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ORIGINAL ARTICLE

Estimation of effective number of breeders and effective population size in an abundant and heavily exploited marine teleost

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Abstract

Obtaining reliable estimates of the effective number of breeders (N_b) and generational effective population size (N_e) for fishery-important species is challenging because they are often iteroparous and highly abundant, which can lead to bias and imprecision. However, recent advances in understanding of these parameters, as well as the development of bias correction methods, have improved the capacity to generate reliable estimates. We utilized samples of both single-cohort young of the year and mixed-age adults from two geographically and genetically isolated stocks of the Australasian snapper (*Chrysophrys auratus*) to investigate the feasibility of generating reliable N_b and N_e estimates for a fishery species. Snapper is an abundant, iteroparous broadcast spawning teleost that is heavily exploited by recreational and commercial fisheries. Employing neutral genome-wide SNPs and the linkage-disequilibrium method, we determined that the most reliable N_b and N_e estimates could be derived by genotyping at least 200 individuals from a single cohort. Although our estimates made from the mixed-age adult samples were generally lower and less precise than those based on a single cohort, they still proved useful for understanding relative differences in genetic effective size between stocks. The correction formulas applied to adjust for biases due to physical linkage of loci and age structure resulted in substantial upward modifications of our estimates, demonstrating the importance of applying these bias corrections. Our findings provide important guidelines for estimating N_b and N_e for iteroparous species with large populations. This work also highlights the utility of samples originally collected for stock structure and stock assessment work for investigating genetic effective size in fishery-important species.

KEYWORDS
effective population size, fisheries genomics, fisheries management, genetic diversity, overfishing

1 | INTRODUCTION

Interest in estimating the genetic effective population size of exploited marine fishes continues to grow as fisheries scientists and managers pay increasing attention to the genetic state of fish stocks (Hare et al., 2011; Marandel et al., 2019; Ovenden et al., 2015). The two genetic effective size parameters, N_b (effective number of breeders) and N_e (effective population size), are applicable in a fisheries management context (Hare et al., 2011). The parameter N_b refers to the effective number of breeders in a single reproductive cycle, which provides important insight into eco-evolutionary processes taking place during reproduction (Waples, 1989, 2024; Waples & Antao, 2014). This parameter is largely shaped by the number and size of families contributing to the sampled cohort, which is influenced by factors like adult density, mate choice, individual variation in fecundity and reproductive success, and habitat quality and quantity (Whiteley et al., 2015). The parameter N_e represents generational effective population size, which is defined as the size of an idealized population experiencing the same rate of genetic drift or change in genetic diversity per generation as the focal population (Wright, 1931). This parameter is thus valuable for determining the effectiveness of selection and population viability, and for developing hatchery-based supportive breeding programs (Charlesworth, 2009; Hare et al., 2011). When N_e is low, increased rates of genetic drift cause genetic variation to erode, the effectiveness of selection to be reduced and deleterious alleles to become fixed, which all cause reductions in fitness, adaptive potential, and the probability of population persistence (Hare et al., 2011; Luikart et al., 2010). In exploited species, selective- or over-harvesting and environmental changes can lower N_e and N_b due to impacts on demographic parameters like census population size, sex ratios, and variance in reproductive success (Hare et al., 2011, Luikart et al., 2010).

Despite the value of effective size parameters in wildlife management, they have proven difficult to estimate accurately and precisely, particularly in abundant and iteroparous (i.e., multiple reproductive cycles over the course of a lifetime) marine species (Hare et al., 2011). This is because a considerable proportion of the census population size needs to be genotyped (>1%; Marandel et al., 2019), and also because age structure (Waples et al., 2014), population genetic structuring (Neel et al., 2013), and physical linkage (Waples et al., 2016) can bias estimates considerably. However, recent developments in understanding these biases, as well as improvements in effective size and confidence interval estimators, mean that our ability to generate accurate and precise estimates has increased considerably. The temporal and single-sample estimators are the most widely used methods for estimating effective size in marine populations (Marandel et al., 2019). However, the temporal method requires genotyping of at least two samples separated by time intervals much larger than the generation time of the focal population (in the case of species with overlapping generations), which is difficult to achieve for long-lived and late maturing species like many exploited marine teleosts (Waples, 1989). Single-sample estimators such as the linkage disequilibrium (LDN_e) method have therefore become increasingly popular due to their relative practicality (Marandel et al., 2019). The accuracy and precision of the LDN_e method has also recently been improved through the inclusion of options for screening out rare alleles and the addition of a jackknife confidence interval estimator (Do et al., 2014; Jones et al., 2016). Although employing large numbers of genetic markers (i.e., 1000s of SNPs) generally increases precision of effective size estimates, overprecision can occur due to the resulting large number of comparisons. However, the jackknife confidence interval estimator can be utilized to reduce such overprecision when using large SNP datasets (Jones et al., 2016).

Advances in understanding of the magnitude of the biases caused by age structure and physical linkage has led to the development of correction formulas. Waples et al. (2016) developed a formula incorporating information on chromosome number to correct for bias in effective size estimates due to physical linkage. Additionally, Waples et al. (2014) produced formulas integrating information on age at maturity and adult lifespan to correct for biases caused by age structure. Besides these bias corrections, it has also been demonstrated that the best approach for obtaining reliable effective size estimates is to employ a sample of individuals from a single cohort (Waples et al., 2014). Using the LDN_e method, a sample from a single cohort produces an estimate of N_b relating to the pool of parents that gave rise to the cohort. Generational N_e can also be calculated from this N_b estimate using a formula from Waples et al. (2014) and information on age at maturity and adult lifespan. Although capacity to generate reliable effective size estimates requires basic genetic and life-history information, as well as large samples of individuals of known ages, such resources and data are often readily available for fishery important species.

