



Genetic population structure of Yellowtail Kingfish (*Seriola lalandi*) in temperate Australasian waters inferred from microsatellite markers and mitochondrial DNA

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ABSTRACT

Expansion of finfish aquaculture will see increased incentive for translocation of stocks across geopolitical boundaries. The potential for genetic contamination of stocks arising from translocation and subsequent release or escape of translocated and/or genetically mixed stocks may be a significant risk to wild populations. Assessment of risk requires knowledge of the local population structure for the species across the range that translocation might occur and it is in this context we undertook a population genetic survey of stocks of Yellowtail Kingfish across temperate Australia and New Zealand. Seven polymorphic microsatellite loci were used to analyse a total of 272 individuals sampled from New Zealand, New South Wales, Victoria, South Australia and Western Australia. A subset of individuals from each sample locality was also assessed for variation at the mitochondrial gene ND4. Pairwise analysis of sample location and Bayesian analysis showed that Western Australia *S. lalandi* were genetically distinct from *S. lalandi* sampled from the other localities. No difference was found between New Zealand *S. lalandi* and eastern (New South Wales) or central (South Australia and Victoria) Australian fish. The mitochondrial analysis supported the microsatellite data with western samples possessing unique haplotypes compared with all other sites which shared haplotypes. With the expansion of the Yellowtail Kingfish aquaculture industry and likely translocation of stocks, there is a need for a review of translocation policies that consider genetic diversity as a factor in the development of Yellowtail Kingfish aquaculture in the region.

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1. Introduction

The Yellowtail Kingfish, *Seriola lalandi*, (Perciformes: Carangidae) is widespread in the Atlantic and Pacific Oceans and is an important species for both commercial and recreational fishing in Japan, Australia and New Zealand (Nugroho et al., 2001). In Australia the distribution of *S. lalandi* extends from North Island (10°S) in Queensland, across the eastern and southern coasts of the continent, including the east coast of Tasmania, Lord Howe Island (31°S) and Norfolk Island (29°S), to Trigg Island in Western Australia (32°S) (Love and Langenkamp, 2003). In New Zealand, *S. lalandi* occurs from the Kermadec Islands (29°S) to Foveaux Strait (46°S) (Poortenaar et al., 2003). Yellowtail Kingfish can grow to 2.5 m in length and weigh around 70 kg (Gomon et al., 2008). The ideal water temperature for this species is between 18 and 24 °C (Wolvaardt, 2007).

Kingfish usually spawn between October and January in the southern hemisphere (Poortenaar et al., 2001). Juvenile Yellowtail Kingfish are found in surface waters offshore and often shelter within flotsam and floating seaweed suggesting passive dispersal of juvenile *S. lalandi* is possible (Diggles, 2002). Currently, there is limited information on the biology and behaviour of the species and it is unknown whether they exhibit active homing or philopatry; moreover, little is known about the location of spawning grounds for the species.

Several *Seriola* spp. (amberjacks) are important aquaculture fishes. Japan currently leads production with 139,000 t per annum (US \$1.1 billion per annum; Poortenaar et al., 2003). In Japan, culture of *Seriola* spp. (*S. quinqueradiata*, *S. dumerili* and *S. lalandi*), accounts for approximately 57% of all Japanese marine fish aquaculture (Ohara et al., 2005). Yellowtail Kingfish are currently cultured in South Australia with production expanding considerably since its initiation in 2001. Annual production is currently 3000–4000 t per annum and is expected to increase in the near future to ≥5000 t (ABARE, 2009). There has been some culture of the species in New South Wales (NSW) and Western Australia (WA) but growth of the sector has been constrained to date by limited access to production sites, high mortality rates, disease and growth deformities (Stephens and Savage, 2010; Tachihara et al., 1997). Aquaculture of this species is also under development in New Zealand (NIWA, 2011). Plans have

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been made to initiate a breeding programme for the genetic improvement of Yellowtail Kingfish in Australia which could involve the translocation of germplasm between different locations in the formation of a genetically diverse base population.

