Assessing the genomic population structure of Jackass Morwong (*Nemadactylus macropterus*) in South-Eastern Australian waters

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Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution. This thesis, to the best of my knowledge, does not contain any material previously published or written by another person, accept where due reference is acknowledged within the text.

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Abstract

Recent evaluations have revealed that over half of Tier 1 (a robust, integrated quantitative stock assessment for that species has been conducted) commercial species in the Southern and Eastern Scalefish and Shark Fishery (SESSF) rely on biological data more than 20 years old (FRDC project 2019-027, Evans et al. 2022). Among the uncertainties found, knowledge on the population structuring of the depleted Eastern stock of jackass morwong (*Nemadactylus macropterus*) was highlighted as a critical gap. This project aimed to resolve spatial and temporal uncertainties using Single Nucleotide Polymorphism (SNP) genotyping to provide updated insights into the species' genomic population structure, following previous studies conducted by Elliot & Ward (1994), and Richardson (1982). Samples were collected during the 2023–2024 Southeast Australia Marine Ecosystem Study (SEA_MES) voyages. All analyses undertaken have suggested a panmictic population along the South East coast of Australia. The low value of population-level structure ($F_{ST} = 0.0003$) reflects a single panmictic population, suggesting high gene flow or recent divergence across the sampled range. Therefore, drivers of structure such as sex, cohort, and temporal sampling were not examined in this study. These findings are consistent with earlier allozyme and SNP studies (Elliot & Ward 1994; Richardson 1982; Papa et al. 2022). Furthermore, reinforcing the scientific basis for the current single-stock management approach for *N. macropterus* in the SESSF. However, this study recognises the importance of balanced sampling and careful SNP filtering to avoid obscuring localised genetic differentiation. Future research could expand spatial and temporal sampling, integrate genomic with ecological and fishery data, and employ adaptive management frameworks, all of which will potentially enhance overall stock assessments, and support the long-term sustainability and recovery of *N. macropterus.*

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Chapter 1. Literature Review

1. Fisheries management; defining stock structure and populations

1.1 Sustainable fisheries management

Sustainable fisheries management is complex and requires a multifaceted approach. This process involves identifying the structure of fish stocks and evaluating independent populations (Bessell-Browne et al. 2021). For optimized yield, managers carefully consider the distribution of fishing effort and mortality across each stock (Bessell-Brown et al. 2021), balancing exploitation with conservation to ensure long-term sustainability (Cope & Punt 2011). Effective management requires methods encompassing various contexts—social, economic, political, and biological—understanding why some fish stocks recover more quickly than others after fishing pressure is reduced, and identifying and implementing appropriate fisheries assessment, management, and enforcement techniques in regions where these practices are currently limited (Hilborn et al. 2020). Additionally, developing and implementing methods to determine population abundance and dispersal is crucial, as these methods must account for both the biological characteristics of the species and the intensity of fishing activities (Hilborn et al. 2020). By addressing these aspects comprehensively, fisheries managers can work towards ensuring the long-term sustainability of fish stocks while balancing the needs of fishing communities and ecosystems. Effective fisheries management hinges on a comprehensive understanding of stock structure and dynamics. As fisheries science develops, a multifaceted approach that combines stock assessments, biological data, genomic data, and considers the ecosystem, is essential for maintaining the sustainability of species and creating holistic management strategies.

1.2 Stock structure

A stock can be defined as a population of fish that inhabits a particular area and sustains itself through all aspects of their life cycle, including reproduction, survival and migration (Waples & Gaggiotti 2006). A population is also isolated from other groups of the same species, where immigration or emigration does not substantially influence the population dynamics (Waples & Gaggiotti 2006). This relative independence of stocks allows it to be considered a distinct unit for management purposes (Green et al. 2022). To effectively manage a fishery, the identity and characteristics of a species stock structure must be well understood, and the effects of mortality and fishing effort on the population should be considered, as each stock is recommended to be managed separately to optimise their yield (Grimes et al. 1987). Biological processes (processes that are necessary for an organism to survive and shape its capabilities for interacting with their environment), such as genetic drift should also be considered, as this may have significant implications for fisheries management (Marty et al. 2014) - specifically in terms of maintaining genetic diversity and the sustainability of fish populations (Marty et al. 2014). Fishing may induce natural and adaptive pressure affecting life-history traits with molecular studies showing that genetic diversity has declined in exploited populations (Marty et al. 2014). Harvesting may increase genetic drift as it reduces population size, and alters population structure in size, age, and maturity status (including fecundity), also potentially modifying sex ratios (Marty et al. 2014). This demonstrates the importance of accounting for population genetic variability in predictions of co-evolutionary dynamics and the long-term impacts of commercial fishing (Marty et al. 2014). Without a clear concept of stock structure which considers the biological characteristics of a species and fishing activity, current fishing practises may potentially lead to large-scale shifts in biological attributes, productivity rates, genetic diversity, and the overall fitness of a species (Altukhov 1981; Ricker 1981; Smith et al. 1991; Begg et al. 1999).

Various methodologies can be utilized to determine the stock structure of populations; method selection is dependent on sample size and quality, along with specific aims and research objectives (Bessell Browne et al. 2021). Population parameters, such as age classes and growth rates, are useful for identifying assumed stocks in fisheries management; behavioural and physiological traits, like temperature tolerance, or spawning migration timing, are typically used to assess how stocks adapt to changing environments (Ihssen et al. 1981). These delineation methods provide differentiated but useful information based on various timescales, therefore, the choice in technique for determining a stock will depend on the specific information desired, resourcing, and the broader implications (Green et al. 2022).

2. Understanding genomic techniques in fisheries management

2.1 Molecular techniques

The selection of molecular techniques is an important component of investigating population structure (Begg et al. 1999). Population structure can develop across varying time scales, encouraging the combination of multiple genetic markers to improve detection power and accurately resolve patterns (Green et al. 2022). Furthermore, sampling at scale determines how much of the variation in the population is putatively assessed, with lower sample sizes providing a less robust representation of the level of genetic diversity in the broader population or species (Bailey & Smith 1981).

Molecular markers can be classified as ‘genetic’, which is the process of sequencing or genotyping a specific gene region, or as ‘genomic’, which is the high throughput sampling of the partial or entire genome (Nielsen et al. 2020). Genetic markers include microsatellites, nuclear DNA (nDNA), mitochondrial DNA (mtDNA), and Amplified Fragment Length Polymorphisms (AFLPs) (Nielsen et al. 2020). These techniques are standardised, easy to interpret, and are cost effective due to fewer markers sequenced (Nielsen et al. 2020). These methods provide less power to detect genetic differentiation, typically only detecting historical measures of diversity (except microsatellites) (Nielsen et al. 2020).

In comparison, genomic markers can include thousands to millions of loci, representing a larger portion of the genome (Lowe & Allendorf 2010; Garner et al. 2016; Nielsen et al. 2020). Genome-wide single nucleotide polymorphisms (SNPs) provide the advantage of detecting low levels of genetic structure at smaller scales, indicating genome-wide diversity, due to the abundance of markers for both neutral and adaptive loci, and low associated error rates (Helyar et al. 2011; Puritz et al. 2012; Fischer et al. 2017; Nielsen et al 2020). SNPs are beneficial for genomic, or diversity/connectivity studies as it permits the combination of temporal and spatial datasets, allowing for population structuring to be assessed (Helyar et al. 2011). For example, Vendrami et al. (2017) genotyped the same individuals using microsatellites and SNP markers in great scallop populations (*Pecten maximus*). The results demonstrated that a higher number of SNP markers could detect genetic structure, compared with a panel of microsatellites which did not detect heterogeneity (Vendrami 2017).

The use of SNPs in population genomics involves identifying informative genetic markers, and SNP array and testing (Andersson et al. 2023), see Figure 1 for an example of whole genome sequencing and development of genomic markers in non-model organisms. These steps require careful selection of methods based on the study’s criteria, particularly for non-model organisms where SNPs must be identified through laboratory screening of genome segments from multiple individuals (Morin et al. 2004) (Figure 1).

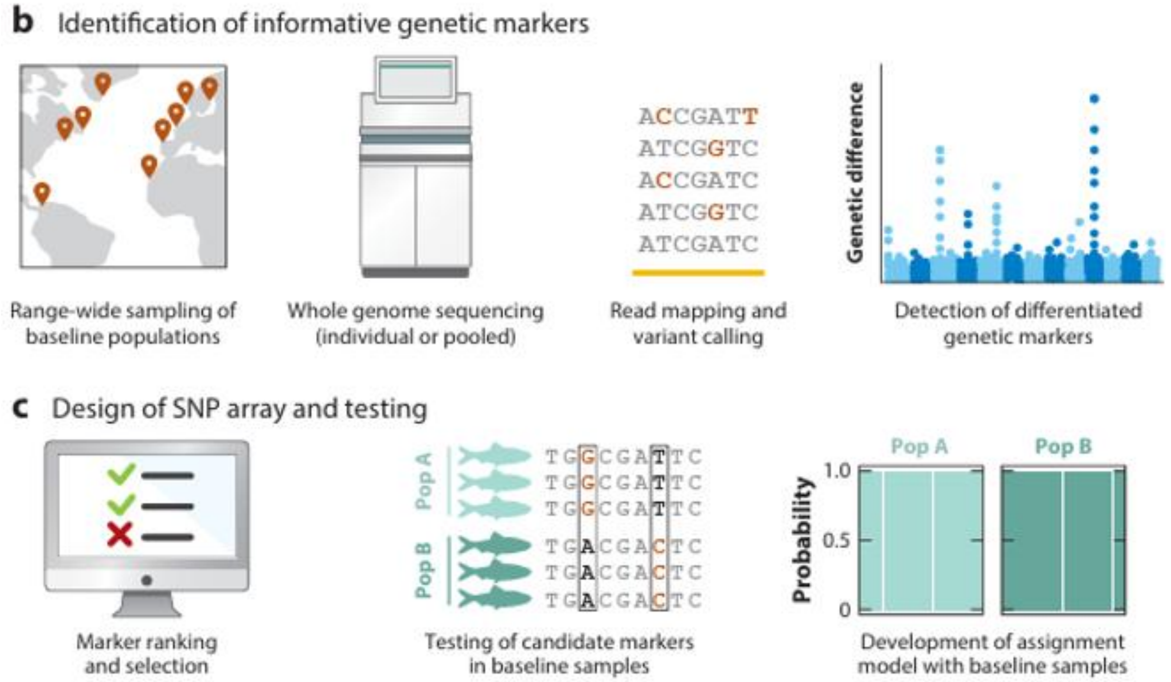

Figure 1. Genomic process for identifying SNPs and analysis. ***(b) Baseline sampling and marker discovery****: Collecting representative biological samples across the species' range and identifying diagnostic markers through comparative genomic analysis.* ***(c) Population structure analysis****: Conducting population genomics analyses to define stock boundaries, connectivity patterns, and population differentiation. (Figure adapted from Andersson et al. 2023).*

2.2 Population genomics in fisheries management

Population genetics/genomics has been effectively applied in several fisheries management scenarios, offering important insights into stock structure and informing management decisions (Zhang et al. 2020). Genetic analysis of stock structure, obtained by utilising allozymes, microsatellite DNA, and mtDNA sequencing, can provide insights into the most appropriate scale of management on a species-specific basis (Ovenden et al. 2015). A study by Pampoulie et al. (2023) reviews 60+ years of genetic studies on Atlantic cod (*Gadus morhua*) in Iceland waters. SNP marks revealed finer population structure than earlier allozyme and mtDNA work, identifying distinct behavioural ecotypes (e.g. migratory versus stationary) (Pampoulie et al. 2023). The genomic data also challenged previous assumptions regarding gene flow, showing unexpected complexity in connectivity patterns despite high dispersal potential (Palaiokostas et al. 2022; Pampoulie et al. 2023). The integration of genomic data with behavioural monitoring demonstrated how spawning site and habitat preferences maintain genetic differentiation, therefore, informing targeted conservation strategies (Palaiokostas et al. 2022; Pampoulie et al. 2023). A study on two related redfish species (*Sebastes mentella and Sebastes fasciatus*) employed genotype-by-sequencing (GBS) to analyse 24,603 SNPs across 860 individuals, revealing clear genetic distinctiveness of the two species, and identified three ecotypes within *S. mentella* and five populations in *S. fasciatus* (Benestan et al. 2021). Spatial distribution and depth influenced genomic variation, indicating environmental drivers of adaptive divergence (Benestan et al. 2021). Demographic modelling revealed that secondary contact models best explained inter- and intragenomic divergence (Benestan et al. 2021). These findings highlight the need to refine fishery management units to protect evolutionarily distinct groups and reduce overharvesting risks.