We investigated the potential to generate robust LDN_e-based effective size estimates in a highly abundant iteroparous species, the Australasian snapper (*Chrysophrys auratus*), using genome-wide SNPs and both single-cohort young of the year (YOY) and mixed-age adult samples. Snapper is a long-lived abundant sparid that inhabits coastal waters of temperate and subtropical Australia as well as northern New Zealand (Gomon et al., 2008). Throughout its range, snapper is a highly important recreational and commercial species, generating significant economic and social benefits (Jalali et al., 2022; McLeod & Lindner, 2018; Steven et al., 2021). Because of its abundance and fishery importance, much is known about the biology of snapper and the status of most stocks is assessed regularly (Fowler et al., 2021; Parsons et al., 2014). This means that considerable resources are readily available for estimating the effective size of snapper stocks, including a reference genome, tissue samples from a range of life stages, information on stock structure, as well as population specific data on age at maturity and longevity (Catanach et al., 2019; Fowler et al., 2021; Parsons et al., 2014).

Here, we utilized tissue samples taken from snapper belonging to two genetically distinct and geographically isolated stocks, one from southeastern Australia and the other from southwestern Australia,

that were originally sampled for stock assessment purposes and for population genetic structure work (Bertram et al., 2022, 2023; Conron et al., 2020; Fairclough et al., 2021). For the two stocks, both single-cohort YOY and adults of mixed ages were available for effective size estimation, allowing us to generate estimates of both N_b in a single reproductive cycle and generational N_e using the LDN_e method. We also compare generational N_e made from the YOY-based N_b estimates and the samples of mixed-age adults. We apply the bias adjustments to our effective size estimates to account for physical linkage (based on chromosome number; Waples et al., 2016) and age structure (based on age at maturity and adult lifespan; Waples et al., 2014, Waples, Grewe, et al., 2018). To the best of our knowledge, this is the first study to compare empirical N_e estimates from both single-cohort and mixed-age adult samples in a highly abundant teleost using genome-wide SNPs. Thus, our study improves understanding of the performance of the LDN_e method across samples of highly abundant, iteroparous species with different age compositions.

2 | MATERIALS AND METHODS

2.1 | Sampling

Population genomic work has shown that the Australian locations selected in this study are represented by two geographically and genetically isolated snapper populations, known as the southwest (Bertram et al., 2022) and the southeast (Bertram et al., 2023) stocks. Muscle samples were obtained from 202 0+ aged YOY snapper recruits from the southwest stock (Cockburn Sound), as well as 202 YOY from the southeast stock (Port Phillip Bay; Table 1, Figure 1). These YOY snapper were originally collected for annual recruitment surveys via trawling by the Department of Primary Industries and Regional Development Western Australia and the Victorian Fisheries Authority. The southwest YOY hatched during the breeding season of 2016, while the southeast recruits hatched during the breeding season of 2017/2018. Muscle or fin samples were also obtained from adults of mixed ages belonging to the stocks during 2011, 2014, 2018, and 2019 (Table 1). These adult snapper, which were landed by commercial or recreational fishermen, or by fisheries researchers as part of fisheries independent surveys, were originally sampled for population genetic structure work (Bertram et al., 2022, 2023; Gardner et al., 2022). The southwest adult sample contained 150 individuals caught in Cockburn Sound, Busselton, and Albany (Table 1, Figure 1; Bertram et al., 2022). The southeast adult sample included 185 individuals caught in Kingston SE, Portland, Port Phillip Bay, and Western Port Bay (Table 1, Figure 1; Bertram et al., 2023). Where possible, biological data on age and length were obtained for sampled fish (Table 1). Tissue samples were placed in 100% ethanol and stored at −20°C until DNA extraction.

2.2 | DNA extraction, library preparation, and sequencing

For all samples, DNA was extracted using a modified salting-out protocol (Sunnucks & Hales, 1996). DNA quality was assessed with

TABLE 1 Catch and biological data for the young of the year (YOY) and adult snapper samples from the southwest and southeast snapper stocks in Australia. Average fork lengths (FL) and ages are followed by standard deviations in parentheses. Sample sizes represent the number of individuals after removing those with >20% missing data.

Samples	*N*	Avg. lat.	Avg. lon.	Catch dates (mm/yy)	Avg. FL (mm)	Avg. age (years)	Sector
Southwest							
Southwest YOY	201	−32.2	115.7	04/17	86 (14)	0+	Research
Adults							
Cockburn Sound (CS)	39	−32.2	115.7	10/18	713 (30)	9.7 (0.6)	Research
Cockburn Sound 2014 (CS14)	29	−32.2	115.7	10/14	794 (42)	—	Research
Busselton (BUS)	40	−33.6	115.3	07,08/18	703 (72)	9.0 (1.5)	Recreational
Albany (ALB)	39	−35.2	118.4	08,09,10,11/18	611 (163)	8.9 (5.5)	Commercial
Southeast							
Southeast YOY	200	−38.0	144.9	03,04/18	-	0+	Research
Adults							
Kingston SE (KSE)	35	−36.5	139.4	04/19	514 (98)	7.9 (2.5)	Recreational
Portland (PLD)	39	−38.4	142.0	01,02,05,06/19	331 (42)	—	Recreational
Port Phillip Bay (PPB)	40	−38.0	144.9	11,12/18; 01,02/19	592 (61)	—	Commercial
Port Phillip Bay 2011 (PPB11)	30	−38.2	144.8	n.a./11	504 (69)	8.9 (1.3)	Recreational
Western Port Bay (WPB)	40	−38.3	145.3	11/18	438 (139)	6.5 (3.3)	Recreational

