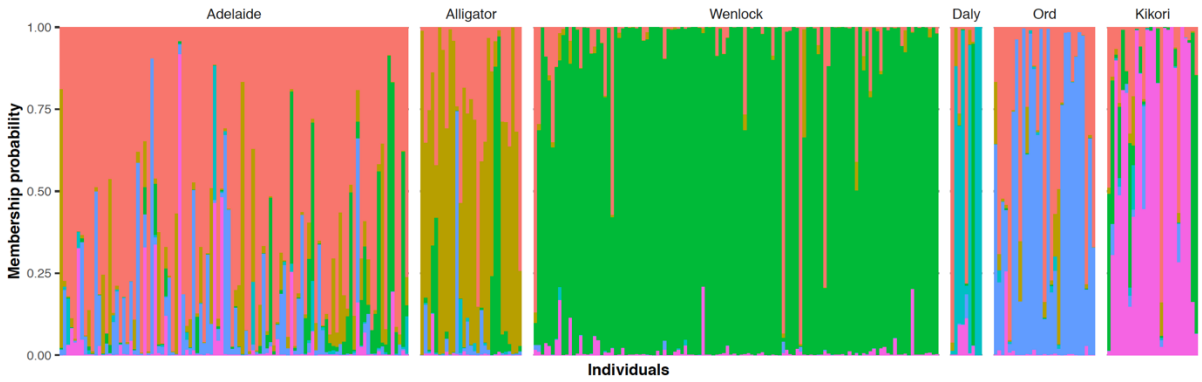

Figure 3: Discriminant Analysis of Principal Component membership probabilities for *Glyphis glyphis* across its range.

4. DISCUSSION

Isolated populations of species which have little demographic exchange represent distinct management units. We provide an analysis of population structure in the threatened *G. glyphis* across its geographic range, comparing previous results (Feutry *et al.* 2014, 2017) with recently 'discovered' populations from northern Australia and a 'rediscovered' population from Papua New Guinea (PNG) (White *et al.* 2015). The pattern of population boundaries established for the species' previously recognised range by Feutry *et al.* (2014, 2017) is supported here, with the Ord and Kikori Rivers representing distinct populations. Results from the Daly River also suggest that this is a distinct population, although sample size was small and power limited to infer statistical significance with the nuclear SNP data.

The geographic range of *G. glyphis* is greater than previously recognised (Pillans *et al.* 2009 *cf.* this study). This provides an insurance policy for this threatened species, although each population is likely to be small (Patterson *et al.* in prep.) and each is genetically distinct. A historical population in the Bizant River of Queensland has not been recorded since 1983 (Pillans *et al.* 2009) and was not included in this study due to a lack of samples. Dedicated surveys are needed to confirm the species' contemporary occurrence there. The Bizant River on eastern Cape York is geographically well separated from the closest known Australian population in the Wenlock River on western Cape York and from southern PNG. It would therefore be expected that the Bizant River represented a genetically distinct population given the results here and of Feutry *et al.* (2014, 2017).

Samples available from PNG covered one river where the species has recently been documented. In addition to the Kikori River, *G. glyphis* has been recorded from the Fly River and the south Fly Coast (White *et al.* 2015, Grant *et al.* submitted). Both the Kikori and Fly Rivers flow into the Gulf of Papua and their estuaries are separated by <40 km. Samples are required from the Fly River to identify if these two rivers harbour distinct populations, or if there is a broader Gulf of Papua population. Several other rivers occur along the Gulf of Papua coast including the Aramia and Bamu Rivers which lay between the Fly and Kikori Rivers. It is likely that *G. glyphis* also occur in these rivers, although they were not documented in recent surveys (Grant *et al.* submitted).

Sample size is an important consideration in population genetic studies. Higher sample sizes can result in greater accuracy of population genetic inferences (Fumagalli 2013) but may be

constrained by such factors as research budget, accessibility to species' habitat and range, or a species' natural rarity. The latter can influence a species' catchability and hence the ability to sample a sufficient proportion of the population. While we considered that an adequate number of samples were available from the Ord River (n=32) and the Kikori River (n=33), sample size from the Daly River (n=9) was lower than planned. Catch rates of *G. glyphis* on the Daly River were extremely low suggesting that the species may be rare or sparsely-distributed in that river; 1 *G. glyphis* was caught per 59 hook hours in the Daly River vs 1 *G. glyphis* per 14 hook hours in the Ord River (P.M. Kyne *et al.*, unpubl. data).

Threats persist across the species' range although the species receives considerable refuge in Australia due to its occurrence in protected areas and its protected status. The Alligators rivers population occurs within Kakadu National Park and World Heritage Area where commercial fishing is prohibited. Further, commercial gillnet fishing is not permitted within the Adelaide and Daly Rivers of the Northern Territory. However, fishing occurs adjacent to the Alligator rivers and Daly Rivers, including in estuarine areas and *G. glyphis* is a bycatch of these operations (Field *et al.* 2013). Localised commercial gillnetting also occurs in the species' Queensland and Western Australian range. In PNG, the species is facing increasing fishing pressure from the rapid expansion of gillnetting and catch levels could well prove to be unsustainable there given the full utilisation of catches and a lack of regulatory management (Grant *et al.* submitted).

5. ETHICS STATEMENT

Sampling in Australia was approved by the Charles Darwin University Animal Ethics Committee (Approval No. A11041 and A19008) and undertaken through Northern Territory *Fisheries Act* Special Permits S17/3364 and S17/3467, and Western Australian *Fish Resources Management Act* Exemption No. 2630 and 3264. Samples in Papua New Guinea were collected with consent from local communities in Gulf Province, and under supervision of the Gulf Provincial Fisheries Office. Samples were imported under AQIS permit number 0002424804 issued to James Cook University.

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