The South Australian Yellowtail Kingfish aquaculture industry currently relies on hatchery production derived from wild fish captured in the northern Spencer Gulf (34°S). With the majority of temperate Australasian culture of Yellowtail Kingfish taking place in Spencer Gulf using locally derived broodstock, escapees from aquaculture currently pose no significant risk to the genetic structure of this species. However, with the likelihood of expansion of the industry throughout southern Australia and New Zealand and the prospect of genetically composite and eventually genetically improved stocks of mixed origin being used in aquaculture across the region, it is becoming increasingly important to conduct a comprehensive assessment of the risks associated with translocations of stocks of the species. Whilst a major component of this risk will relate to biosecurity and the threat of transmission of pathogens, the potential for genetic contamination of stocks arising from translocation and subsequent release or escape of translocated and/or genetically mixed stocks may also be a significant component of the risk. Risk assessment requires knowledge of the local population structure for the species across the range over which translocation might occur. Escapees from aquaculture or even deliberate releases of hatchery reared stock, if not sourced from the same location, have the potential to interbreed with wild fish, thus possibly modifying the genetic structure of wild populations. This may result in the contamination of potentially important reservoirs of genetic diversity and break up co-adapted gene complexes in locally adapted stocks. Interbreeding of fish from genetically distinct stocks can potentially reduce the fitness and viability of a species and makes it more vulnerable to extinction over time (Chauhan et al., 2007).

Whilst these issues relate to conservation of indigenous genetic diversity, knowledge of genetic structure is also important to the optimal exploitation of this diversity. Maximising genetic diversity in the formation of a base population for a long term breeding programme is an important consideration. The desire to maximise genetic diversity has to be balanced against the risks of future genetic contamination arising from aquaculture (McClelland and Naish, 2007).

Population genetic surveys can reveal genetic resources available as a base for breeding programmes and determine the potential genetic risk of translocation (Johnson, 2000). It is thus evident that understanding the genetic diversity of an economically important species, such as the Yellowtail Kingfish, is vital to optimising its management and ensuring the long term sustainability of both wild and captive stocks (Jeong et al., 2003).

Little is known about the population structure of Yellowtail Kingfish in Australia and New Zealand. Tag and recapture studies in Australia suggest that most Yellowtail Kingfish are relatively sedentary; with some (both juvenile and adults) moving large distances (Gillanders et al., 2001; Hutson et al., 2007a, b). Recaptures show that wild Yellowtail Kingfish migrate naturally between Australia and New Zealand (Holdsworth and Saul, 1998; Gillanders et al., 2001) which is consistent with evidence from microsatellite and mitochondrial DNA (mtDNA) markers that show no significant difference amongst fish sampled from New South Wales and New Zealand (Nugroho et al., 2001). However, Japanese and New South Wales/New Zealand populations show significant genetic divergence (Nugroho et al., 2001) and there are no records of Yellowtail Kingfish movements between Australian and Asian waters.

The aim of this research was to determine if there are genetically distinct populations of *S. lalandi* in temperate Australasia. The present study builds on previous research by Nugroho et al. (2001) through sampling a wide geographical range across southern Australian waters and utilising several microsatellite markers and mtDNA gene

sequences to discriminate populations of *S. lalandi*. MtDNA is known to evolve at a much slower rate compared to microsatellite markers, thus this analysis can provide information on historical changes within this species (Anderson et al., 2010). Population structure is an important factor that should be taken into account by the appropriate regulatory authorities when considering applications for translocation of fish.

2. Materials and methods

2.1. Sample collection and DNA extraction

A total of 272 wild *S. lalandi* were sampled from 17 sites and grouped into the five regions, New South Wales ($n=111$) and New Zealand ($n=91$; eastern), South Australia ($n=37$) and Victoria ($n=18$; central), and Western Australia ($n=15$; western) (Figs. 1 and 2). Fin clips (approx 0.5 cm²) were taken from each individual and stored in 70% molecular grade ethanol. Total DNA was extracted from tissue samples using the Genra Puregene® DNA Extraction Kit (Qiagen) following the manufacturer's instructions.