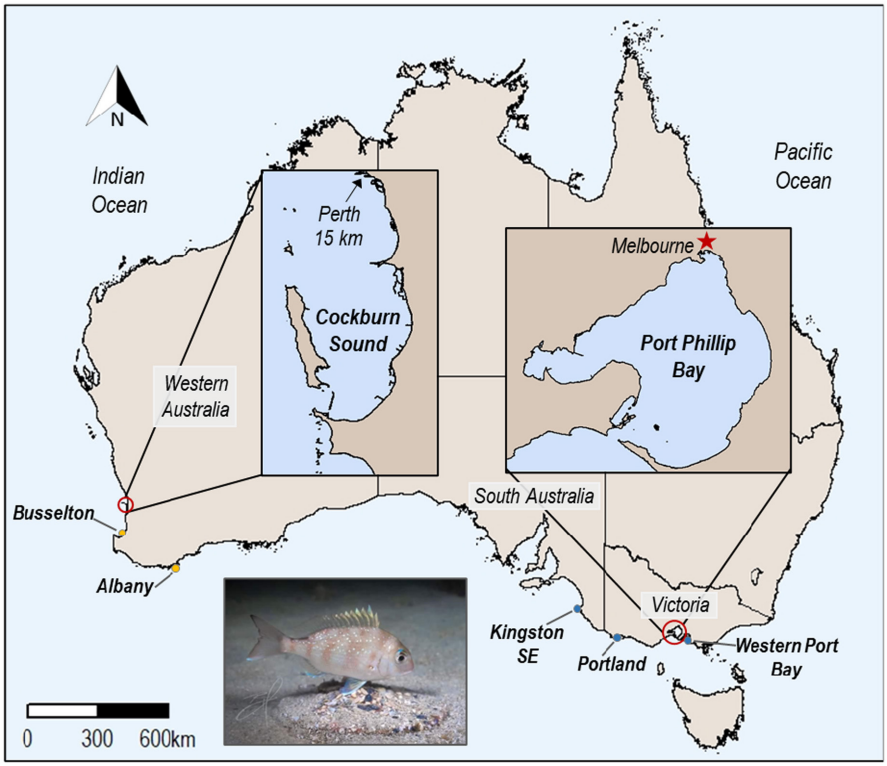

FIGURE 1 Map of sampling locations for the young of the year (YOY) and adult snapper (*Chrysophrys auratus*) from the southwest and southeast stocks. For the southwest, the YOY were obtained from Cockburn Sound ($n = 202$), while the adults were sourced from Cockburn Sound, Busselton, and Albany ($n = 147$). For the southeast, the YOY were obtained from Port Phillip Bay ($n = 202$), while the adults were sourced from Kingston SE, Portland, Port Phillip Bay, and Western Port Bay ($n = 184$). Photo of YOY snapper taken in Cockburn Sound courtesy of Brian Hoehn.

agarose gel electrophoresis (1% TBE gel) and extracts were quantified with Qubit v2.0 (Life Technologies). Double-digest restriction site-associated DNA (ddRAD) libraries were then prepared using a protocol modified from Peterson et al. (2012), as detailed in Brauer et al. (2016). Briefly, eight ddRAD libraries, with each comprising 96 DNA samples, were prepared for sequencing. Approximately 200 ng of genomic DNA per sample was digested using the restriction enzymes SbfI-HF and MseI (New England Biolabs). One of 96 unique 6 bp barcodes was then ligated to each individual sample before being pooled into lots of 12. Using a Pippin Prep (Sage Science), DNA fragments between 300 and 800 bp were selected from each pool. Following PCR of the size selected DNA fragments, size distribution was examined using a 2100 Bioanalyser (Agilent Technologies) and quantification was carried out with Qubit. Libraries were sequenced on eight lanes of an Illumina HiSeq 4000 (150 bp paired end) at Novogene (Hong Kong). Replicates were included in each pool of 96 samples for quantification of genotyping and sequencing errors.

2.3 | Bioinformatics

Raw sequence reads were demultiplexed using the *process_radtags* module of STACKS 2 (Catchen et al., 2013). Barcodes, restriction sites, and RAD tags were subsequently trimmed from reads with TRIMMOMATIC 0.36 (Bolger et al., 2014). Trimmed sequence reads were mapped to a high-quality snapper genome (Catanach et al., 2019) using BOWTIE 2 (Langmead & Salzberg, 2012) before calling single nucleotide polymorphisms (SNPs) with BCFTOOLS 1.16 (Narasimhan et al., 2016). Using VCFTOOLS 0.1.16 (Danecek et al., 2011), individuals with >20% missing data were identified and subsequently excluded before conducting the filtering steps detailed in Table S1. All utilized scripts are available at https://github.com/Yuma248/SNPcallingPipe.

2.4 | Categorizing neutral loci

Loci under selection are expected to bias effective size estimates (Waples et al., 2016). Therefore, we removed loci from our dataset determined to be under selection based on an analysis using BAYESCAN 2.1 (Foll & Gaggiotti, 2008). Twenty pilot runs were undertaken, each with 5000 iterations, followed by 100,000 iterations with a burn-in length of 50,000 iterations. Outlier loci were identified using a 5% false discovery rate (FDR) using prior odds of 10.