Genomic techniques are useful for defining population structures in species with high gene flow, which often indicates some level of population connectivity. For example, using thousands of SNP loci instead of six genetic microsatellites and one mtDNA gene, improved the delineation of population structuring for Japanese anchovy *(Engraulis japonicus)* (Zhang et al. 2020). A study by Green et al. (2019), highlighted the increased statistical power of SNPs compared to microsatellites for detecting the population structure of the silvertip shark (*Carcharhinus albimarginatus*) within the Indo-West Pacific region. Samples were analysed using a mtDNA gene, microsatellite and SNPs (Green et al. 2019). No gene flow was identified between south-west Pacific locations and Seychelles, but mtDNA indicated significant population structuring between PNG and east Australia (Green et al. 2019). These markers combined with known telemetry movements for *C. albimarginatus* suggest movement patterns between areas is likely driven by reproductive behaviour (Green et al. 2019). A genomic study for snapper *(Lutjanus johnii*) in northern Australia revealed fine scale population structuring supported by environmental datasets (Taillebois et al. 2021). The distribution of twelve biological stocks suitable for practical management purposes was identified but corresponded poorly with the current fisheries management boundaries, which were established under the Australian government's classification of Integrated Marine and Coastal Regionalisation of Australia (IMCRA) bioregions (Commonwealth of Australia

2006; Taillebois et al. 2021). These examples demonstrate the power and versatility of population genomics in fisheries management, highlighting its ability to reveal fine-scale population structures, detect species local adaptations to environmental shifts, and provide updated biological data. Collectively, the data can be used to re-define stock boundaries to align with population structuring and inform fishing closures. Assessments and management units need to align with biological population structure; therefore, stock boundaries could be assigned to match the spatial scale of biological populations (Kerr et al. 2017).

2.3 Applications and challenges of genomics in fisheries

Traditional biological fisheries data, such as catch, body length, sex, age, and mortality are critical to inform fisheries management (Bernatchez et al. 2017). Fisheries management is now shifting to a new paradigm, which combines traditional biological data with genetic and genomic data integrating adaptive diversity to understand crucial components of fisheries resources (Valenzuela-Quinonez 2016). Outlier loci (loci that demonstrate significantly higher or lower among-population genetic differentiation), than expected under neutrality, offer the potential for accurate genetic stock identification at a fine scale (Feng et al. 2015; Valenzuela-Quinonez 2016). These markers also enhance the opportunity to trace fisheries resources or products to their original locations, offering international regulation and enforcement (Valenzuela-Quinonez 2016). If the population structure of fisheries resources is achieved, the appropriate level to collate data used for fisheries assessment and suitable management areas can be defined (Andersson et al. 2023). Genomics enables scientists to assign the population origins of individuals in mixed-stock commercial catches and scientific surveys to guarantee the validity of data used for stock assessments (Andersson et al. 2023). For this to be achieved, representative samples of individual populations need to be collected, baseline allele frequencies need to be determined, and cost-effective genotyping methods should be utilized (Andersson et al. 2023). The application of genomics, coupled with increasing information and resolution regarding the main causes of marine population differentiation allows for the investigation into the resilience of marine species facing climate change and overfishing, two of the largest challenges in fisheries management (Benestan 2019). Furthermore, scaling up genome data for non-model species leads to refined estimations of population genetic parameters, more so in species that have a weak population structure (Benestan 2019). There is also potential to identify genetic markers that facilitate the classification of management units based on adaptive criteria in addition to the development of diagnostic markers for managing the spread of pathogens or invasive species (Benestan 2019).

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Chapter 2. Manuscript

1. Introduction

Sustainable fisheries management requires integrating stock structure analysis, ecosystem dynamics, and fishing impacts, with genomic tools now complementing traditional biological data to refine population assessments and adaptive strategies (Bessell-Browne et al. 2021; Nielsen et al. 2020). In Australia's Southern and Eastern Scalefish and Shark Fishery (SESSF), a multispecies, multi-gear fishery spanning Commonwealth and state waters, over 50% of biological parameters used in stock assessments rely on data collected over 20 years ago, risking inaccurate biomass estimates and potentially less effective management strategies (Evans et al. 2022; FRDC 2019-027). For example, jackass morwong (*Nemadactylus macropterus*), once a key commercial species, faces unresolved uncertainties in population structure and connectivity with the last major evaluation done in 1994 using genetic techniques (Elliot & Ward 1994). Genomic methods such as single nucleotide polymorphism (SNP) analysis offer higher-resolution insights into stock boundaries and adaptive potential, critical for updating harvest strategies like total allowable catch limits (TACs) and spatial closures under the SESSF's Commonwealth Management Plan (Benestan 2019; Wright et al. 2023).

Although genomic techniques hold significant promise for fisheries management, their practical application is hindered by several challenges. These range from the need of high-quality genomic data, robust analytical capabilities, and standardised protocols to ensure comparability across studies (Andersson et al. 2023). For *N. macropterus,* addressing these obstacles will be crucial to successfully integrate genomic data into existing management frameworks. Furthermore, the integration of genomic data with traditional biological and environmental information will be necessary to provide a comprehensive understanding of the species' population dynamic. While preceding genetic studies on *N. macropterus* have largely shown homogeneity among Australian populations (Richardson 1982; Elliott & Ward 1994; Grewe et al. 1994; Burridge & Smolenski 2003), these studies utilized older genetic techniques with limited resolution. Higher-resolution genomic methods, such as single nucleotide polymorphisms (SNPs), offers an opportunity to re-assess the population structure of *N. macropterus* along the South East coast of Australia at a finer scale, providing insights useful for stock assessments and management strategies (Helyar et al. 2011; Papa et al. 2022).

2. Study species – jackass morwong (*Nemadactylus macropterus*) in the South-Eastern Shark and Scalefish Fishery (SESSF).

2.1 The biology of *N. macropterus*

Nemadactylus macropterus, a member of the Latridae family (Ludt et al. 2019), is a moderately long-lived (up to 30 years) demersal fish species (Figure 1), found in coastal and continental shelf waters of southern Australia, New Zealand, South America, and South Africa, ranging in depths down to 450m (Wayte 2013). In Australia, *N. macropterus* is caught in northern NSW, Tasmania, and along the Western edge of the Great Australian Bight (Bessell-Browne et al. 2021). Currently, tagging experiments provide no evidence of large-scale migration of *N. macropterus* individuals around Australia (Bessell-Browne et al. 2021). Spawning occurs during March and May, peaking in mid to late April in Southern Australia (Bruce et al. 2001). Additionally, *N. macropterus* have been observed to spawn more than once during the season, occurring at night in the midwater, and throughout the entire geographical species range (Bessell-Browne et al. 2021). Larvae reside offshore for a significant period of nine to 12 months before metamorphosing into the adult form, when the young adult reaches between 70-90 mm in length and, individuals move to coastal shelf areas (Bessell-Browne et al. 2021). Females grow faster and live longer than males, but both reach maturity at roughly the same age at approximately 24.5cm and grow to a maximum length of ~50cm (Female age at maturity = **3.5 ± 0.5 years**, Male = **3.5 ± 0.5 years)** (Bessell-Browne et al. 2021).

Figure 1. *Photo of jackass morwong (N. macropterus) caught by trawl operations onboard SEA_MES 3.*

2.2 *Nemadactylus macropterus* in the SESSF

Jackass morwong is one of 34 quota-managed species under the SESSF, a Commonwealth-regulated fishery spanning the Australian Fishing Zone (Figure 2). Management areas include both Commonwealth waters and state waters under Offshore Constitutional Settlement arrangements, with stock assessments conducted across the entire fishery (Wayte 2013; Wright et al. 2023). This species is managed as two separate stocks, an Eastern stock (Commonwealth, New South Wales, Tasmania and Victoria), which is considered ‘Depleted’, and a Western stock (Commonwealth, South Australia, Tasmania, Victoria), which is classified as ‘Sustainable’ (Australian Bureau of Agricultural and Resource Economics and Sciences, 2023). Tasmania and Victoria are unique in that they contribute to both stocks, depending on the precise location of catch or assessment within those states (Australian Bureau of Agricultural and Resource Economics and Sciences, 2023). The boundary between east and west occurs at a longitude of 147° East, the east includes SESSF zones 10, 20 and 30 and the west encompasses SESSF zones 40 and 50 (Figure 3) (Bessell-Browne et al. 2021).

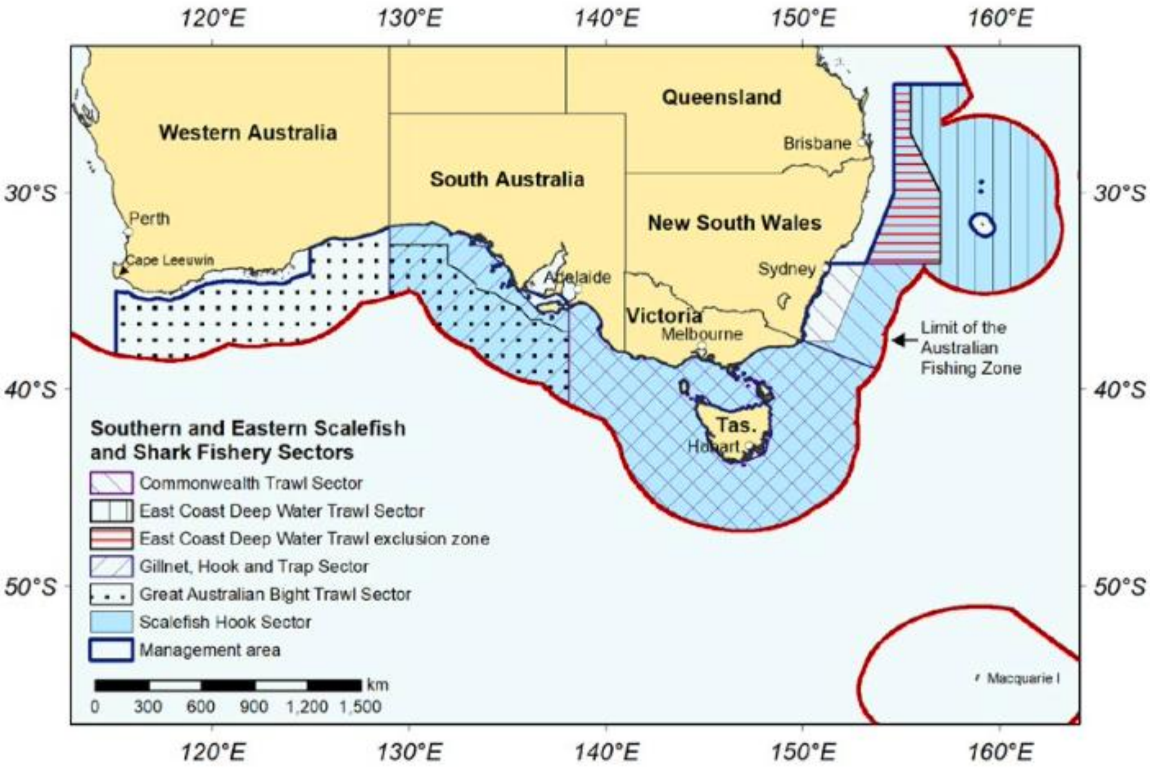

Figure 2. *Area and sectors of the Southern and Eastern Scalefish and Shark Fishery (SESSF) around Australia. (Figure from Wright et al. 2023).*

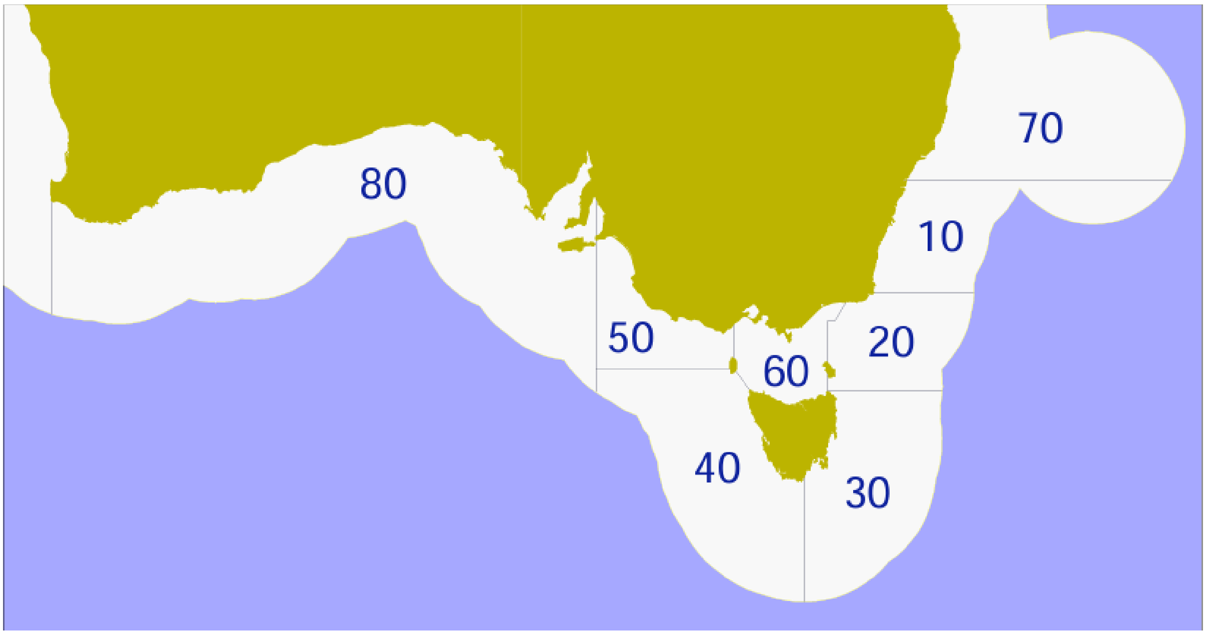

Figure 3. *Map of the SESSF showing zones in the East (10, 20, 30), and zones in the West (40 and 50). (Figure from Bessell-Browne et al. 2021).*

The SESSF employs a harvest strategy framework that integrates data collection, quantitative stock assessments, and harvest control rules aligned with the Commonwealth Harvest Strategy Policy (Smith et al. 2014). Key objectives include maintaining biomass above limit reference points (to avoid high extinction risk) and ensuring stocks remain above these thresholds ≥90% of the time (Smith et al. 2014).