2.2. Microsatellite analysis

Nine previously published microsatellite markers *Sdn03* (Nugroho and Taniguchi, 1999), *Sdu 01*, *Sdu10*, *Sdu16*, *Sdu27* (Renshaw et al., 2006), *Sdu 29*, *Sdu32*, *Sdu37* and *Sdu46* (Renshaw et al., 2007) were successfully amplified by polymerase chain reaction (PCR) in preliminary trials and genotyped for all individuals. Primers were synthesised by Geneworks (Adelaide, Australia) and Applied Biosystems (Foster City, USA) with the reverse primer 5'-labelled with a fluorescent tag: FAM, PET, VIC or NED. Polymerase chain reactions were carried out in 15 µl volumes comprising 10x Hotmaster *Taq* buffer with magnesium, 200 µM dNTPs, 0.4 µM of each forward and labelled reverse primer, 0.03 U Hotmaster *Taq* DNA polymerase (5Prime) and 2–15 µg genomic DNA. Thermal cycling conditions for each locus were: 2 min at 94 °C, followed by 34 cycles of 94 °C for 30 s, annealing (as previously published) for 45 s and extension at 68 °C for 1 min, with a final extension temperature of 68 °C for 10 min.

Samples were analysed on an ABI 3770 (Applied Biosystems) sequencer using LIZ 500 (–250) size standard by the Australian Genome Research Facility (AGRF, Adelaide). Alleles were scored using Genemapper v. 3.7 software (Applied Biosystems). A minimum 5%, blindly scored, sample repeats were performed within and across plates to reduce genotyping errors.

2.3. MtDNA analysis

Twenty six samples were selected for mtDNA analysis from across the 17 sites: New South Wales ($n=6$), New Zealand ($n=6$), South Australia ($n=4$), Victoria ($n=3$) and Western Australia ($n=7$). An approximately 700 bp fragment of the mitochondrial genome, including the 3' end of the *NADH dehydrogenase subunit 4 (ND4)* gene, the tRNA genes *tRNA^{His}*, *tRNA^{Ser}*, *tRNA^{Leu}* and the 5' end of *ND5*, was amplified and sequenced using the forward primer ND4 5' CACATGACTAC-CAAAAGCTCATGTAGAAGC 3' (Arevalo et al., 1994) with the reverse primer H12293-Leu 5' TTGCACCAAGAGTTTTGGTTCTAAGACC 3' (Inoue et al., 2001).

PCR amplifications were performed in a total volume of 25 µl containing, 0.02 U Hotmaster polymerase (5 Prime), 1x Hotmaster *Taq* Buffer with 2.5 mM magnesium (5 Prime), 200 µM of each dNTP and 0.2 µM of each primer. PCR conditions were: 2 min at 94 °C, followed by 34 cycles of 94 °C for 45 s, 52 °C for 45 s, and 70 °C for 1 min; with a final extension of 6 min at 70 °C. PCR products were purified using MultiScreen₃₈₄ PCR Filter Plates (Millipore) following the manufacturer's instructions.

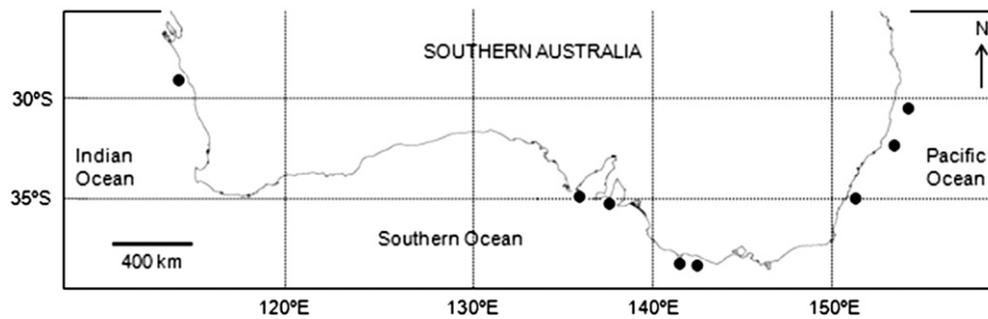


Fig. 1. Sample collection sites (●) of *Seriola lalandi* off mainland southern Australia from west to east: Geraldton, Western Australia (28.8°S, 114.6°E), South Neptune Island, South Australia (35.3°S, 136.1°E), Kangaroo Island, South Australia, (35.5°S, 137°E), Portland, Victoria (38.3°S, 141.6°E), Killarney, Victoria (38.4°S, 142.3°E), Greenwell Point, New South Wales (34.9°S, 150.7°E), Broughton Island, New South Wales, (32.6°S, Longitude, 152.3°E), South West Rocks, New South Wales (30.9°S, 153.1°E).