2.5 | Population genomic structure

To confirm that the YOY and adult samples taken from the same geographical region belong to the same genetic population, thereby allowing for effective size estimates to be directly compared, we tested for the presence of population genetic structuring using the maximum-likelihood approach of ADMIXTURE 1.3 (Alexander et al., 2009; Alexander & Lange, 2011). We used the software to perform a fivefold cross-validation for the K values 1–5. Ancestry proportions for the most likely K value were visualized using GGPLOT 3.3.3 (Wickham, 2016) in R. We then carried out a Principal Components Analysis (PCA) using VEGAN 2.6-4 (Oksanen et al., 2018) in R,

substituting missing genotypes (~0.4% of data matrix) with the most common genotype at that locus. Finally, we calculated pairwise F_{ST} values in ARLEQUIN 3.5 (Excoffier & Lischer, 2010), with significance assessed with 1000 permutations. *P*-values were corrected for multiple comparisons with the Benjamini and Hochberg (1995) FDR method.

2.6 | Genomic diversity

The genome-wide genetic diversity parameters observed heterozygosity (H_O), expected heterozygosity (H_E), and the F_{IS} population inbreeding coefficient, were calculated for the YOY and adult samples using the *populations* module in STACKS 2 (Catchen et al., 2013).

2.7 | Effective size estimation (N_b and N_e)

Following Waples et al. (2014), linkage disequilibrium (LD)-based effective size estimates *calculated from* a single-cohort reflect N_b in one reproductive cycle, while those calculated from adults of mixed ages reflect N_e per generation. Using the LDN_e method in NEESTIMATOR 2.1 (Do et al., 2014), we estimated N_b for the southwest and southeast stocks from the YOY samples (which were also subsequently converted to N_e estimates using equation three detailed below), and estimated N_e per generation from the two mixed-age adult samples. For the adults, N_e was calculated both including and excluding the samples collected prior to 2018 to assess the effects of adding extra cohorts on our estimates. We ran the software using the no singleton alleles option and calculated 95% confidence intervals (CIs) using a jackknife method that accounts for pseudoreplication due to linkage and overlapping loci (Jones et al., 2016). Bias corrections were applied to the resulting estimates and their CIs to account for both physical linkage and age structure. The first correction, which was applied to both the raw single-cohort N_b and the mixed-age N_e estimates, adjusts for downward bias due to physical linkage, which cannot be fully accounted for by r^2 filtering methods due to difficulties with identifying loosely linked loci (Waples et al., 2016):

$$N_{b/e(\text{adj1})} = \frac{N_{b/e(\text{raw})}}{0.098 + 0.219 \times \ln(\text{chr})} \quad (1)$$

The above formula approximately accounts for the increased LD of linked loci, occurring due to limited recombination, using the number of haploid chromosomes (24 for snapper; Ashton et al., 2019). The process of recombination, including chromosome number, is strongly negatively associated with the magnitude of the bias in N_e due to linked loci (Waples et al., 2016).

Next, the $N_{b(\text{adj1})}$ estimates were adjusted to account for bias due to age structure using information on adult lifespan (AL) and age at maturity (α; Waples et al., 2014):

$$N_{b(\text{adj2})} = \frac{N_{b(\text{adj1})}}{1.103 - 0.245 \times \log(\text{AL}/\alpha)} \quad (2)$$

Since the longevity of snapper in Australia is ~40 years (Norriss & Crisafulli, 2010), the AL values used for each stock were 40 minus α estimates. For the southwest YOY sample, α was set to 5.7 (Wakefield et al., 2015) and AL to 34.3, while for the southeast YOY sample, an α of 4.9 and an AL of 35.1 was used; (Coutin et al., 2003). From these $N_{b(\text{adj2})}$ estimates, N_e per generation was estimated using the same two life history parameters following Waples et al. (2014):

$$N_e = \frac{N_{b(\text{adj2})}}{0.485 + 0.758 \times \log(\text{AL}/\alpha)} \quad (3)$$

The $N_{e(\text{adj1})}$ estimates made from the mixed-age adults were adjusted upward to account for expected downward bias due to age structure using the approach of (Waples, Grewe, et al., 2018) for bluefin tuna. According to Waples et al. (2014), N_e estimates based on mixed-age samples of iteroparous species with life history traits comparable to snapper (e.g., AL and α) are likely downwardly biased by ~20%. As a result, we adjusted the two $N_{e(\text{adj1})}$ estimates upward by dividing them by 0.8.

3 | RESULTS

3.1 | SNP genotyping

After completing strict quality filtering (Table S1), the YOY and adult datasets comprised 6839 SNPs. Twenty-one SNP loci determined to be under selection were removed, leaving 6818 neutral SNPs for our analyses. Of the 739 genotyped snapper, seven were found to have >20% missing data (three YOY and four adults) and therefore were subsequently removed (Table 1). The remaining 401 YOY (201 from the southwest; 200 from the southeast) had an average of 0.6% missing data (range: 0.01%–14.84%), while the remaining 331 adults (147 from the southwest; 184 from the southeast) had an average of 0.2% missing data (range: 0%–1.5%).

3.2 | Population genomic structure

Our ADMIXTURE analysis confirmed a lack of population genomic structure between the YOY and adult samples from the southwest, as well as between the YOY and adult samples from the southeast ($K=2$ most supported; Figure S1). This indicates that the YOY and adult samples taken from the same geographical region belong to the same genetic populations, allowing for subsequent comparisons of generational N_e estimates. Additionally, the analysis indicated a lack of temporal genetic structure between the adult samples within each region collected at different time periods (i.e., between the 2014 and 2018 southwest fish, and the 2011 and 2018/19 southeast fish). The PCA reflected these ADMIXTURE results (Figure S2), and all pairwise F_{ST} values between regions were significant (Table S2). Within regions, significant pairwise F_{ST} were obtained only for the comparisons between the Albany and the southwest YOY and 2018 Cockburn Sound samples ($F_{ST}=0.0021$ and 0.0024, respectively).