Since 2021, the Eastern stock of *N. macropterus* has been classified as ‘overfished’ due to historical overexploitation; catches exceeded 2,500 tonnes annually in the 1960s with sustained declines since the 1980s (AFMA 2023; Australian Bureau of Agricultural and Resource Economics and Sciences, 2023). Fishing mortality was above the target reference point for the past 27 years, with previously high levels from 1997 to 2012, compounded by reduced recruitment post 2007 (AFMA 2023). Another large driver is a depletion in biomass, the 2021 Status of Australian Fish Stocks Report estimated spawning stock biomass in 2020 to be 14% of the unfished level, well below the limit reference point (AFMA 2023; Sharples et al. 2024). AFMA has implemented spatial closures and reduced catch limits to aid recovery, particularly for the overfished eastern stock. In contrast, the Western stock remains classified as ‘sustainable’ under current management (Sharples et al. 2024).

2.3 Catch reporting within the SESSF framework

All commercial catches of *N. macropterus*, whether in Commonwealth or state waters are managed under the SESSFs jurisdiction and reported to AFMA. In New South Wales, the commercial catch of Eastern *N. macropterus* is primarily taken in the Line and Ocean Trap Fishery, with smaller catches from other fisheries (AFMA 2023). In the last 10 years, the annual commercial catch (ACC) has ranged between 3.4 and 10.3 tonnes, representing only 1.8% to 7.4% of the total SESSF catch each year and thus comprising a minor component of overall fishing mortality for the stock (AFMA 2023).

In Victoria, commercial catches have been consistently less than 1 tonne per year for more than 25 years, with many years recording zero landings. Although some recreational catch occurs in Victoria, it is considered small relative to other sources of fishing mortality and unlikely to affect the stock biomass significantly (AFMA 2023).

In Tasmania, *N. macropterus* (predominantly from the Eastern stock) are taken in the multi-gear, multi-species Tasmanian Scalefish Fishery (TSF), which is managed under the SESSF framework (Sharples et al. 2024). Commercial TSF catches peaked at 33.2 tonnes in 1997–98, but since 2011–12, annual commercial catches have been below 5 tonnes, with a total catch of 3.4 tonnes recorded in 2021–22 (Australian Bureau of Agricultural and Resource Economics and Sciences, 2023). Additionally, *N. macropterus* is also a popular recreational species in Tasmania, with recreational catches generally higher than commercial landings; peak recreational catches have historically exceeded 30 tonnes (31.9 tonnes in 2000–01), and in more recent years, 8.4 tonnes were recorded in 2017–18 (AFMA 2023; Sharples et al. 2024).

Catch per unit effort in the TSF (CPUE) shows the trend of catches fluctuating with fishing effort, which has stabilized at lower levels since 2007/08, influenced by effort reductions and spatial management (Tasmanian Wild Fisheries Assessments 2024) (Figure 4).

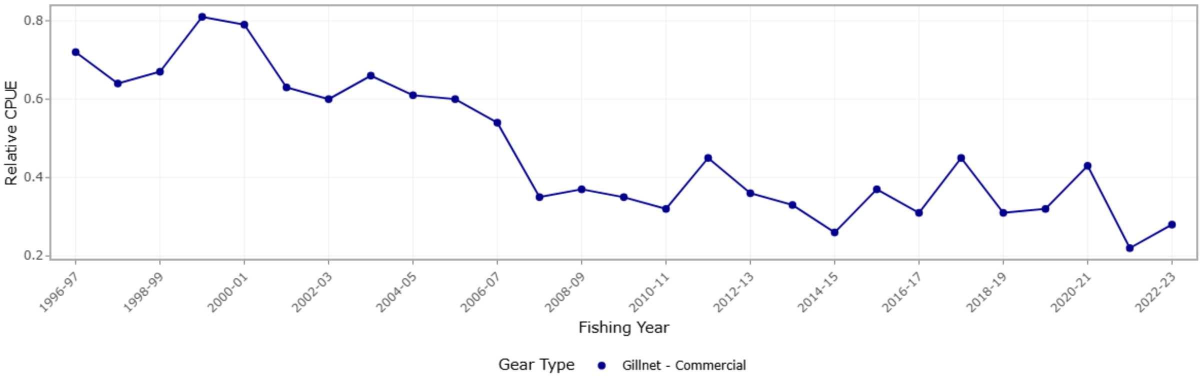

Figure 4. *Relative CPUE of N. macropterus against fishing year. Relative CPUE is calculated using the geometric mean, normalising data relative to the first representative values of the catch and effort time series (i.e. the reference year). (Figure from Tasmanian Wild Fisheries Assessment 2024).*

3. Population genomics of *N. macropterus*

3.1 Previous findings based on population genetics/genomics in *N. macropterus*

Numerous genetic studies based on allozymes, microsatellites, and mtDNA have been undertaken on *N. macropterus* around Australia. Richardson (1982) examined the polymorphisms of five enzymes but found no significant differences in populations. Similarly, a study by Elliott & Ward (1994), also examining allozyme variation, yielded the same results. Further genetic based studies conducted on Australian and New Zealand populations, have revealed no spatial heterogeneity, and no significant divergence between populations (Grewe et al. 1994, Burridge & Smolenski 2003). Within New Zealand, Halliwell (2019) found no genetic differentiation using mtDNA suggesting *N. macropterus* has a panmictic genetic structure (characterized by random mating within a breeding population, usually genetically connected), and relatively high levels of genetic diversity.

The first identification of genetic differentiation of *N. macropterus* across regions was outlined by Papa et al. (2022), who used whole genome resequencing of 175 individuals, (183,443 high-quality SNPs) which highlighted fine-scale adaption and a temperature-associated cline. The analysis suggested the existence of two stocks between New Zealand and Tasmania (Papa et al. 2022). Collectively, while genetic studies have largely shown homogeneity among *N. macropterus* populations in Australia, the detection of differences between Australian and New Zealand populations using genomic techniques highlights the potential for detection of regional stock differentiation, due to genomics detecting finer-scale resolution. Prior to this study, there has been no genomic research conducted on *N. macropterus* in the Eastern stock.

4. Scope of present study

Considering the limited literature which largely focuses on traditional genetic techniques, combined with the previous commercial significance of *N. macropterus*, there is a recognised need for updated biological parameter information. This can partially be achieved through genomic connectivity assessments. With advancements in genomic technologies, this project aims to provide updated data on the species' genomic population structure in the Eastern stock, updating the previous evaluation for the species conducted ~30 years ago in 1994 (Elliott & Ward 1994). Earlier genetic studies have indicated no latitudinal structuring within Australia (Elliott and Ward 1994; Thresher et al. 1994), but more recent studies using whole genome approaches have provided evidence of regional differentiation between Australian and New Zealand populations (Papa et al. 2022). Understanding the genomic connectivity and population structure of *N. macropterus* in the SESSF will help inform stock assessments for the Eastern stock, with implications for effective fishery management. This project investigated if there was latitudinal and temporal structuring of *N. macropterus* in the Eastern stock, and what relevance this might have on current SESSF stock assessments. Assessing the population structuring can further inform the current management efforts to address overfishing through re-assigning spatial closures. This research was achieved through utilising samples collected from south eastern regions of the SESSF fishery collected under the South East Australian Marine Ecosystem Study (SEA_MES) and by examining the genomic structure of *N. macropterus*. The findings of this project will guide stock assessments to accommodate any population structuring that might be present and provide insight for conservation measures to ensure the sustainability of the species in the SESSF.

5. Project aims and objectives

This project aimed to investigate the genomic population structure of *N. macropterus* in the SESSF, specifically the Eastern stock, where biological parameters are outdated.

H0: Given the results from Richardson (1982), Elliott & Ward (1994), Grewe et al. (1994), Burridge & Smolenski (2003), Halliwell (2019) and Papa et al. (2022) papers, it was hypothesised that *N. macropterus* have a panmictic population structure in the SESSF, with no significant genetically distinct populations present across the sampling design.

H1: The alternate hypothesis states that *N. macropterus* population structuring is occurring in the SESSF, with independent genetically distinct populations, and genetic heterogeneity observed.

6. Materials and Methods

Muscle samples from *N. macropterus* were utilized from three CSIRO led South East Australian Marine Ecosystem Survey (SEA_MES) voyages. DNA extractions of tissue samples and SNP genotyping were completed by Diversity Arrays Technology in Canberra (DArT, https://www.diversityarrays.com/). Statistical analyses were then undertaken in R Studio (v2024.12.1; R Core Team 2025), using *dartRverse* (v1.0.6; Gruber et al. 2018), and associated and linked packages.

6.1 Site and sample collection

Samples of *N. macropterus* were obtained via trawling operations (McKenna Trawl/ McKenna semi V-wing fish trawl; average trawl time: 31.55 min; average depth: 186m) from three of CSIRO's SEA_MES voyages in 2023 – 2024. The selection for sub-sampling was based on an average of 27 samples from each latitude (-36° through to -42°) along the South East coast of Australia (Figure 5; Figure 6). The sample design aimed to capture individuals of various sizes to include varying cohorts (Supplementary Table 1). Samples selected per voyage were split relatively evenly, allowing for temporal stability to be investigated. The approach taken to investigate connectivity was through assigning populations based on latitude; they are not 'true' populations (Table 1). For consistency, here on the sample groups will be referred to as 'populations', or 'assigned populations'.

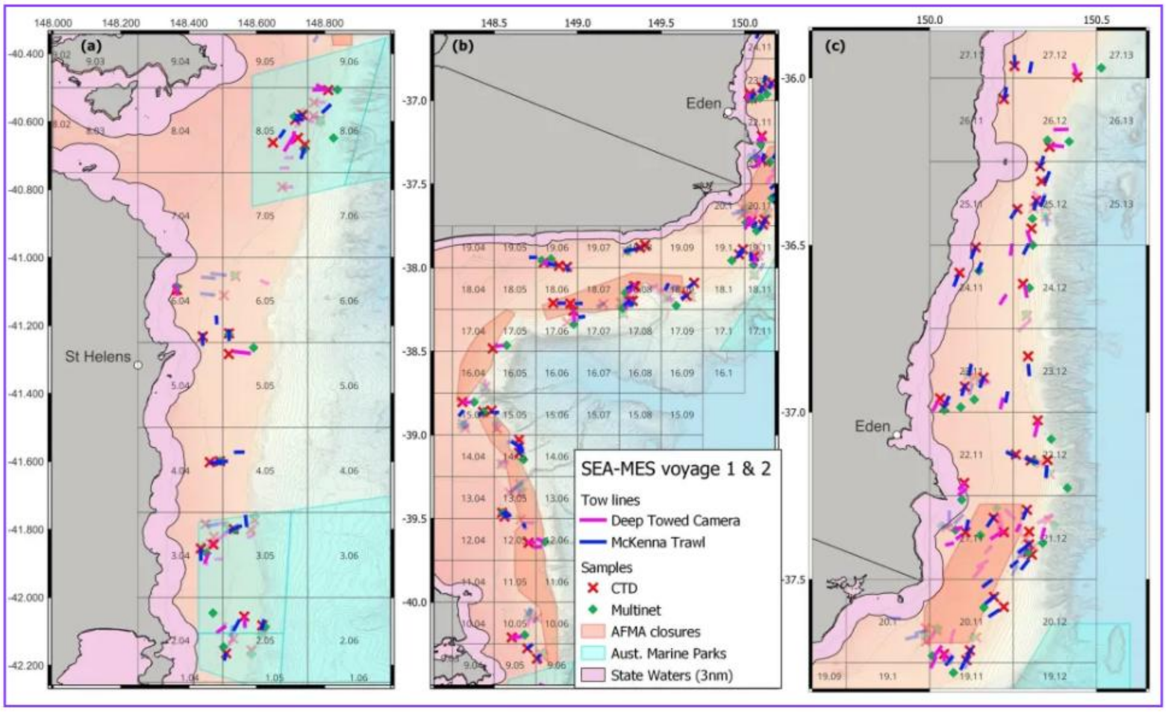

Figure 5. *SEA_MES voyages 1 and 2, route and tow lines where samples were harvested. The blue line indicates trawl sites where samples were harvested. (Figure from SEA_MES voyage operations 2023-2024).*

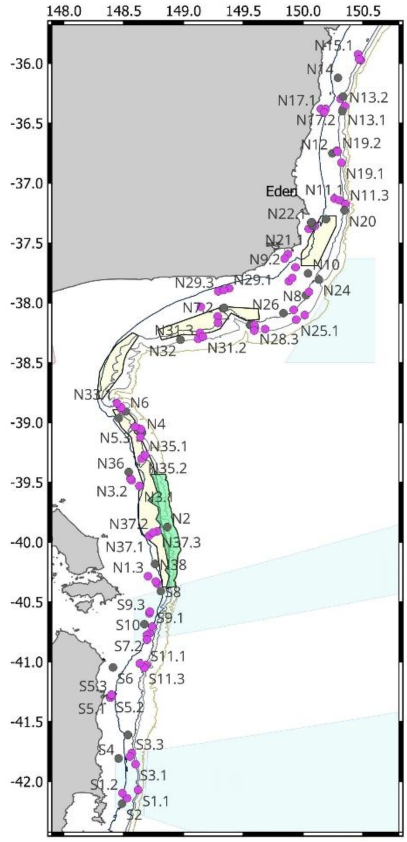

Figure 6. *SEA_MES voyage 3 site map along the South East coast of Australia. Trawls and sample collection were conducted at each site indicted in purple. (Figure from SEA_MES voyage operations 2023-2024).*