PCR products were sequenced in both directions using the same primers as those used for PCR amplification using the BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems), products purified using MultiScreen₃₈₄-Seq Filter Plates (Millipore) and then run on an ABI Prism 3730xl capillary sequencer at the AGRF, Adelaide. Sequences were edited using SEQED v 1.0.3 (Applied Biosystems) and aligned manually using SE-AL v. 1.0.3 (Rambaut, 1995). Sequences were deposited in the GenBank database under Accession numbers JF345183–JF345208.

2.4. Data analysis

2.4.1. Measures of genetic diversity

Deviations from Linkage and Hardy–Weinberg Equilibrium (HWE) for each microsatellite locus were tested using GENEPOP v. 4.0 (Rousset, 2008). Linkage disequilibrium and HWE exact test were tested using the Markov chain method (10,000 dememorization steps, 100 batches, 5000 iterations). Given that different sample sizes were

used in this study, FSTAT v. 2.9.3 (Goudet, 1995) was used to calculate allelic richness (A_r) using the rarefaction procedure based on a minimum sample size of 14 diploid individuals. This measure calculates the number of alleles expected independent of sample size. FSTAT v. 2.9.3 (Goudet, 1995) was also used to determine the inbreeding coefficient (F_{IS}). GENALEX v. 6 (Peakall and Smouse, 2006) was used to calculate observed and expected heterozygosity. ADZE v. 1.0 (Szpiech et al., 2008) was used to determine the number of private alleles using standardised sample sizes.

To account for sample size differences, α error (probability that the null hypothesis is incorrectly rejected) and power analysis (probability of rejecting a false null hypothesis) were performed using both Pearson's traditional contingency chi-square (χ^2) and Fisher's exact test analysis in POWSIM v. 4.0. Simulations were run in this programme, using the real sample sizes, loci and allele frequencies, to determine the study's power to detect divergence at different expected F_{ST} values (0.001–0.013). The default parameters for the number of dememorizations, batches, and iterations per batch were used (1000, 100 and 1000 respectively). Different numbers of generations of random drift ($t = 1–50$) and effective base population sizes ($N_e = 500–2000$) were tested.

2.4.2. Measurements of population differentiation – microsatellites

Genetic subdivision was determined amongst pre-defined sample sites, using an unbiased estimator of F_{ST} (Weir and Cockerham, 1984). To test differences in allele distributions between localities an exact test of genic differentiation, suitable when sample sizes are small, was performed (Raymond and Rousset, 1995). The pairwise tests of F_{ST} and genic differentiation were both calculated using GENEPOP v. 4.0. The Markov chain method (same parameters as the exact test above) was utilised to obtain unbiased estimates of the probability. According to Jost (2008), G_{ST} and its relatives (including F_{ST}) may not be a good representation of genetic differentiation when there is high within population diversity, as often found with microsatellites. Jost (2008) demonstrates that when there are many common alleles G_{ST} can be close to zero, even if there is complete population differentiation. The computer programme SMOGD v. 1.2.5 (Crawford, 2010) was used to calculate an estimate of D (recommended by Jost, 2008) in order to validate the F_{ST} results (bootstrap replicates = 1000). To provide a visual representation of population subdivision, pairwise population assignment and Principal Component Analysis (PCA) were performed in GENALEX v. 6 (Peakall and Smouse, 2006).

2.4.3. Bayesian analysis

Bayesian analysis of population structure was assembled using three methods implemented in BAPS v. 5.1 (Corander et al., 2004), BAYESSASS v. 1.2 (Wilson and Rannala, 2003) and GENELAND v. 2.0.12 (Guillot et al., 2005). Bayesian analysis was used in order to reduce biases associated with designations due to sampling locality. The programme grouped the individuals together in genetic clusters