This result reflects the slight isolation by distance uncovered with a spatial autocorrelation analysis in Bertram et al. (2022).

3.3 | Genomic diversity

Genomic diversity was high and similar across the different snapper samples, with observed and expected heterozygosity (H_O and H_E) ranging between 0.206 (southwest YOY) and 0.209 (southeast adults 2), and 0.209 (southwest YOY and adults 1 and 2) and 0.210 (southeast YOY and adults 1 and 2), respectively (Table 2). Values of F_{IS} were close to zero for all samples, ranging between 0.012 (southeast adults) and 0.020 (southwest YOY and adults 2; Table 2). The southeast samples had slightly higher H_O and H_E and slightly lower F_{IS} than the southwest samples.

3.4 | Estimates of N_b in a single reproductive cycle

The bias corrections to account for physical linkage and age structure resulted in upward adjustments of the raw southwest and southeast YOY N_b estimates and their 95% confidence intervals (CIs) by 41% and 43%, respectively (Table 3). Adjusted N_b was greater for the southwest than the southeast YOY sample (3754 vs. 2684). The lower bounds of the 95% CIs for the southwest and southeast YOY N_b estimates were similar (1702 vs. 1362), while their upper bounds were indeterminate (i.e., infinite) and 35,587, respectively.

3.5 | Estimates of generational N_e

Generational N_e based on the southwest and southeast YOY samples, which we calculated from the adjusted N_b estimates, was 3333 and 2282, respectively (95% CIs: 1511–inf and 1158–30,256; Table 3, Figure 2). The bias adjustments (to account for physical linkage and age structure) applied to the raw N_e estimates for the southwest and southeast adult samples resulted in upward modifications of 74% (Table 4). Adjusted N_e was similar across the adult samples, albeit slightly higher for the southeast than the southwest (1958 vs 1834; Table 4, Figure 2). Like the YOY based N_e estimates, the lower bounds of the 95% CIs for the adult N_e estimates were similar (southwest, 79-9; southeast, 953). Additionally, the 95% CIs for southwest adult N_e estimate also had an indeterminate upper limit (i.e., infinite). The upper limit of the 95% CIs for the southeast adult N_e estimate was 126,951. N_e estimates including the fish collected prior to 2018 were slightly higher for both stocks (southwest, 2631; southeast, 2687; Table 4, Figure 2). The lower bounds of the 95% CIs for these estimates were also higher (southwest, 1183; southeast, 1339). The southwest estimate continued to exhibit an indeterminate upper limit, while the southeast upper limit was less than half of that obtained for the smaller sample (54,282).

TABLE 2 Summary of sample sizes and genomic diversity (based on 6818 SNPs) for the young of the year (YOY) and adult snapper samples excluding (adults 1) and including (adults 2) the extra fish obtained prior to 2018. Abbreviations are expected heterozygosity, H_E; observed heterozygosity, H_O; inbreeding coefficient, F_{IS}.

Sample	N	H_O	H_E	F_{IS}
Southwest YOY	201	0.206	0.209	0.020
Southeast YOY	200	0.208	0.210	0.017
Southwest adults 1	118	0.207	0.209	0.018
Southwest adults 2	147	0.207	0.209	0.020
Southeast adults 1	154	0.208	0.210	0.012
Southeast adults 2	184	0.209	0.210	0.013

4 | DISCUSSION

Although estimating genetic effective size (N_e and N_b) is challenging, particularly in abundant and iteroparous species, advances in our understanding of these parameters have improved our ability to generate reliable effective size estimates. There are very few published estimates of genetic effective size in age-structured non-model marine fishery species that are reliable. The vast majority of genetic effective size estimates are calculated as part of population genetic structure surveys using 10s of individuals of mixed ages and bias corrections to account for age structure and physical linkage of loci are rarely applied. We assessed the potential to generate reliable N_e and N_b estimates for an abundant, iteroparous species using genome-wide SNPs and samples from both single-cohort YOY and adults of mixed ages. To explore this, we focused on two genetically and geographically distinct Australian stocks of the fishery-important teleost, the Australasian snapper (*C. auratus*), utilizing fish originally sampled for stock assessment and population genetic structure work. Results from the different sample types were similar for both stocks. Upper bounds of the 95% CIs around our N_e and N_b estimates were achieved for one of the two stocks, from both the mixed-age adult and YOY samples. For this stock, N_e estimates based on single-cohort YOY were more precise than those based on the adults of mixed ages. The bias corrections applied resulted in considerable upward modifications of our genetic effective size estimates, highlighting their importance. Although we cannot be certain of the actual genetic effective sizes of the two stocks, the application of bias corrections and the similarity of results between the different sample types increases our confidence in the validity of our estimates. Our study indicates that it is possible to generate reliable genetic effective size estimates for abundant, iteroparous species using large samples and genome-wide SNPs, especially if samples from a single cohort are available for genotyping and if the relevant bias corrections are applied. This work also demonstrates the potential additional uses of specimens originally collected to address other research questions. The design and results of this study can inform the development of strategies for estimating genetic effective size for other abundant, iteroparous species.

TABLE 3 Raw and adjusted effective size estimates based on 6818 SNPs for the two young of the year (YOY) snapper samples. Raw estimates were calculated using the linkage disequilibrium method in NEESTIMATOR 2.1 (Do et al., 2014; Waples & Do, 2008), and reflect the effective number of breeders (N_b) in one reproductive cycle. The first and second adjustments made to the N_b estimates were applied to account for bias due to physical linkage of loci and age structure, respectively. Generational effective population size (N_e) was calculated from the final adjusted N_b estimates using an equation from Waples et al. (2014) that incorporates information on two life-history traits (adult lifespan and age at maturity). In parentheses are 95% confidence intervals generated using the jackknife method in NEESTIMATOR.