Table 1. *Assigned populations based on latitude for the selection of N. macropterus samples along the South East coast of Australia.*

Code[a]	Latitude	Number of samples	Sex[b]
A	-36 °	27	NA: 11, M: 10, F: 6
B	-37 °	27	NA: 10, M: 6, F:11
C	-38 °	31	NA: 18, M: 6, F: 7
D	-39 °	26	NA: 4, M: 6, F: 16
E	-40 °	29	NA: 17, M: 2, F: 10
F	-41 °	35	NA: 19, M: 8, F: 8
G	-42 °	13	NA: 6, M: 0, F: 7
P (total)	ALL	188	NA: 85, M: 38, F: 65

[a]*Individuals of N. macropterus, were assigned a population code based on latitude in the SESSF.* [b]*Number of individuals sampled at each location, and the corresponding ratios of na:males:females.*

6.2 Sub-sampling process

N. macropterus muscle tissues were sub-sampled at CSIRO laboratories in Hobart, and all samples were labelled with barcodes from the CSIRO SEA_MES voyages and documented. A sterilised scalpel and forceps were used to slice 15-20mg of tissue from the middle of the sample, ensuring the sub-sample was not contaminated by exterior sources. Each of the 188 tissue sub-samples were placed into two Axygen (California, USA) plates in plastic vials of rows of eight, submerged with 500µl of 80% ethanol, and sealed with strip caps (MTS-8CP-C-S) (California USA). Samples were boxed up securely and packaged with frozen gel packs. Ambient temperature freight was arranged through LabCabs (https://labcabs.com.au/, Hobart, Australia), and samples travelled from IMAS Taroona laboratories (Hobart, Australia) on the 5th of February 2025 and were received by Diversity Arrays Technology (DArT) (Canberra Australia) on the 6th of February 2025. Samples were sent to DArT for DNA extractions and high throughput SNP ascertainment and genotyping.

DArT employs methods to reduce genome complexity, focusing on regions rich in genes, and then uses high-throughput, open-access microarray platforms for analysis (Killian et al. 2012). The quantitative design of the assay enables researchers to estimate allele frequencies across populations (Killian et al. 2012). Typically, a DArT assay surveys tens of thousands of loci for genetic variation, with the number of markers ultimately reported, ranging from several hundred to several thousand, reflecting the amount of DNA sequence diversity detected in the sample (Killian et al. 2012). DArT markers are designed to focus on gene-rich regions and are generally distributed evenly throughout the genome (Petroli et al. 2012). This broad and uniform coverage makes them highly effective for genetic mapping, as well as for genome-wide studies in breeding and diversity research (Petroli et al. 2012).

6.3 SNP data analyses

Following DNA extraction and sequencing SNP data were obtained from DArT on April 7, 2025. The SNP dataset was generated using a random and reproducible selection of small DNA fragments exhibiting variation at single base pairs (Gruber et al. 2018). Metadata files were compiled in Excel (v250) to include sample-specific information such as sample ID, population designation (based on latitudinal groupings; Table 1), latitude, longitude, and sex (see Appendix 2; Table 2.1). Two metadata files were created: (1) a ‘panmictic population’ file where all individuals were assigned a single population labelled ‘P’, and (2) a file which divided individuals into population groups based on latitude (according to Table 1). Samples were separated into latitude to test if any population structure could be identified using the SNP dataset.

Analyses were performed on both data files and yielded similar results. Filtering and quality-control was performed with both files, and the Hardy-Weinberg Equilibrium (HWE) analyses in section 7.2 examined the data from the overall (P) dataset (file 1). For consistency purposes, the population-based results presented after 7.2 were deducted from file 2 (samples split latitudinally). All data has been archived at CSIRO Hobart marine labs, inclusive of excel files and raw sequencing data.

All data manipulation and statistical analyses were conducted using R Studio (v 2024.12.1+563; R Core Team 2025). Filtering and quality control processes were performed using functions from the *DartR* package (Gruber et al. 2018). These steps included filtering loci based on reproducibility (0.98) minimum allele frequency (MAF = 0.02), read depth, (lower = 5; upper: 100), call rate (0.98), removal of monomorphic loci, heterozygosity (lower = 0; upper: 0.20), and linked loci (best) (see Appendix 1; Supplementary Table 2 for specific thresholds applied and SNPs retained).

Population structure analyses were conducted on the file 2 filtered SNP dataset using the *dartR.base* package (v0.98*;* Gruber et al. 2018). Metrics such as number of polymorphic SNP loci, observed heterozygosity, expected heterozygosity, linked disequilibrium, the inbreeding coefficient (F_{IS}), and fixation index (F_{ST}) were calculated in R Studio (v 2024.12.1; R Core Team 2025; *adegenet;* v2.1.11; Jombart & Ahmed 2011). File 1 was used to calculate HWE deviations (*HardyWeinberg;* v1.7.8; Graffelman 2015). These analyses were used to assess genetic variation within and between populations. Statistical significance of fixation indices (F_{ST} and F_{IS}) was evaluated using p-values derived from 1,000 bootstrap iterations across loci, with associated 95% confidence intervals.

A Principal Component Analysis (PCA) was performed to visualise genetic structure among individuals. Additionally, Shannon information indices were calculated using *dartR.base* (v0.98*;* Gruber et al. 2018), to quantify genetic diversity across populations. All analyses were conducted using standard workflows implemented in *DartR* (v0.98*;* Gruber et al. 2018) and complementary R Studio packages.

Additional population genetic analyses were undertaken using alternative R Studio (v 2024.12.1; R Core Team 2025) packages to ensure robust results. A Discriminant Analysis of Principal Components (DAPC) using the *adegenet* package v2.1.11 (Jombart & Ahmed 2011; Jombart & Collins 2015), which identifies and describes genetic clusters was utilised. An Analysis of Molecular Variance (AMOVA) was also generated using the package *hierfstat* (v0.5-11; Goudet & Jombart 2022), to test the presence of nested population differentiation.

7. Results

7.1 SNP filtering across the data set

The initial dataset contained 72,794 SNPs across 188 individuals. After applying quality control filters, including thresholds for repeatability (≥0.98) and removing loci with excessive missing data, 9,879 high-quality polymorphic SNPs remained across 187 individuals (Supplementary Table 2). The average repeatability of SNPs was 1.0, indicating high reliability in genotype calls. One individual (10098639) was excluded due to a low call rate (<0.9), leaving 187 individuals for downstream analysis (Supplementary Figure 1).

7.2 Hardy-Weinberg Equilibrium and F-statistics based on the SNP data in the overall (P) sample set

The F-statistics showed low genetic differentiation (F_{ST} = 0.003) and a deficiency in heterozygotes (F_{IS} = 0.232), (statistically indicating potential inbreeding) when the SNP data set was treated as one (Table 2). The Hardy-Weinberg Equilibrium (HWE) analysis had non-significant p-values for FST and FIS. Genetic diversity values were also calculated based on the data set being treated as a single stock (Table 2). This can indicate that sampling has not been extensive enough, so the full complement of variation has not been sampled.

Table 2. *Genetic diversity values of N. macropterus from east coast sampling (n=187).*

Genetic Diversity	Value
Observed heterozygosity (Ho)	0.1477
Expected heterozygosity within populations (Hs)	0.1923
Expected heterozygosity in total population (Ht)	0.1924
Genetic differentiation within subpopulations (D_{ST})	0.0001
Fixation index (F_{ST})	0.0003
Inbreeding coefficient (F_{IS})	0.2318
Hardy-Weinberg Equilibrium (HWE) p-value for FST and FIS	0.0000

Values calculated were based on a panmictic structure around South East Australian waters.

7.3 Minor Allele Frequency distribution across the data set

The MAF distribution revealed a skewed pattern with most SNPs having MAF values close to 0.0, indicating a prevalence of rare variants in the population. As MAF increased, the number of SNPs at higher frequencies decreased, suggesting that common variants were less frequent than rare ones (Figure 7). This pattern aligns with expectations for populations with limited genetic diversity.

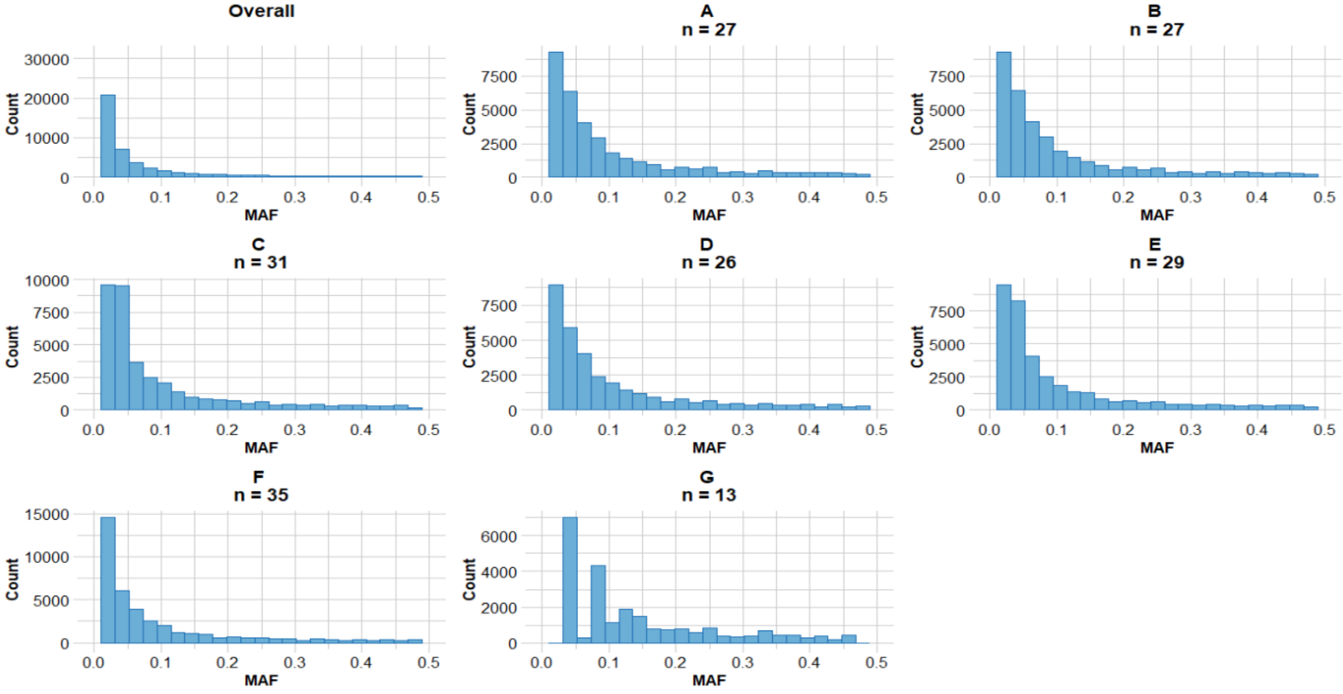

Figure 7. *MAF for each N. macropterus assigned population (A-G). Sample size (n) is indicated above each graph. All populations are skewed to the left, with most SNPs sitting between 0.0-0.1.*

7.4 Read depth and missing data in the SNP data set

Analysis of read depth showed that most loci had low coverage concentrated between 0–50 reads, with an upper threshold set at 100 reads to exclude loci with excessive coverage (Supplementary Figure 2). Missing data analysis on the raw data, revealed that approximately 26% of loci had missing genotype calls (missing rate = 0.259), while individual call rates were generally high (>0.9), these were then filtered out. Filtering on read depth and missing data parameters ensured robust genotype calling across all samples.

7.5 Genotype composition and heterozygosity across the genotyped individuals

A smear plot visualized genotype calls across loci, showing that most individuals were homozygous for the reference allele, with fewer heterozygous and homozygous alternate genotypes (Figure 8). Observed heterozygosity clustered narrowly around ~0.15, indicating a lower genetic variability across the whole data set (Supplementary Figure 3). Filtering based on heterozygosity thresholds (<0.20) further support a homogeneous population.