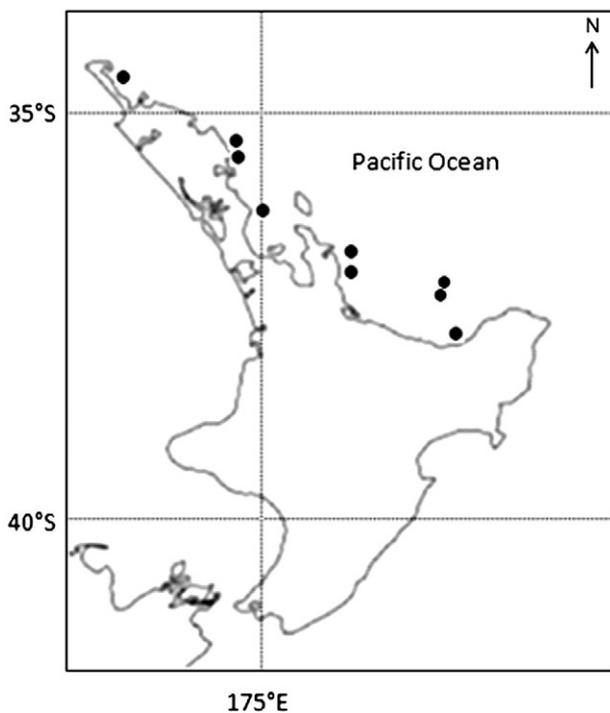


Fig. 2. Sample collection sites (●) of *Seriola lalandi* off the north east coast of New Zealand from west to east: Tutukaka (35.6°S, 174.5°E), Bream Bay (35.9°S, 174.5°E), Simpson Rock (36.1°S, 175°E), Bowentown Heads and Mair Island (37.45°S, 176°E), Alderman (37°S, 176.1°E), White Island (37.3°S, 177.1°E), Whakatane (37.6°S, 177.1°E), Opotiki (38°S, 177.2°E).

Table 1
Summary statistics for genetic variation across 5 Australian localities at 7 microsatellite loci in *Seriola lalandi*.

Locality (N)	Locus								Average
		<i>Sdu03</i>	<i>Sdu10</i>	<i>Sdu16</i>	<i>Sdu27</i>	<i>Sdu29</i>	<i>Sdu32</i>	<i>Sdu46</i>	
NSW (111)	A	8	3	3	2	19	18	6	8
	Ar	3.6	1.4	1.5	2.0	11.1	11.8	3.7	5
	H _O	0.51	0.03	0.04	0.20	0.80	0.75	0.59	0.42
	H _E	0.51	0.03	0.04	0.19	0.89	0.91	0.61	0.45
	F _{IS}	0.008	−0.007	−0.01	−0.02	0.11	0.18	0.04	0.09
NZ (91)	A	6	3	3	2	21	18	7	9
	Ar	3.4	1.3	1.6	1.8	11.1	11.5	5.3	5.16
	H _O	0.46	0.01	0.06	0.11	0.82	0.82	0.66	0.42
	H _E	0.47	0.02	0.05	0.10	0.89	0.90	0.71	0.45
	F _{IS}	0.02	0.5	−0.02	−0.05	0.07	0.09	0.07	0.07
SA (37)	A	3	2	1	2	15	15	4	6
	Ar	2.9	1.6	1.0	2.0	11.0	11.8	3.6	4.84
	H _O	0.50	0.04	0.00	0.16	0.69	0.82	0.62	0.41
	H _E	0.49	0.04	0.00	0.15	0.88	0.91	0.62	0.44
	F _{IS}	−0.01	0	NA	−0.08	0.23	0.11	0.006	0.09
VIC (18)	A	3	2	2	2	11	12	3	5
	Ar	2.9	2.0	1.8	2.0	11.0	11.6	3.0	4.90
	H _O	0.33	0.07	0.06	0.35	0.86	0.77	0.56	0.43
	H _E	0.37	0.07	0.06	0.36	0.86	0.90	0.56	0.45
	F _{IS}	0.14	0	0	0.05	0.04	0.18	0.04	0.09
WA (15)	A	3	2	1	1	9	10	6	5
	Ar	2.9	2.0	1.0	1.0	8.9	9.9	5.9	4.52
	H _O	0.60	0.07	0.00	0.00	0.73	0.73	0.67	0.40
	H _E	0.59	0.44	0.00	0.00	0.87	0.86	0.68	0.48
	F _{IS}	−0.13	0.85	NA	NA	0.19	0.19	0.06	0.20

Locations: NSW = New South Wales; NZ = New Zealand; SA = South Australia; VIC = Victoria; WA = Western Australia. A = number of alleles; Ar = allelic richness; H_O = observed heterozygosity; H_E = expected heterozygosity; F_{IS} = inbreeding coefficient; NA = data not available due to monomorphic locus.