Samples	*N*	$N_{b(raw)}$	$N_{b(adj1)}$	$N_{b(adj2)}$	N_e
Southwest YOY	201	2670 (1210–inf)	3363 (1524–inf)	3754 (1702–inf)	3333 (1511–inf)
Southeast YOY	200	1875 (951–24,854)	2361 (1198–31,302)	2684 (1362–35,587)	2282 (1158–30,256)

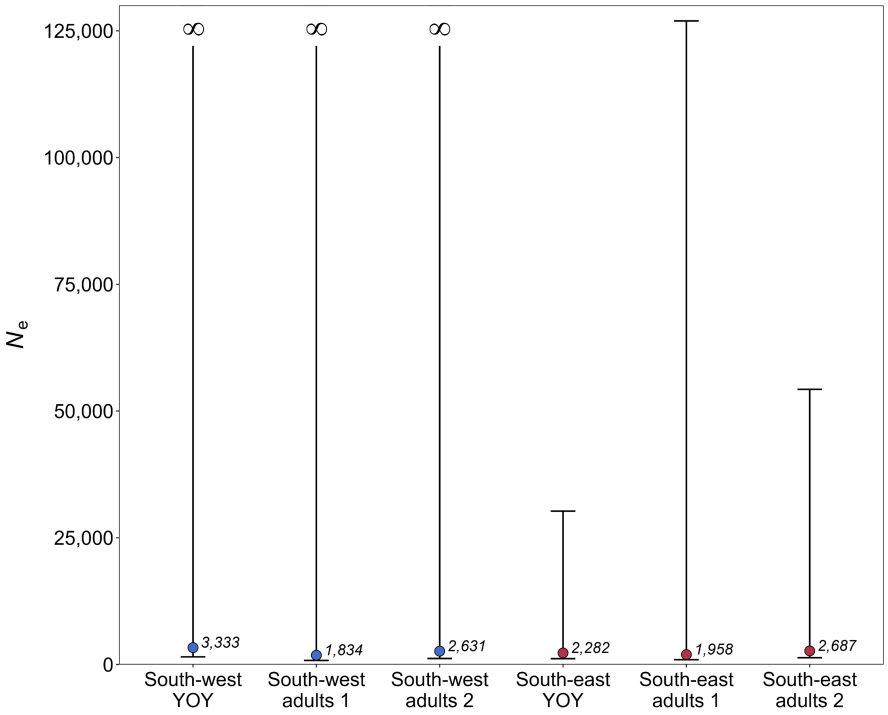

FIGURE 2 Comparison of generational effective population size (N_e) based on 6818 SNPs for the young of the year (YOY) and adult snapper from the southwest (blue) and southeast (red) stocks in Australia. The first and second estimates for the mixed-age adult samples exclude and include the extra fish obtained prior to 2018 respectively. Data labels represent the N_e estimates after correcting for biases due to physical linkage and age structure.

TABLE 4 Raw and adjusted effective size estimates based on 6818 SNPs for the mixed-age adult snapper samples excluding (adults 1) and including (adults 2) the extra fish obtained prior to 2018. Raw estimates were calculated using the linkage disequilibrium method in NEESTIMATOR 2.1 (Do et al., 2014; Waples & Do, 2008) and reflect generational effective population size (N_e). The first and second adjustments applied to the N_e estimates were to account for bias due to physical linkage of loci and age structure, respectively. In parentheses are 95% confidence intervals generated using the jackknife method in NEESTIMATOR.

Samples	*N*	$N_{e(raw)}$	$N_{e(adj1)}$	$N_{e(adj2)}$
Southwest adults 1	118	1056 (460-inf)	1330 (580-inf)	1834 (799-inf)
Southwest adults 2	147	1515 (681–inf)	1907 (858–inf)	2631 (1183–inf)
Southeast adults 1	154	1127 (549–73,079)	1420 (691–92,040)	1958 (953–126,951)
Southeast adults 2	184	1547 (771–31,247)	1948 (971–39,354)	2687 (1339–54,282)

4.1 | Genetic effective size bias corrections

The corrections applied to account for bias due to physical linkage of loci and age structure resulted in considerable upward modifications to our effective size estimates. Estimates based on the southwest and southeast YOY samples were adjusted upward by 41% and 43% respectively, while those based on the mixed-age adult samples were adjusted upward by 74%. Species with

at least 60 chromosomes will produce genetic effective size estimates with minimal bias due to physical linkage of loci (Waples et al., 2016). However, downward bias occurs in species like snapper that have <60 chromosomes, particularly if chromosomes are short in length (<100 cM), because smaller genomes contain fewer independently assorting loci. With respect to age structure, downward bias in effective size estimates increases as the ratio between adult lifespan and age at maturity increases (Waples et al., 2014). Therefore, effective size estimates can be highly inaccurate if these bias corrections are not applied, particularly in species that have less than 60 chromosomes, and in species that have long lifespans with early maturity.