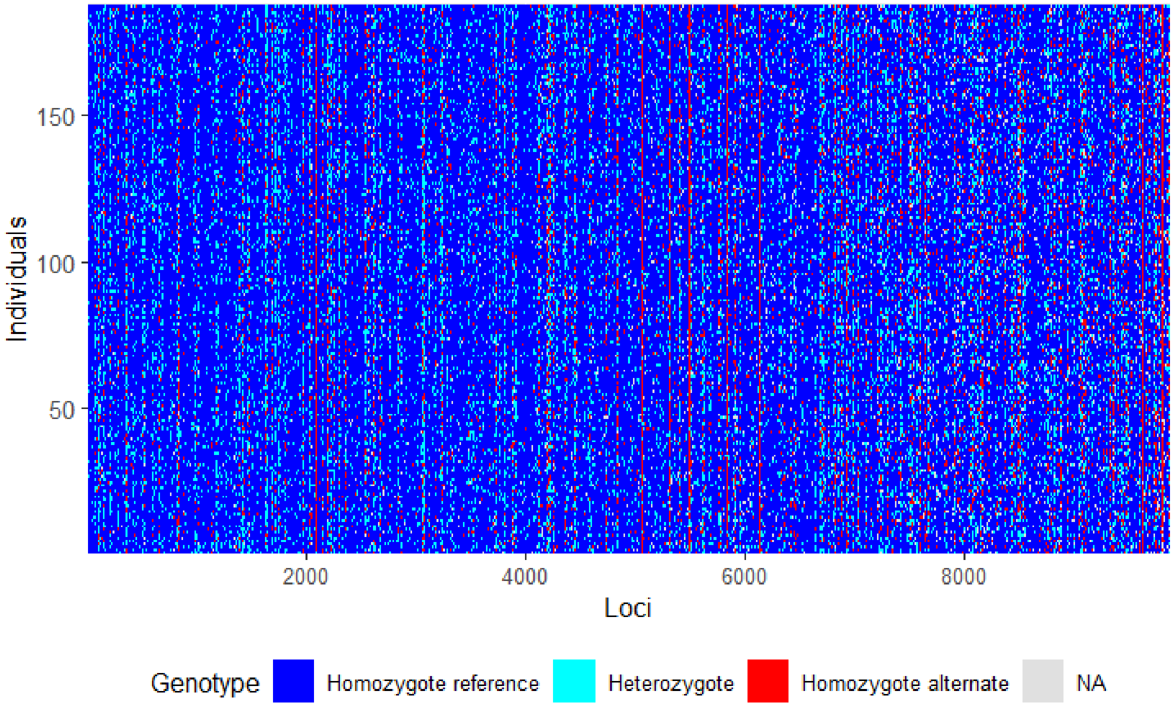

Figure 8*. Smear plot of individuals across 9,879 polymorphic loci genotyped in the 187 N. macropterus individuals. Blue represents the homozygote reference, cyan with heterozygote reference and red, a homozygote alternative. Missing data is shown in white, where some loci have low call rate, and some individuals have low call rate.*

7.6 Genetic diversity metrics per latitudinal population

Genetic diversity was assessed using observed heterozygosity (H_o), unbiased expected heterozygosity (uH_e), and allelic richness ($q = 0$) metrics. Across populations, H_o values were consistent (0.150), while uH_e values were slightly higher (0.20), reflecting a deficiency of observed heterozygotes compared to expectations under HWE assumptions (Table 3). Allelic richness was slightly lower in Population G, which had the smallest sample size of all latitudinally split populations ($A_R = 1.754$). Allelic richness for Populations A-F sat at around 1.90.

Table 3. *Summary of measures of genetic diversity based on 9,879 SNPs of N. macropterus across the South East waters of Australia, according to latitudinal 'populations'.*

Population							
Code	**Latitude**	**N**	**$N_{polyloci}$**	**A_R**	**Ho**	**He**	**F_{IS}**
A	-36°	27	8908	1.902	0.147	0.188	0.195
B	-37°	27	8924	1.903	0.146	0.186	0.199
C	-38°	31	9144	1.926	0.148	0.189	0.198
D	-39°	26	8791	1.890	0.147	0.188	0.191
E	-40°	29	9052	1.916	0.148	0.189	0.191
F	-41°	35	9277	1.939	0.148	0.189	0.191
G	-42°	13	7448	1.754	0.150	0.182	0.166

The number of samples per latitude and the corresponding code, N = number of individuals sampled, the number of polymorphic loci ($N_{polyloci}$), the observed (Ho) and expected (He) heterozygosity, the inbreeding coefficient (F_{IS}), and allelic richness (A_R).

7.7 Latitudinal Population Comparisons

The Alpha diversity, which measures genetic variation within the overall population data set through assessing allele richness or heterozygosity (Ma et al. 2020), P was low (= 0.319).

Beta diversity, which quantifies genetic differences between populations (Ma et al. 2020), (here equivalent to the 'latitudinal populations'). Population G had the fewest polymorphic loci (7,448) and smallest allelic richness (1.754), likely due to sample size (n = 13). Comparatively, Population F had the largest sample size (n = 35), and number of polymorphic loci (9,277), with an allelic richness of 1.939. This could suggest subtle differences in genetic composition influenced by geographic or demographic factors; however, it is more likely attributed to the sample size of Population G being at least 50% smaller than the other six 'populations'.

Table 4. *Shannon Information (q = 1) for beta diversity of N. macropterus using SNP data.*

	A	B	C	D	E	F	G
A	*	0.053	0.051	0.055	0.053	0.049	0.070
B	0.012	*	0.051	0.055	0.052	0.049	0.070
C	0.009	0.010	*	0.053	0.049	0.046	0.068
D	0.011	0.012	0.010	*	0.053	0.050	0.071
E	0.010	0.011	0.009	0.011	*	0.047	0.069
F	0.010	0.011	0.008	0.010	0.009	*	0.067
G	0.018	0.019	0.017	0.019	0.017	0.017	*

Below diagonal; pairwise beta diversity values. Above diagonal: standard deviations.

7.8 Principal Component Analysis (PCA)

The PCA indicated no population structure, with PC1 and PC2 explaining only ~0.7% of genetic variance each (Figure 9). The lack of distinct clustering suggests minimal genetic differentiation among individuals.

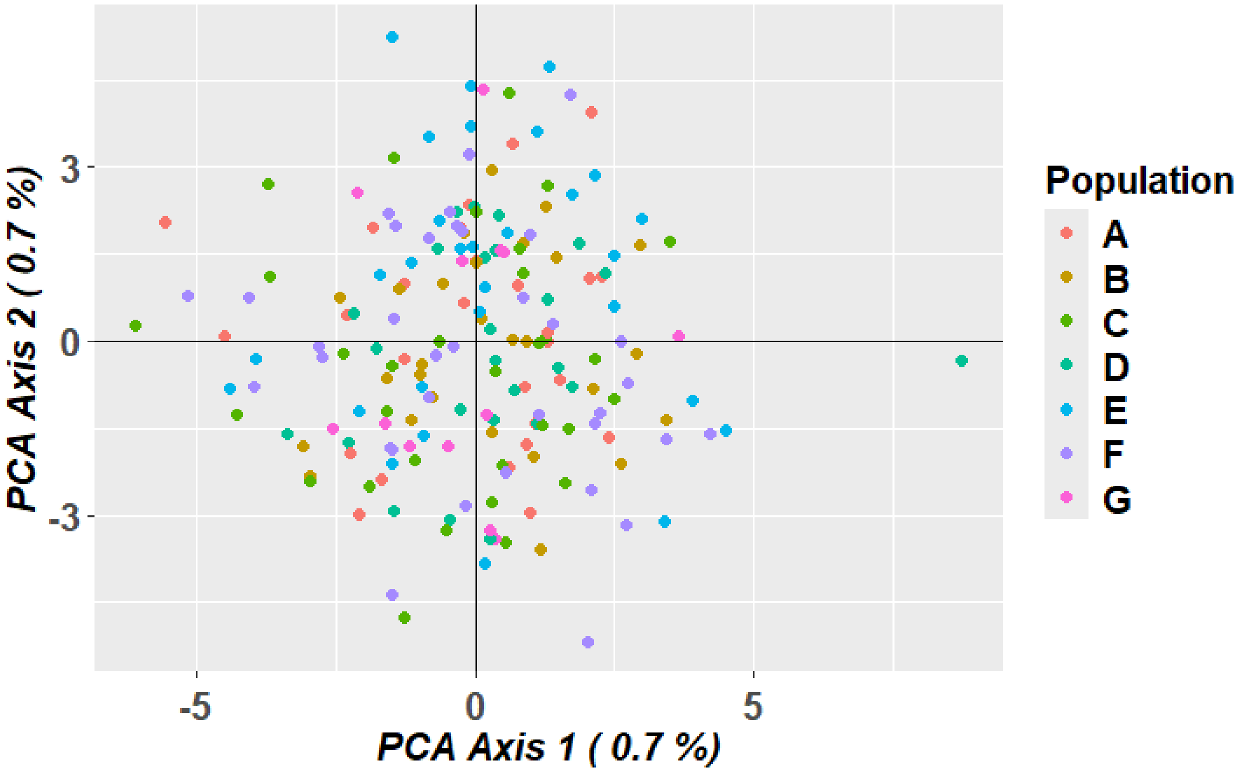

Figure 9. *PCA plot based on SNP data from N. macropterus in South East Australian waters. Each point represents an individual, assigned populations (represented by colours) are divided by latitude.*

7.9 Discriminant Analysis of Principal Components (DAPC)

A DAPC was run for an alternative assessment of the population clustering as the model used differs from PCA analysis, as it maximises separation using pre-defined groups (Miller et al. 2020). Initial plots of variances explained by PCA, the value of Bayesian Information Criterion, (BIC; a statistical tool used to determine the optimal number of genetic clusters (*k*) in the data), versus number of inputted clusters (7), and discriminant analysis eigenvalues (DF = 2) were generated. The DAPC was run with 7 clusters, 25 PCs and 3 discriminant functions (Figure 10).

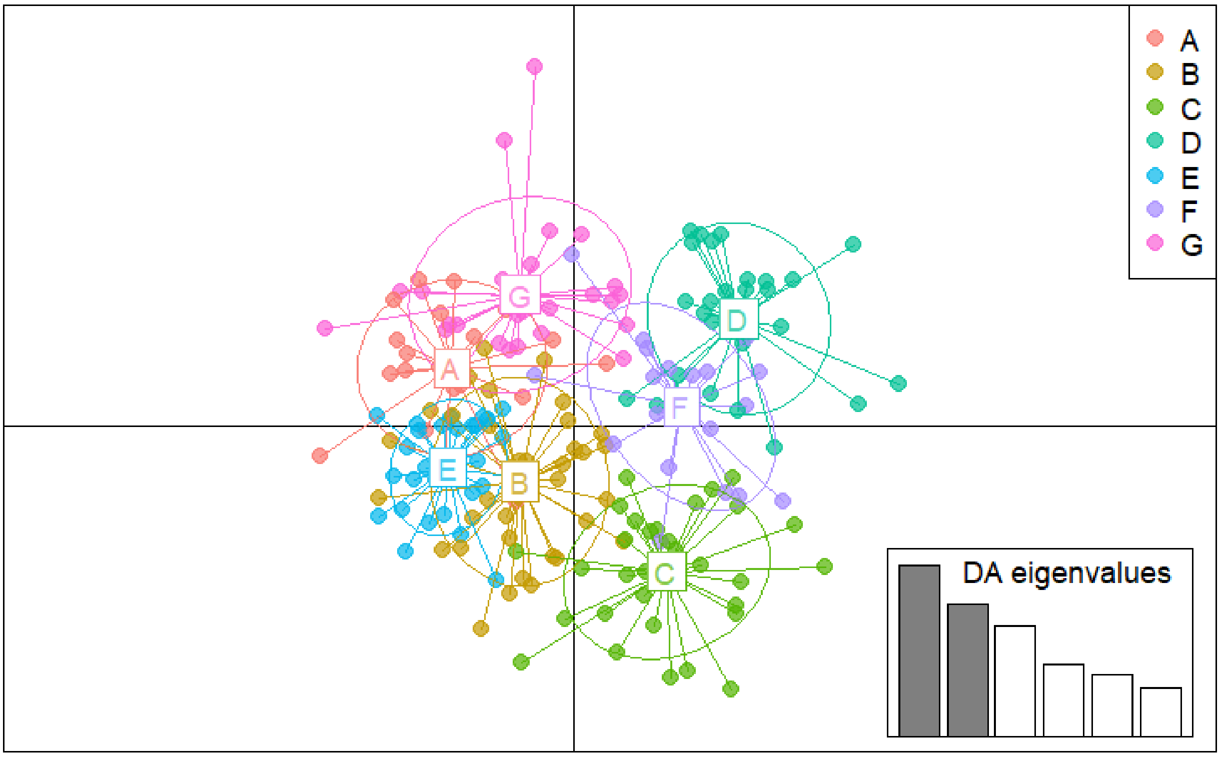

Figure 10. *DAPC plot of N. macropterus in South East Australian waters. Each dot is an individual, with colours representing a genetic cluster. The letters indicate the mean position of each group, the ellipses around each group show the dispersion and spread of individuals within the group. The DA Eigenvalues shows the relative contribution of each discriminant function (axes x and y) to the overall discriminant among groups. Assigned populations to the data set (A through to G) are represented as colours.*

8.0 Analysis of Molecular Variance – AMOVA

The AMOVA (Table 5) revealed minimal genetic differentiation among pre-defined populations of *N. macropterus*, with 0.03% of total genetic variation (Φ_{ST} (which can be interpreted as F_{ST}) = 0.0003), separated among populations and 99.7% occurring among individuals within populations (F_{IS} = 0.233).

Table 5. *Analysis of Molecular Variance (AMOVA) results for N. macropterus based on assigned latitudinal populations.*

Source of Variation	**Sum of Squares**	**Variance Components**	**% of Variation**	**F-Statistic**
Among populations	0.623	0.0003	0.03%	F_{ST} = 0.0003
Among individuals within populations	441.874	0.2325	99.70%	F_{IS} = 0.2325
Within individuals	1458.792	-	-	-
Total	-	0.2327	100%	-

Pairwise FST genetic differences are presented with their p-values (following 1000 bootstraps) in Table 6. This analysis revealed no significant differentiation among populations once Bonferroni corrections were conducted. For example, while the uncorrected p-value for the comparison between populations C and E was 0.004, the Bonferroni-adjusted significance threshold (0.05/21 pairwise comparisons ≈ 0.002) rendered this non-significant. Similarly, pairwise comparisons involving population G yielded FST values of 0.001, but none approached significance, even before **correction.** These low FST values (many pairwise comparisons were 0.000), combined with the minimal population-level structure (FST = 0.0003), reflect a single panmictic population and suggest high gene flow (or recent divergence across the sampled range). All analyses conducted herein have indicated a panmictic population structure along the southeast coast of Australia. Therefore, putative drivers of structure such as sex, cohort, and temporal sampling were not examined further in the dataset.