(populations) that reduce Hardy–Weinberg and genetic disequilibrium and not in a priori groupings. For the BAPS programme, clustering of groups of individuals was calculated using the admixture model (1000 iterations, 200 reference individuals and 10 admixture coefficients). This method takes into account the priori locations of the samples and is considered sensitive at detecting population structure (Waples and Gaggiotti, 2006). In BAYESASS, a Monte Carlo Markov chain (MCMC) calculation (3 million iterations; burn-in 200,000; sampling frequency 2000; allele frequency, migration rate and inbreeding coefficient all set at 0.15) was performed to evaluate recent migration rates between populations. In GENELAND, a MCMC calculation (1 million iterations; sampling frequency of 1000) was performed under the non-spatial model, assuming null alleles and correlated allele frequencies. GENELAND and BAYESASS analyses did not utilise any a priori information.

2.4.4. mtDNA analysis

A median-joining (MJ) network was constructed using NETWORK v. 4.6 (Bandelt et al., 1999) with settings following the software instructions.

3. Results

3.1. Conformance to Hardy–Weinberg Equilibrium

Polymorphism varied between microsatellite loci, ranging from two (*Sdu27*) to 25 (*Sdu29*) alleles. The accuracy of scoring *Sdu01* was reduced due to large allele sizes (>500 bp) so it was not used in further analysis. All microsatellite markers, except *Sdu37*, conformed to HWE within each sample locality after applying sequential Bonferroni corrections (Rice, 1989). *Sdu37* showed significant ($P < 0.05$) heterozygote deficiency within all sample localities, so was excluded from all further analysis. Linkage disequilibrium analysis of microsatellite locus pairs showed no significant linkage between any pair of loci ($P > 0.05$). Hence, all the markers were considered to be independently segregating.

The average allelic richness per locality ranged from 5.16 to 4.52 with the western stock samples displaying the lowest richness. Average observed heterozygosity was also lowest (0.401) in the western samples. The mean F_{ST} was much greater in the western samples compared to the eastern/central samples (0.20 and ≤ 0.09 respectively). This difference can be partly explained by the very large value (0.85) of F_{IS} reported for locus *Sdu10* in the western samples; however, excluding this locus from the analysis still resulted in western having the highest F_{IS} value (0.11; Table 1). Regardless, the western F_{IS} value, even with the inclusion of *Sdu10*, fell within the 95% confidence interval (mean 0.091; 95% confidence 0.01–0.13). The number of private alleles per locality when sample size was standardised was slightly higher in the western samples (average = 0.82) compared to eastern/central (0.41), however all private allele values were relatively low (Fig. 3).

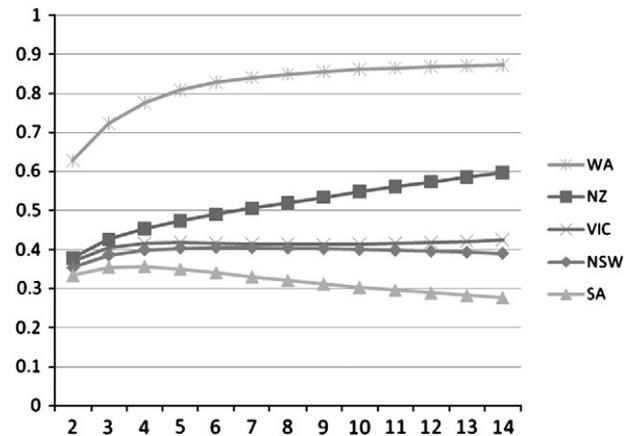


Fig. 3. The number of *Seriola lalandi* private alleles present per locality when sample size is standardised. Calculated in ADZE v. 1.0 (Szpiech et al., 2008). Locations: NSW = New South Wales, NZ = New Zealand, SA = South Australia, VIC = Victoria, WA = Western Australia.

Table 2

Estimation of F_{ST} (above diagonal) and exact test of genic differentiation (below diagonal) of *Seriola lalandi* samples collected from each location. Pairwise F_{ST} calculated using Weir and Cockerham (1984). The Markov chain method (10,000 dememorization steps, 100 batches, 5000 iterations) was utilised to obtain unbiased estimates of the exact P-value. Calculations performed in GENEPOP v. 4.0. * Indicates significance after Bonferroni correction. NSW = New South Wales, NZ = New Zealand, SA = South Australia, VIC = Victoria and WA = Western Australia.