4.2 | Effective number of breeders (N_b) in a single reproductive cycle

The most straightforward approach for obtaining reliable genetic effective size estimates with the LDN_e method is to genotype a large sample of a single cohort (Waples et al., 2014). The resulting estimates reflect the effective number of breeders (N_b) that gave rise to the sampled cohort. This is the first study to generate empirical estimates of N_b for snapper. Our N_b estimates based on the single-cohort YOY snapper from the southwest and southeast stocks were 3754 and 2684, respectively (95% CIs: 1702–inf and 1362–35,587). These results suggest that a greater number of effective breeders contributed to the 2016 southwest cohort than the 2017/2018 southeast cohort. Factors that can influence N_b include individual variation in fecundity, population density, sexual selection, spawning and nursery habitat quality and quantity, and the suitability of environmental conditions for spawning and larval survival (Whiteley et al., 2015). Long-term studies on N_b may be valuable for understanding the factors influencing interannual variation in individual reproductive contribution and therefore may facilitate predicting the impacts of anthropogenic development, different harvest strategies and environmental changes on stock resilience and productivity (Bacles et al., 2018; Luikart et al., 2021). For example, a long-term study by Whiteley et al. (2015) determined that interannual changes in N_b in two brook trout (*Salvelinus fontinalis*) populations were significantly correlated with temporal variation in stream flow. N_b monitoring may be particularly feasible in situations where regular sampling of recruits is carried out as part of an existing stock or population monitoring strategy, as is the case for the snapper stocks in this study.

4.3 | Generational effective population size (N_e)

Generational effective population size (N_e) refers to the theoretical size of a population facing the same rate of genetic drift or change in genetic diversity per generation as the one in question (Wright, 1931). This parameter is the most informative in wildlife conservation and management as it indicates the vulnerability of a population to environmental changes and exploitation. We calculated N_e for the two Australian snapper populations using two approaches. First, we calculated N_e from our YOY-based N_b estimates using population-specific information on adult lifespan and age at maturity (Waples et al., 2014). Second, we estimated N_e from samples of mixed-age adults and used the ratios of observed to expected N_e for species similar to snapper from Waples et al. (2014) to roughly correct for bias due to age structure. Our N_e estimates based on the YOY samples were higher than those based on the mixed-age adult samples. Additionally, the southeast YOY-based estimate exhibited improved precision. The YOY-based N_e estimates were 3333 and 2282 for the southwest and southeast snapper stocks, respectively (95% CIs 1511–inf and 1158–30,256), while those based on the southwest and southeast mixed-age adult samples (sampled in 2018 and 2019) were 1958 and 1834, respectively (95% CIs: 779–inf and 953–126,951). Including the additional adult snapper collected for prior population genetic work (Cockburn Sound in 2014, $n = 29$; Port Phillip Bay in 2011, $n = 30$) resulted in higher point estimates for both stocks (south-west, 2631; southeast, 2687). Precision was also improved for the southeast stock (95% CIs south-west, 1183–inf; southeast, 1339–54,282), likely due to the increase in sample size. The inclusion of additional cohorts therefore did not appear to result in extra downward bias due to age structure. These N_e estimates are perhaps more reliable than those generated without these additional samples as they exhibited precision (or a lower 95% CI value in the case of the southwest) that was more comparable to the estimates based on the YOY samples, demonstrating the importance of sample size for N_e estimation.

Similarities between the N_e estimates based on the different sample types increase our confidence in their validity. Our N_e estimates for the southwest stock were generally higher than those obtained for the south-east stock, and the upper 95% CI for the southwest estimates were both indeterminate (i.e., infinite). Since the southwest point estimates were generally highest and precision is inversely related to true N_e (Waples & Do, 2010), we can conclude that the N_e of the southwest stock, when sampled, was larger than that of the southeast stock. This does not necessarily mean that the former stock has a larger census population size than the latter stock, as no simple relationship between N_e and census population size has been determined and the ratio between the two parameters can vary between populations of the same species (Palstra & Fraser, 2012; Pierson et al., 2018). In fact, the relative biomass of the southwest stock is considered to be lower than that of the southeast stock (depleted vs sustainable; Fowler et al., 2021), and historic landings have generally been higher in the latter (Conron et al., 2020; Fairclough et al., 2021). Additionally, in 2018, the abundance of YOY in Port Phillip Bay (the primary nursery area for the southeast stock) was the highest since recruitment surveys began 30 years ago (Bell et al., 2021). Although no spawning biomass estimates are available for the southwest snapper stock, population dynamic modelling estimated that in 2016, the southeast stock contained >1000,000 spawning individuals (Hamer et al., 2019). This suggests that the N_e and N_b of the southeast may

be a small proportion of the census population size, and therefore that individual variation in reproductive contribution is likely to be substantial. This hypothesis is consistent with the vast interannual variation in spawning success of snapper in Port Phillip Bay, where larval survival and juvenile recruitment is linked to changes in abundance and composition of their planktonic diet (Murphy et al., 2013).

Since snapper appear to have colonized the Australian coastline in an east to west direction, the southwest and its two adjacent stocks are likely the most recently formed (A. Bertram et al., unpublished data). These three stocks (the mid-west, southwest, and south-coast stocks) are therefore weakly differentiated, and they are also not completely contemporarily isolated. As a result, it is possible that the southwest estimates reflect the effective size of a broader region, or are inflated due to contemporary gene flow from these weakly differentiated adjacent stocks (Neel et al., 2013; Waples & England, 2011). Alternatively, the lower N_e of the southeast compared to the southwest could be due to higher individual variance in reproductive success in the former stock.