Table 6. *Pairwise genetic differences calculated from SNPs of N. macropterus. A correction factor for multiple comparisons has been considered for P values.*

	A	**B**	**C**	**D**	**E**	**F**	**G**
A	*	0.241	0.386	0.261	0.340	0.139	0.134
B	0.000	*	0.317	0.338	0.444	0.294	0.115
C	0.000	0.000	*	0.153	0.004	0.582	0.159
D	0.000	0.000	0.000	*	0.386	0.256	0.097
E	0.000	0.000	0.001	0.000	*	0.648	0.076
F	0.000	0.000	0.000	0.000	0.000	*	0.169
G	0.001	0.001	0.001	0.001	0.001		*

Above diagonal; p-values, below diagonal; pairwise F_{ST} values. P-values calculated following 1000 bootstraps.

8. Discussion

Population genomics offers the detailed genetic information required to more accurately predict how populations respond to environmental and anthropogenic changes, providing valuable insights for addressing and managing these impacts on important marine resources (Oleksiak & Rajora 2019). In this study, the population genomics of *N. macropterus* within the SESSF was analysed, building on the last major genetic evaluation conducted in 1994 by Ward and Elliot. Through analysing samples collected during the 2023–2024 SEA_MES voyages, this study resolved the longstanding uncertainties regarding the species' latitudinal structuring. The findings presented here provide updated insights into the genomic population structure of *N. macropterus*. Integrating these genomic insights into management can improve the accuracy of stock assessments and support the long-term sustainability and recovery of Australian *N. macropterus* stocks.

8.1 Key Genomic Findings in *N. macropterus* from eastern Australia

The investigation of *N. macropterus* in South Eastern Australian waters revealed no significant population structure, with individuals forming a single panmictic population. Genetic diversity, measured by heterozygosity, showed a narrow range (0.150) across all sampled groups (Supplementary Figure 3). Principal Component Analysis, a conservative method for exploring genetic structure without prior group assumptions (Miller et al. 2020), supported this finding: the first principal components explained minimal variance (0.7% each), and no clear clustering was observed among individuals (Figure 9). In contrast, DAPC, which maximized between-group differences using predefined clusters (Miller et al. 2020), highlighted subtle divergence in Population C (Figure 10), despite overlapping genetic distributions among the other populations. This aligns with Miller et al. (2020), suggesting that DAPC's reliance on group priors can artificially amplify minor genetic differences, particularly in species with high gene flow. The eigenvalues from DAPC further emphasised that discriminatory power was concentrated in the first two dimensions, highlighting the limited biological differentiation.

The F_{ST} (0.0003 from the AMOVA; 0.0004 panmictic dataset) was not significant and indicated a lack of genetic differentiation between populations, consistent with high connectivity and gene flow typical of marine species with broad dispersal (Holsinger & Weir 2009). Conversely, the F_{IS} (0.2325 from the AMOVA; 0.2325 panmictic dataset) potentially suggested inbreeding or cryptic sub-structure, however, this is more likely a reflection that larger sample sizes per latitudinal grouping (and hence increased sampling of the variation present in the population) would be required (particularly for Population G). Furthermore, the panmictic population structure detected from other analyses (e.g., PCA, AMOVA, connectivity tests) contradicts localised inbreeding. Similar patterns were observed in a genomic study of skipjack tuna (*Katsuwonus pelamis*) in the tropical Western and Central Pacific Ocean, which has historically been assumed to be panmictic (Anderson et al. 2020). The study attributed panmixia to the species very large population size, high reproductive output, rapid growth and early maturity, high mobility, and the absence of barriers to movement or breeding—all of which promote extensive gene flow and genetic mixing (Anderson et al. 2020).

While small but significant pairwise F_{ST} values emerged, clustering analyses, heterozygosity measures, and AMOVA supported a panmictic population. This parallels the findings of this study, where minor allele frequency (MAF) distributions across *N. macropterus* groups suggested shared genetic heritage (Figure 7).

The smaller sample size in Population G limits any further analyses or extrapolation. The broader conclusions based on the genomic SNPs screened in the 187 individuals, indicate panmixia and genetic homogeneity across the sampling areas. The among-individual variance (99.7%) highlights low genetic diversity within *N. macropterus*, with only 0.03% of total genetic variance occurring between the pre-defined populations. Future studies should prioritise balanced sampling and adaptive locus analysis to disentangle neutral and selective processes. Overall, genomic analyses support a panmictic population structure for *N. macropterus* in southeastern Australia, with high gene flow outweighing subtle signals of divergence.

8.2 Updated *N. macropterus* assessment in context of previous genomic studies

In this study, a comprehensive analysis of *N. macropterus* across southeastern Australian waters revealed no significant population structure, with 187 individuals screened using 9,879 SNPs (from 77,794 unfiltered SNPs), and multiple analytical methods. These findings align with earlier studies; Richardson (1982) supported spatial and temporal genetic stability, analysing 374–510 individuals across south-eastern Australia using five polymorphic allozyme loci (*ADA, ADH*, GPI-1, PGDH, PGM-2; Ho = 0.15). Elliot & Ward (1994) further examined 33 enzyme loci in Australian and New Zealand samples, reporting 10.1% (Ho = 0.101) average heterozygosity and minimal differentiation within Australia (0.17% variation attributed to sampling error). Collectively, these results suggest long-term genetic homogeneity in southeastern Australian *N. macropterus*, contrasting with subtle divergence in New Zealand, where distinct populations may have occurred as a result of passive gene flow. It should also be noted that the observed heterozygosity values from SNP, protein, and microsatellites are not directly comparable due to differences in mutation rates, selection, and genomic context (Allendorf et al. 2013). Recent research by Papa et al. (2022) conducted a genome-wide analysis of 175 *N. macropterus,* (also referred to as terakihi) from New Zealand and Tasmania and identified 7.5 million SNPs, (pruned dataset of 183,443 for downstream analysis), which were used to assess population structure and local adaptation. The study found a weak but significant divergence between New Zealand and Tasmania (F_{ST} = 0.0054–0.0073, $p \leq 0.050$*)*, supporting the hypothesis of two stocks within the Tasman Sea (Papa et al. 2022). Similar to the current study, (in which an overall F_{ST} = 0.0003 was observed), in New Zealand alone, no population structure was detected ($F_{ST} < 0.001$, $p = 0.770$) in *N. macropterus* populations. The genetic homogeneity observed in South Eastern Australian *N. macropterus* populations, supported by both historical allozyme studies and modern genomic SNP analyses suggests the presence of a single panmictic stock.

8.3 The ecology and behaviour of *N. macropterus* driving panmixia

The extended pelagic larval duration (PLD) of *N. macropterus* (9–12 months) facilitates extensive offshore dispersal, with larvae occupying surface waters of the southwestern Tasman Sea and adjacent oceanic regions (Bruce et al. 2001). Spawning occurs in mid to outer shelf waters, and larvae remain concentrated in surface layers, a behaviour that promotes offshore transport via currents such as the East Australian Current (EAC) (Kailola et al. 1993; Bruce et al. 2001). Oceanographic features, such as eddies, promote widespread larval dispersal across hundreds of kilometres, resulting in an extensive distribution of homogenous genetic material across spatial scales (Bruce et al. 2001). Interannual variability in stratification and current strength has minimal impact on larval retention, supporting consistent gene flow between geographically separated adult populations (Kailola et al. 1993; Bruce et al. 2001). This prolonged larval phase, combined with passive dispersal in surface currents, enables mixing across putative stock boundaries, supporting panmixia (Bruce et al. 2001; Jordan 2014; AFMA 2023). Despite adults inhabiting demersal coastal and continental shelf environments (rocky reefs, sandy habitats to 400m depth; Wayte 2013; Ludt et al. 2019), the lack of physical dispersal barriers and broad larval connectivity likely drive genetic homogeneity (Jordan 2014; Bessell-Browne et al. 2021). Genomic studies (here and elsewhere) further confirm panmixia with subtle adaptive divergence linked to temperature gradients rather than geographic isolation (Papa et al. 2022).

A parallel can be drawn with the European eel *(Anguilla anguilla*), which also exhibits a long pelagic larval stage, with larvae transported thousands of kilometres from the Sargasso Sea to European and North African coasts over a period estimated at 7–12 months, and potentially up to two years (Deelder 1984; Dannewitz et al. 2005; Huang et al. 2005; Bonhommeau et al. 2010). Spawning occurs in a single oceanic location, and larvae drift with major ocean currents, resulting in widespread mixing and gene flow across the species' range (Dannewitz et al. 2005; Huang et al. 2005; Bonhommeau et al. 2010). Whole-genome and microsatellite analyses consistently reveal extremely low genetic differentiation among continental samples (global $F_{ST} = 0.0014$), no significant isolation by distance, and no evidence of persistent population substructure, supporting the hypothesis of a single, panmictic population (Dannewitz et al. 2005; Huang et al. 2005). This pattern is attributed to the species' long pelagic larval stage, the absence of physical barriers during larval dispersal, and the homogenising effect of large-scale oceanographic processes, closely paralleling the mechanisms described for *N. macropterus*.

8.4 Reliability of SNPs

Single nucleotide polymorphisms are highly sought after for marine population genomics due to their genome-wide abundance, reproducibility in high-throughput sequencing, and have the capacity to detect fine-scale genetic structure and adaptive divergence (Rasal et al. 2017).

However, SNP data requires the correct filtering and examination to provide robust results, particularly for studies with low genetic structure (Larson et al. 2021). Rigorous filtering and the removal of loci with missing data is essential when conducting population structure analysis (Larson et al. 2021). Following the recommendation outlined in Larson et al. (2021), and to ensure the *N. macropterus* data was robust and assisted with providing a clear understanding of the potential population structuring, thresholds specific for the data which filtered out lower quality SNPs (Supplementary Table 2) were applied. Correct data handling and filtering are vital for SNP analysis and the accurate representation of genetic patterns, allowing for accurate scientific conclusions to be made.

8.5 Limitations of current study and SNP analyses

This study aimed to resolve spatial and temporal population connectivity patterns in *N. macropterus* within the SESSF using genomic data collected across three voyages (2023–2024). While the sampling design incorporated individuals from multiple size classes, uneven sample sizes across latitudinally defined "populations" introduced potential biases, notably, Population G (-42° latitude, Tasmania) comprised only 13 individuals compared to approximately 27 samples per other assigned populations. Small sample sizes reduce statistical power to estimate genetic diversity accurately and increase variance in allele frequency estimates (Bailey & Smith 1981), potentially obscuring subtle population structure. Further analytical limitations may have arisen from SNP filtering protocols: stringent thresholds (MAF ≥ 0.1; missing data $\geq 90\%$) removed ~86% of loci, consistent with previous studies demonstrating that such filters disproportionately eliminate rare alleles and reduce resolution for fine-scale genetic differentiation (Nazareno & Knowles 2021). For small or recently diverged populations, including Population G, this loci loss may have reduced signals of subtle structure, as rare alleles critical for detecting localized divergence are often excluded. While these filters improve data quality by removing low-confidence variants, the trade-off between noise reduction and marker retention requires careful consideration in systems where weak differentiation is anticipated. Alongside these technical and sampling challenges, there are broader limitations to effectively applying genomic approaches in fisheries management.

Although DNA provides a significant range of information applicable to fisheries management, it represents only one aspect of the knowledge required for policymaking (Bernatchez et al. 2017). The acquisition of high-quality genomic data can also be expensive and time-consuming (Andersson et al. 2023), and the interpretation of such data requires robust analytical software and expertise that may not be available in all management contexts (Andersson et al. 2023). Finally, standardized protocols are necessary to ensure that genomic data is comparable across studies and regions, allowing for accurate and meaningful conclusions to be drawn (Benestan 2019).

8.6 Implications for *N. macropterus* fishery management

Understanding the genetic structure of marine species and the connectivity patterns which are defined over spatial and temporal scales should be considered in the design and implementation of management strategies (Grandra et al. 2021). The amount of genetic diversity within and among populations, influences species ability to adapt to environmental and anthropogenic pressures (Grandra et al. 2021). This study has revealed a panmictic stock structure (across samples from 2023 and 2024) consistent with previous work that stock assessments have been based on. While comparing the Western stock to the Eastern stock and population connectivity, was outside the scope of this study, currently based on jurisdiction, the populations are managed separately. In the SESSF, *N. macropterus* is managed as a Tier 1 stock under the Harvest Strategy Framework, with the stock classified as 'depleted', and the stock is considered to be recruitment impaired (AFMA 2021). Currently management strategies for *N. macropterus* in the SESSF include a quota system, with both total allowable catch (TAC) limits and individual fisher quotas (AFMA 2023). Fishery closures were also implemented along the East Coast of Australia (AFMA 2021). These measures have all been based on the assumption of a single Eastern stock. The genomic findings of this study support the current single-stock management approach for *N. macropterus* in the SESSF, providing an updated scientific understanding to the genomic population structure, which is important for ongoing conservation efforts.