	NSW	NZ	SA	VIC	WA
NSW	–	0.005	–0.002	0.007	0.15*
NZ	< 0.001*	–	0.002	0.012	0.15*
SA	0.53	0.14	–	–0.001	0.14*
VIC	0.29	0.005	0.44	–	0.15*
WA	< 0.001*	< 0.001*	< 0.001*	< 0.001*	–

The estimated α error for both the chi-squared (0.033) and Fisher's (0.036) was less than the standard accepted error rate of 0.05, indicating that the risk of incorrectly rejecting the null hypothesis is small. The power of this study to detect an F_{ST} value of 0.013 and higher was 100% for both the χ^2 and Fishers test. This expected F_{ST} value is much lower than any observed for the western and central/eastern sample pairwise analysis. The power of this study to detect an F_{ST} value similar or lower to that observed between the eastern and central pairwise analyses (0.001), however, was very low ($\chi^2 = 28\%$, Fisher = 20%).

3.2. Population differentiation inferred by microsatellites

The pairwise F_{ST} results and the genetic differentiation exact test showed a significant genetic difference between the individuals sampled from the western location compared to those from the central and eastern locations (Table 2). Surprisingly the exact test also indicated a significant difference between New Zealand and NSW samples. This test was primarily run to ensure that the small sample sizes of Western Australia and Victoria were not biasing the results. Given that New Zealand and NSW had large sample sizes, and this difference was not seen anywhere else in the data, it is unlikely to be biologically significant. The estimates of D , whilst presenting higher values, were similar to F_{ST} values with no further structure identified. Pairwise population assignment showed that individuals sampled from the central and eastern locations were tightly clustered together, whereas central/eastern versus western samples were much more distinct (data not shown). Furthermore, the PCA showed the western samples to be genetically distinct from the other localities (Fig. 4). The PCA also suggested that Victorian samples could be genetically distinct from samples from the other localities; however this was inconsistent with the pairwise population assignment and F_{ST} tests.

Table 3

Recent migration between pairs of sample localities. Source populations are given in columns and recipient populations in rows. Values along the diagonal (bold) line are the self recipient rates into the source population. 95% confidence intervals are indicated in brackets.

	New South Wales	New Zealand	South Australia	Victoria	Western Australia
New South Wales	0.99 (0.96, 1)	0.004 (0, 0.02)	0.004 (0, 0.02)	0.002 (0, 0.009)	0.003 (0, 0.01)
New Zealand	0.3 (0.25, 0.33)	0.69 (0.67, 0.75)	0.003 (0, 0.02)	0.002 (0, 0.01)	0.003 (0, 0.01)
South Australia	0.3 (0.26, 0.33)	0.01 (0, 0.04)	0.68 (0.67, 0.7)	0.005 (0, 0.03)	0.005 (0, 0.03)
Victoria	0.28 (0.2, 0.32)	0.01 (0, 0.07)	0.01 (0, 0.06)	0.69 (0.67, 0.73)	0.01 (0, 0.05)
Western Australia	0.034 (0.002, 0.01)	0.01 (0, 0.06)	0.01 (0, 0.05)	0.008 (0, 0.05)	0.94 (0.86, 0.99)

3.3. Bayesian analysis of population structure

All three Bayesian methods uncovered two genetically distinct populations within *S. lalandi*. BAPS found the majority of individuals sampled in New South Wales, New Zealand, South Australia and Victoria were assigned to cluster 1; whereas the majority of individuals from Western Australia were allocated to cluster 2. The only exceptions to this were two individuals amongst the New South Wales samples that displayed genotypes of which half corresponded to cluster 1 and half to cluster 2 (putative hybrids), and 1 individual from the Western Australian samples which appeared to be from cluster 1.