Our results suggest that while samples of mixed-age adults are valuable for assessing relative population differences in N_e, they can produce more downward biased and less precise estimates than samples from a single cohort. Waples et al. (2014) showed that downward bias of N_e estimates made from adults of mixed ages increases as the ratio between adult lifespan and generation length increases. Therefore, if the study species is long lived, matures early, and reproduces for its entire mature lifespan (like snapper and many other marine fishes), then considerable downward bias in N_e estimates is expected if they are generated from adults of mixed ages. Compared with a single cohort, N_e estimates made from mixed-age adults are more difficult to adjust accurately to account for bias due to age structure. Therefore, as already recommended by others, we advise that the most suitable approach for estimating N_e in species like snapper is to base calculations on a single cohort. Based on the guidelines of Frankham et al. (2014), our single cohort-based N_e estimates for the southwest and southeast snapper stocks are likely sufficiently large to avoid inbreeding ($N_e > 100$) and loss of adaptive potential ($N_e > 1000$).

4.4 | Effects of population genetic structure on effective size estimates

Downward bias in N_e is expected when population genetic structure occurs within the genotyped sample. This is because the inclusion of genetically divergent individuals generally results in downward biased N_e estimates due to mixture LD (Neel et al., 2013). It is possible that the weak signal of isolation by distance in the southwest (Bertram et al., 2022) caused additional downward bias of our mixed-age adult N_e estimates. However, we believe the impact of this slight genetic structuring on our N_e estimates was low, since the most differentiated southwest samples had an F_{ST} of only 0.003 (Cockburn Sound vs Albany; Bertram et al., 2022). Additionally, F_{IS} was no higher for the adult sample than for the YOY sample that was obtained from one location (i.e., Cockburn Sound). We would expect inflated F_{IS} if genetic structuring due to the Wahlund effect was significant enough to downwardly bias our N_e estimate (Neel et al., 2013; Waples, Scribner, et al., 2018). Alternatively, the lower N_e estimate obtained from the mixed-age adult sample could be due to its age composition causing more downward bias than expected or due to the slightly different time period the estimate relates to (Waples, 2005).

4.5 | Comparisons with effective size estimates of other species and previous snapper studies

Our N_e estimates are within the range of those reported for marine species exhibiting very large populations (Marandel et al., 2019), and are similar to N_e estimates generated for species with reproductive strategies comparable to snapper, including the giant black tiger shrimp (*Penaeus monodon*; Vu et al., 2020), Sydney rock oyster (*Saccostrea glomerata*; O'Hare et al., 2021), green abalone (*Haliotis fulgens*; Gruenthal et al., 2014), Pacific cod (*Gadus macrocephalus*; Suda et al., 2017), white hake (*Urophycis tenuis*; Roy et al., 2012), and redbelly yellowtail fusilier (*Caesio cuning*; Ackiss et al., 2018). As expected, the two snapper N_e estimates are generally larger than those for anadromous fishes (Barría et al., 2019; Ferchaud et al., 2016; Miller et al., 2022; Waldman et al., 2019) and elasmobranchs (Dudgeon & Ovenden, 2015; Pazmiño et al., 2017; Reid-Anderson et al., 2019; Venables et al., 2021), and are smaller than those for southern bluefin tuna (*Thunnus maccoyii*; Waples, Grewe, et al., 2018), albacore tuna (*Thunnus alalunga*; Laconcha et al., 2015) and New Zealand hoki (*Macruronus novaezelanidae*; Koot et al., 2021), which support far more productive fisheries than snapper. Although fewer studies have explored N_b in marine species, due to the close relationship between N_e and N_b, similar trends to those described above occur between our results and similar studies with regard to N_b (Davenport et al., 2021; King et al., 2023; Puritz et al., 2016; Waples, Grewe, et al., 2018; Whiteley et al., 2015).

N_e has previously been estimated for snapper in eastern Australia and New Zealand. Morgan et al. (2018) estimated N_e for samples of mixed-aged adult snapper from nine locations in eastern Australia. However, sample sizes were all <60 individuals and only nine microsatellite DNA markers were used, so three samples produced indeterminate point estimates and all estimates had indeterminate upper 95% CIs. Hauser et al. (2002) estimated N_e for adult snapper from Tasman Bay and Hauraki Gulf ($n = 234$ for each site) in New Zealand using seven microsatellite DNA markers. Estimated N_e was 104 (95% CIs 80–720) for Tasman Bay and 1164 (95% CIs 157–inf) for Hauraki Gulf. Hauser et al. (2002) suggested that the very low N_e for Tasman Bay could partly be due to the population being located at the southern edge of snapper's distribution, which may result in recruitment failure in some years. Jones et al. (2019) used nine microsatellite DNA markers to estimate N_e for snapper within a marine reserve in the Hauraki Gulf. Estimated N_e, which was based on 1044 mixed-age adults, was 10,488 (95% CIs 2818–inf). N_e simulations

conducted with NEOGEN software (Blower et al., 2019) suggested that at least 1500 individuals (~5% of the marine reserve adult population) would need to be genotyped to generate an estimate with a finite upper 95% CI. As with our results, the above studies indicate that large numbers of individuals need to be genotyped to produce precise N_e estimates for very large populations.

5 | CONCLUSIONS

Generating reliable genetic effective size estimates for fishery-important species is challenging since they often have large, connected populations with overlapping generations. However, abundant resources are often available for investigating genetic effective size in fishery-important species because they are commonly sampled for stock structure work and for routine stock assessment. Although we cannot be certain of the 'true' genetic effective sizes of the two stocks, the application of bias corrections and the similarity of results between the different sample types increases our confidence in the validity of our estimates. Our results indicate that it is feasible to obtain reliable effective size estimates for fishery-important species, particularly if large samples from a single cohort are available for genotyping. However, even if such samples are available, estimates can be inaccurate if adjustments are not made to account for factors like physical linkage of loci and age structure. Our study can be used as a guide for others to generate genetic effective size estimates for abundant, iteroparous species.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The SNP dataset is available on figshare: https://doi.org/10.6084/m9.figshare.26310718.

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