8.7 Future Directions

To advance our understanding of *N. macropterus* population dynamics within the SESSF, future studies should prioritize expanded spatiotemporal sampling across its distribution to include both the Eastern and Western stocks. Increased geographic coverage, increased sample sizes, and repeated sampling over time would help disentangle the relative contributions of environmental gradients (e.g., temperature, currents) and demographic processes (e.g., recruitment variability) to observed genetic diversity patterns. Integrating high-resolution genomic data with life-history traits (e.g., spawning behaviour) could further assist with the understanding of stock boundaries. Finally, adopting adaptive management frameworks that are built on a holistic approach which combines biological data, with fishery impacts, and environmental variables will continue to enable *N. macropterus* stocks to be managed appropriately. This approach would enable adjustments to harvest strategies, ensuring genetic diversity while balancing fishery sustainability.

9. Conclusion

This study provides an updated genomic perspective on the population structure of *N. macropterus* in the SESSF. Based on 9,879 nuclear SNPs screened in 187 *N. macropterus* individuals sampled during 2023 and 2024, the null hypothesis was accepted thereby confirming a largely panmictic stock with no genetic differentiation across South Eastern Australian waters. These findings reinforce the scientific basis for the current single-stock management approach, supporting ongoing conservation and recovery strategies for this depleted species. However, the study also highlights critical methodological and sampling limitations, particularly regarding uneven and small sample sizes. Moving forward, a more comprehensive fisheries management approach that expands spatio-temporal sampling, integrates genomic data with ecological and fishery information, and adopts adaptive management frameworks would be of interest. Such strategies can enhance the resolution of population connectivity, ensure the robustness of stock assessments, and better preserve the genetic diversity important for the long-term resilience and sustainability of *N. macropterus* in Australian waters.

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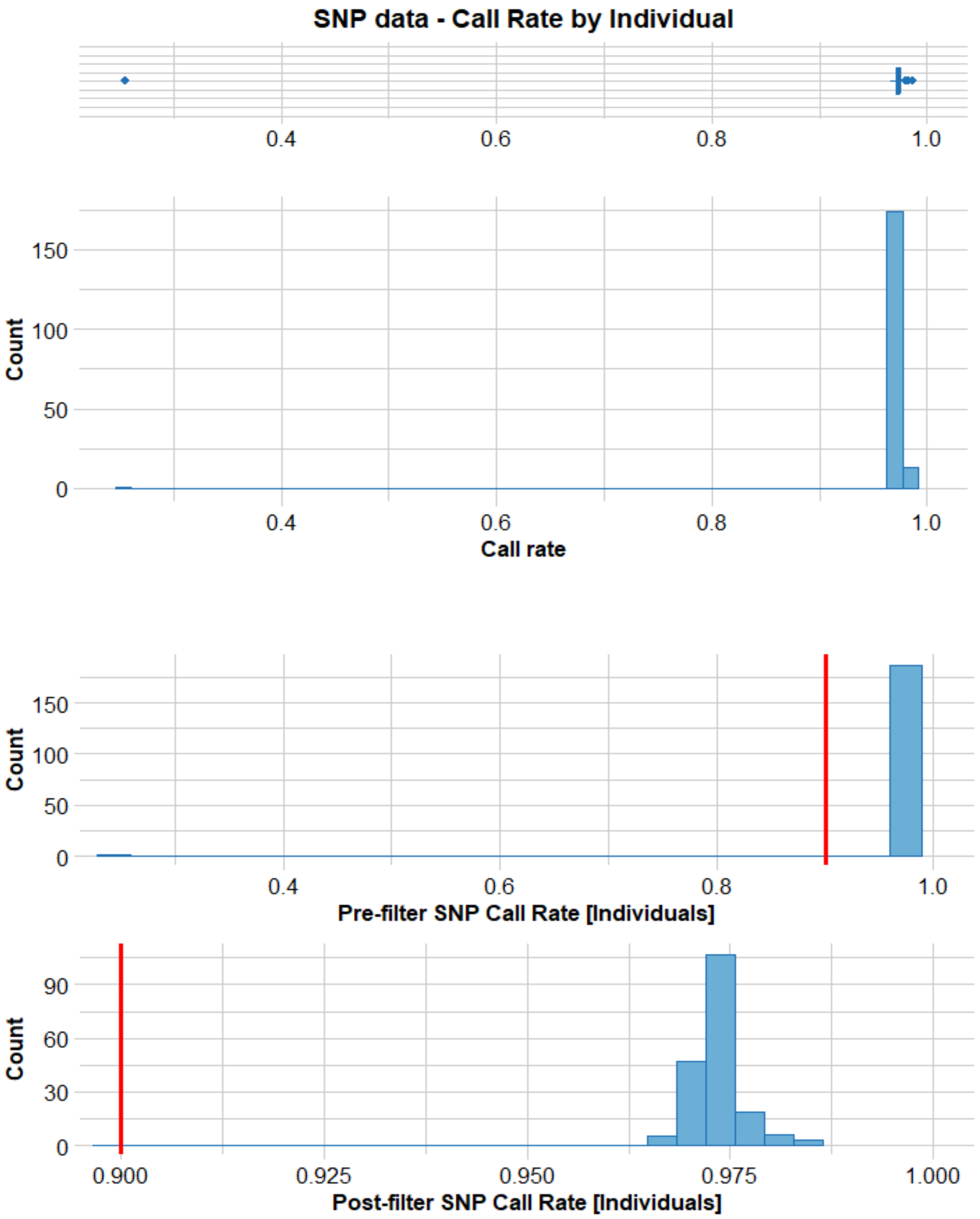
Appendix 1.

Supplementary Table 1. *Sample sites and individual sample information for N. macropterus from SEA_MES voyages 2023-2024.*

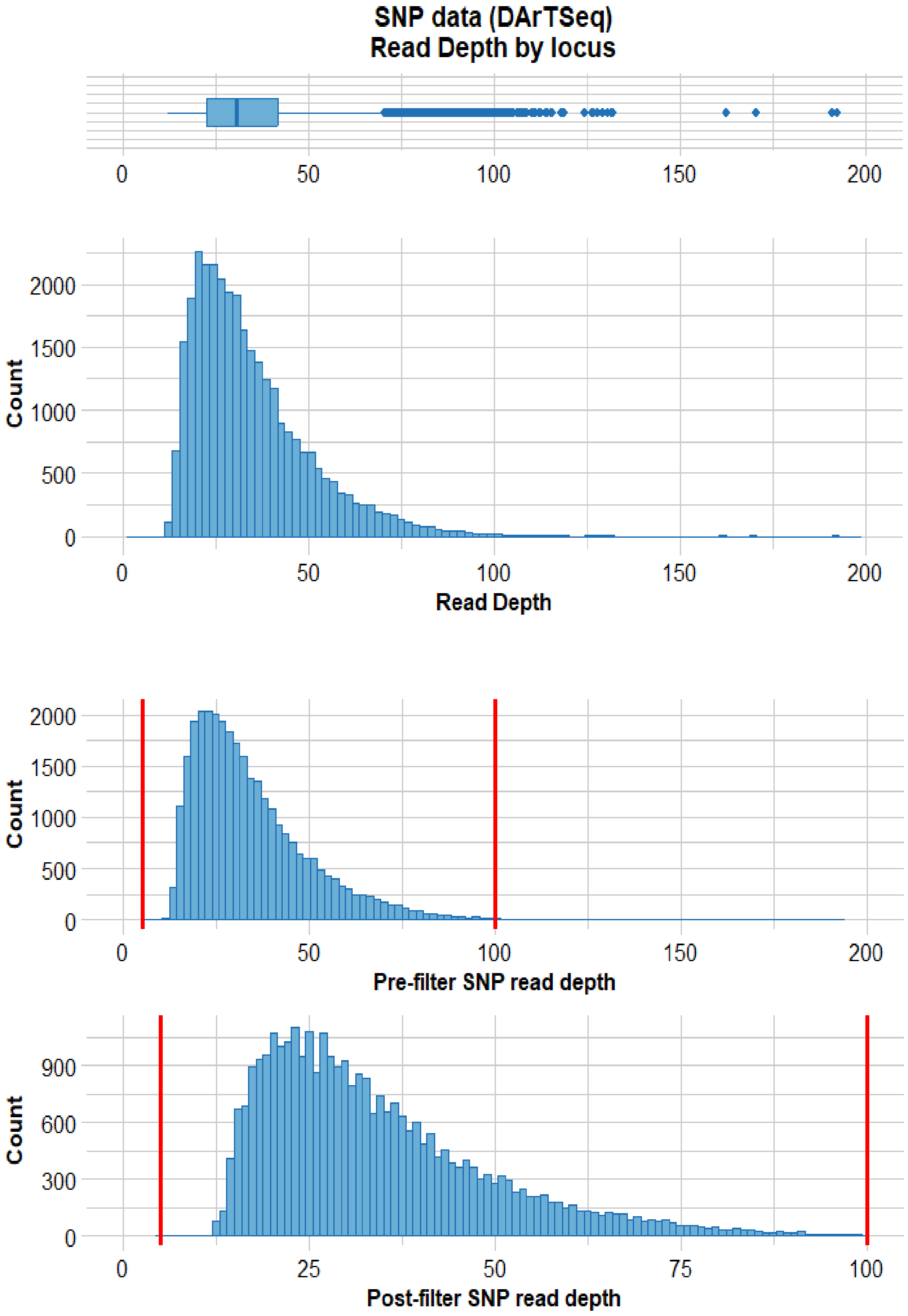
Survey Ops	Site	Latitude	Number of samples
IN2024_V03_216	N31.1	-36	4
IN2024_V03_223	N31.3	-36	4
IN2024_V03_227	N33.2	-36	3
IN2024_V03_238	N37.3	-36	5
IN2024_V03_244	N37.2	-36	1
IN2024_V03_248	N39.1	-36	1
IN2024_V03_256	N39.2	-36	1
IN2024_V05_122	N19.2	-36	8
IN2024_V03_151	N27.1	-37	6
IN2024_V03_186	N21.1	-37	2
IN2024_V03_153	N27.2	-37	5
IN2024_V03_141	N29.2	-37	1
IN2024_V03_184	N21.2	-37	1
IN2024_V03_171	N19.2	-37	3
IN2024_V03_197	N23.2	-37	1
IN2024_V05_065	N9.1	-37	8
IN2024_V03_131	N15.3	-38	4
IN2024_V03_096	N7.2	-38	4
IN2024_V03_095	N7.1	-38	2
IN2023_V05_187	N23.2	-38	9
IN2024_V05_050	N33.1	-38	7
IN2024_V05_048	N33.2	-38	1
IN2023_V05_188	N23.1	-38	1
IN2024_V03_133	N15.2	-38	3
IN2024_V03_076	N3.2	-39	8
IN2024_V03_072	N3.1	-39	3
IN2024_V05_032	N37.3	-39	1
IN2024_V05_040	N3.2	-39	1
IN2024_V05_034	N37.1	-39	1
IN2024_V05_202	N5.3	-39	2
IN2024_V05_209	N35.2	-39	2
IN2023_V05_043	N7.2	-39	8
IN2024_V05_245	S9.3	-40	2
IN2024_V03_045	S9.1	-40	4
IN2024_V03_056	S11.2	-40	2

IN2024_V03_047	S9.3b	-40	1
IN2024_V03_053	S11.1	-40	1
IN2024_V03_066	N1.1	-40	1
IN2024_V03_043	S9.2	-40	1
IN2023_V05_215	S2.2	-40	6
IN2023_V05_214	S2.1	-40	3
IN2023_V05_024	N3.1	-40	1
IN2024_V05_222	N1.1	-40	7
IN2024_V03_034	S7.2	-41	5
IN2024_V03_037	S7.3	-41	2
IN2023_V05_233	S5.1	-41	1
IN2024_V05_022	S5.2	-41	8
IN2024_V05_015	S3.2	-41	2
IN2024_V05_251	S11.1	-41	5
IN2024_V05_253	S11.2	-41	10
IN2024_V05_255	S11.3	-41	2
IN2023_V05_244	S6.1	-42	5
IN2024_V05_007	S1.1	-42	7
IN2024_V05_005	S1.2	-42	1

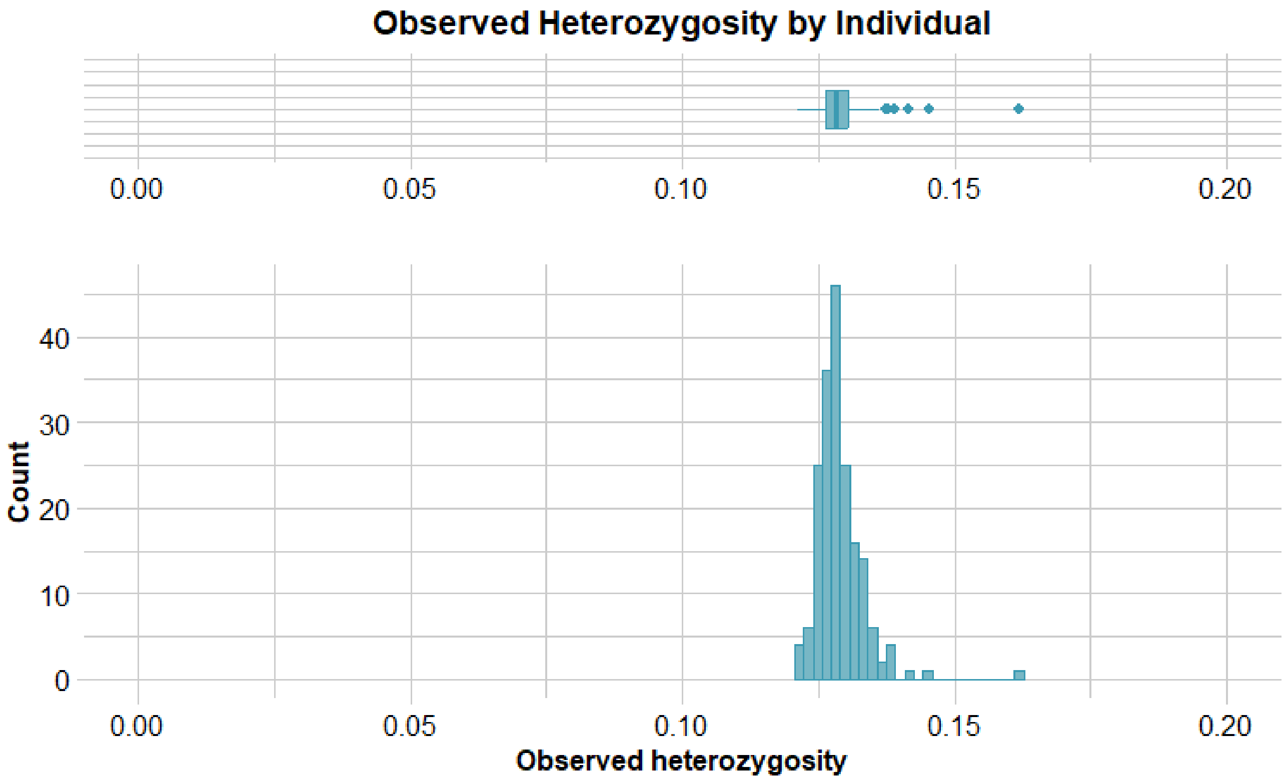
Survey operations from CSIRO SEA_MES voyages one, two and three. Sampling locations and latitudes correspond to the maps in Figures 1 and 2. The number of samples refers to the individuals sampled at each site.



***Supplementary Figure 1**. Individual call rate for SNPs using N. macropterus data. A: reported call rate. B: filtered call rate. The threshold was set to 0.9. One individual ‘10098639’ is a clear outlier and was removed in the filtering. 187 individuals remained.*



Supplementary Figure 2*. Read depth for SNPs using N. macropterus data. A: reported read depth. B: filtered read depth. The lower threshold was set to 5, the upper threshold was set to 100.*



Supplementary Figure 3. *Observed heterozygosity by individual N. macropterus, reported and filtered with a lower limit of 0, and an upper limit of 0.20. The observed heterozygosity values were clustered around a narrow range of ~0.10-0.15.*

Supplementary Table 2. Filtering thresholds applied to the SNP N. macropterus dataset.

Filtering step	Threshold	SNPs	Individuals
start (pop metadata)		77794	188
av repro	0.98	76560	188
MAF	0.2	31605	188
readdepth	lower = 5, upper = 100	31543	188
callrate(loci)	0.9	13959	188
callrate(ind)	0.9	13959	187
monomorphic loci removed		0	0
heterozygosity ind	lower = 0, upper = 0.20	13959	187
linked loci	best	9879	187

Table of the filtering steps with the corresponding threshold applied, the SNP count, and individuals after each filtering process. Downstream analysis was completed using 9879 SNPs, from 187 individuals.

Appendix 2.

Table 2.1. Metadata table for N. macropterus samples from SEA_MES voyages 2023-2024, inclusive of individual ID, population assignment, latitude and longitude, sex and length in mm.

Individual ID	Population	Latitude	Longitude	Sex	Lengths_mm
10095985	A	-36.942913	150.232886	na	321
10095997	A	-36.942913	150.232886	na	282
10096121	A	-36.942913	150.232886	na	253
10096151	A	-36.942913	150.232886	na	315
10095174	A	-36.860557	150.295874	na	231
10095204	A	-36.860557	150.295874	na	238
10095998	A	-36.860557	150.295874	na	248
10096064	A	-36.860557	150.295874	na	248
10095888	A	-36.860351	150.123467	Female	313
10095858	A	-36.860351	150.123467	Female	269
10095977	A	-36.860351	150.123467	Male	297
10097490	A	-36.52339	150.282853	Female	230
10097499	A	-36.52339	150.282853	Male	219
10097521	A	-36.52339	150.282853	Female	243
10097530	A	-36.52339	150.282853	Male	219
10097608	A	-36.52339	150.282853	Female	257
10097319	A	-36.396284	150.258536	na	374
10098735	A	-36.380186	150.333916	na	245
10098684	A	-36.26531	150.331339	na	252
10098774	A	-36.756202	150.278648	Male	254
10098665	A	-36.756202	150.278648	Female	262
10102907	A	-36.756202	150.278648	Male	233
10102477	A	-36.756202	150.278648	Male	268
10102915	A	-36.756202	150.278648	Male	254
10102899	A	-36.756202	150.278648	Male	264
10102910	A	-36.756202	150.278648	Male	256
10102937	A	-36.756202	150.278648	Male	267
10093847	B	-37.313615	150.19154	na	253
10093635	B	-37.313615	150.19154	na	255
10095937	B	-37.733376	150.066029	Female	269
10095847	B	-37.733376	150.066029	Female	292
10093768	B	-37.313615	150.19154	na	294
10093711	B	-37.326541	150.114655	Male	296
10093970	B	-37.140417	150.291077	Female	296
10093398	B	-37.326541	150.114655	Female	298
10096067	B	-37.741031	150.106897	Female	299
10093665	B	-37.313615	150.19154	na	299

10094329	B	-37.890447	149.987369	Female	301
10093516	B	-37.313615	150.19154	na	251
10094157	B	-37.890447	149.987369	na	331
10096029	B	-37.503616	150.183697	Male	331
10094076	B	-37.326541	150.114655	Female	333
10094265	B	-37.890447	149.987369	na	337
10093801	B	-37.313615	150.19154	na	338
10093430	B	-37.326541	150.114655	Female	350
10093638	B	-37.326541	150.114655	Female	364
10102943	B	-37.599212	149.8469	Male	252
10102973	B	-37.599212	149.8469	Female	264
10102940	B	-37.599212	149.8469	Male	246
10102894	B	-37.599212	149.8469	Female	278
10102893	B	-37.599212	149.8469	Male	265
10102970	B	-37.599212	149.8469	na	265
10102913	B	-37.599212	149.8469	Male	254
10102911	B	-37.599212	149.8469	na	246
10093520	C	-38.109721	149.321603	na	189
10092769	C	-38.879973	148.294572	Male	195
10092863	C	-38.879973	148.294572	Female	198
10093746	C	-38.109721	149.321603	na	212
10094059	C	-38.109721	149.321603	na	222
10092833	C	-38.879973	148.294572	Female	223
10093427	C	-38.109721	149.321603	na	215
10092398	C	-38.879973	148.294572	Female	229
10092851	C	-38.875465	148.413842	na	235
10092763	C	-38.875465	148.413842	na	246
10083862	C	-38.204931	149.304733	na	345
10083881	C	-38.204931	149.304733	na	259
10083884	C	-38.204931	149.304733	na	337
10083887	C	-38.204931	149.304733	na	306
10083892	C	-38.204931	149.304733	na	317
10083914	C	-38.204931	149.304733	na	341
10083919	C	-38.204931	149.304733	na	316
10084262	C	-38.204931	149.304733	na	336
10084391	C	-38.204931	149.304733	na	284
10098232	C	-38.878236	148.4092	na	207
10098231	C	-38.878236	148.4092	Male	243
10098685	C	-38.878236	148.4092	na	211
10098572	C	-38.878236	148.4092	Male	239
10098512	C	-38.878236	148.4092	Male	215
10098611	C	-38.878236	148.4092	Male	252
10098719	C	-38.863915	148.487671	Male	335
10098291	C	-38.878236	148.4092	Female	216

10091080	D	-39.537952	148.678491	Female	229
10091082	D	-39.537952	148.678491	Male	225
10091083	D	-39.537952	148.678491	Male	249
10091084	D	-39.537952	148.678491	Female	252
10091125	D	-39.537952	148.678491	Female	200
10091126	D	-39.537952	148.678491	Female	251
10091153	D	-39.537952	148.678491	Female	229
10091202	D	-39.537952	148.678491	Female	240
10091266	D	-39.487866	148.568563	na	254
10091274	D	-39.487866	148.568563	na	193
10091365	D	-39.487866	148.568563	na	205
10081662	D	-39.29805	148.65133	Female	372
10081663	D	-39.29805	148.65133	Female	340
10081721	D	-39.29805	148.65133	Female	325
10081722	D	-39.29805	148.65133	Female	373
10081727	D	-39.29805	148.65133	Female	336
10081856	D	-39.29805	148.65133	Male	359
10098636	D	-39.894756	148.75802	na	175
10098639	D	-39.475514	148.572277	Male	201
10098635	D	-39.948054	148.739887	Male	183
10098240	D	-39.042802	148.607127	Female	382
10098340	D	-39.042802	148.607127	Female	317
10109016	D	-39.296305	148.632432	Female	246
10109809	E	-40.595064	148.632432	Female	264
10108959	D	-39.296305	148.632432	Female	251
10089425	E	-40.680163	148.739391	na	206
10091102	E	-40.58287	148.7187	Female	205
10086122	E	-40.680163	148.739391	na	233
10090200	E	-40.57104	148.795779	Male	239
10089393	E	-40.680163	148.739391	na	240
10090653	E	-40.594909	148.714739	na	248
10091154	E	-40.333214	148.714739	na	236
10091175	E	-40.58287	148.7187	Female	247
10089424	E	-40.680163	148.739391	na	254
10089987	E	-40.628374	148.679936	na	270
10084401	E	-40.593473	148.732722	na	237
10080117	E	-40.593473	148.768471	Female	209
10083946	E	-40.593473	148.732722	na	243
10084003	E	-40.593473	148.732722	na	245
10085393	E	-40.579595	148.734445	na	254
10085205	E	-40.579595	148.734445	na	244
10080761	E	-40.044098	148.734445	na	266
10084589	E	-40.593473	148.734445	na	253
10082332	E	-40.593473	148.732722	na	264

10085248	E	-40.579595	148.734445	na	261
10109106	E	-40.340575	148.756774	Female	246
10108119	E	-40.340575	148.756774	Female	255
10108765	E	-40.340575	148.756774	Female	237
10109338	E	-40.340575	148.756774	Female	253
10108759	E	-40.340575	148.756774	Female	289
10108725	E	-40.340575	148.756774	na	274
10108744	E	-40.340575	148.756774	Male	260
10086169	F	-41.227653	148.439928	na	120
10086137	F	-41.227653	148.439928	na	128
10086370	F	-41.227653	148.439928	na	132
10086139	F	-41.227653	148.439928	na	133
10086202	F	-41.227653	148.439928	na	142
10086121	F	-41.215342	148.517978	na	265
10086401	F	-41.215342	148.517978	na	290
10084752	F	-41.788402	148.456731	na	305
10098606	F	-41.124056	148.405518	na	85
10098549	F	-41.124056	148.405518	na	166
10098779	F	-41.124056	148.405518	Female	145
10098521	F	-41.124056	148.405518	na	190
10098746	F	-41.124056	148.405518	na	172
10098632	F	-41.124056	148.405518	Male	154
10098519	F	-41.124056	148.405518	na	83
10098607	F	-41.781094	148.540289	Female	183
10098489	F	-41.781094	148.540289	Female	233
10098749	F	-41.124056	148.405518	Female	178
10109435	F	-41.641784	148.418549	na	88
10110036	F	-41.641784	148.418549	na	97
10110009	F	-41.641784	148.418549	na	169
10110039	F	-41.641784	148.418549	na	190
10110012	F	-41.641784	148.418549	Female	177
10110406	F	-41.723795	148.444162	Male	210
10110433	F	-41.723795	148.444162	Female	250
10110400	F	-41.723795	148.444162	Male	187
10109465	F	-41.723795	148.444162	Male	190
10083883	C	-38.211941	149.326626	na	366
10085895	G	-42.11222	148.526193	na	307
10085908	G	-42.11222	148.526193	na	324
10085909	G	-42.11222	148.526193	na	305
10085952	G	-42.11222	148.526193	na	304
10085987	G	-42.11222	148.526193	na	331
10098704	G	-42.070728	148.618075	Female	343
10098543	G	-42.070728	148.618075	Female	304
10098655	G	-42.070728	148.618075	na	306

10098672	G	-42.070728	148.618075	Female	380
10098210	G	-42.070728	148.618075	Female	335
10098734	G	-42.070728	148.618075	Female	383
10098669	G	-42.070728	148.618075	Female	356
10099130	G	-42.075914	148.482196	Female	168
10081694	D	-39.29805	148.65133	Male	365
10081719	D	-39.29805	148.65133	Female	344
10093736	C	-38.199809	149.307747	Female	360
10093676	C	-38.199809	149.307747	Female	369
10109495	F	-41.723795	148.444162	Male	207
10110403	F	-41.723795	148.444162	Female	189
10110430	F	-41.723795	148.444162	Female	244
10110449	F	-41.723795	148.444162	Male	191
10110436	F	-41.723795	148.444162	na	184
10107266	E	-40.595064	148.730607	Female	280
10109462	F	-41.723795	148.444162	na	195
10109432	F	-41.7186	148.487493	Male	194
10110063	F	-41.7186	148.487493	Male	250
10093487	C	-38.199809	149.307747	Female	397