The BAYESASS individual population assignments were similar to the BAPS results. The majority of individuals from the central/eastern localities were assigned to one population cluster and the majority of the Western Australian individuals were assigned to a different population cluster. The exceptions were one individual from New South Wales that was assigned to the Western Australian cluster and two individuals from Western Australia that were assigned to the eastern cluster. There were also two individuals from the eastern coast that BAYESASS was unable to assign. The New South Wales and one of the Western Australian individuals were the same as those identified in BAPS as being from a different population cluster than the sampling locality. Recent migration rates between populations, as calculated in BAYESASS (Table 3), were low (<0.034) in most cases. The exception to this was significantly larger (migration values >0.2) migration of fish from New South Wales into each of New Zealand, South Australia and Victoria. The GENELAND results concurred with the BAPS and BAYESASS results. This programme showed two population clusters of *S. lalandi* in temperate Australasia (mean probability

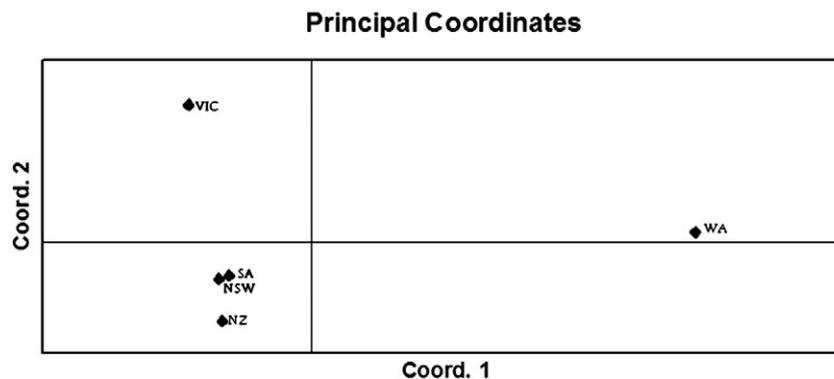


Fig. 4. Principle component analysis of *Seriola lalandi* samples by sampling locality. Locations: NSW = New South Wales, NZ = New Zealand, SA = South Australia, VIC = Victoria, WA = Western Australia.

74.61%), with those individuals from Western Australia being genetically distinct from those from the eastern and central localities.

3.4. mtDNA networks

The mtDNA analysis supports the microsatellite data (Fig. 5). The samples contained five different haplotypes. Except for two unique haplotypes (one from NZ and one from SA), the eastern and central samples shared a single common haplotype. The unique NZ haplotype differed by two substitutions from the common haplotype and the SA haplotype differed by one. The western samples clustered into two haplotype groups, both differing by three nucleotide mutations from the common eastern haplotype. A single substitution separated the western haplotypes from each other.

4. Discussion

The results of this study suggest that there are two distinct genetic clusters of *S. lalandi* in temperate Australasian waters and that the hypothesis of a single panmictic population across temperate Australasia should be rejected. Bayesian analysis, a priori testing and mtDNA examination all indicate that *S. lalandi* sampled from the western locality are genetically different from fish sampled from the eastern and central Australian coast and New Zealand. This finding is unusual for true marine species capable of long distance migration, because high dispersal capacity is expected to result in low genetic structure across a geographic range (Charrier et al., 2006). Ward et al. (1994) determined the average F_{ST} value across 57 different marine finfish species (0.062) and 49 different freshwater fish species (0.14). The differentiation found between western and eastern/central samples in this study (average 0.15) is more similar to that observed in freshwater fish, suggesting a restriction to gene flow.

Other large, pelagic, marine fish in southern Australia, including the southern Bluefin Tuna (*Thunnus maccoyii*; Grewe et al., 1997) and Mulloway (*Argyrosomus japonicus*; Archangi, 2008) show no east–west population structuring. Similarly, no southern Australian population structure was found by Gardner and Ward (1998) in the Gummy Shark (*Mustelus antarcticus*). The lack of population differentiation amongst the central and eastern sampled stocks of Yellowtail Kingfish identified in our study was consistent with the findings from Robinson et al. (2008) on mtDNA variation in Blue-eye

Trevalla (*Hyperoglyphe antarctica*), and Silver Warehou (*Seriola lalandi*) sampled across a similar geographic range. These findings could indicate a geographical or environmental barrier to east–west gene flow exists now, or did so in the past, which is reflected in a signature of east–west subdivision of some marine fish species in southern Australia.

Genetic population structuring of fish species is most often influenced by ecological, behavioural or hydrological factors (Charrier et al., 2006). The Leeuwin current brings warm, tropical flows southward along the Western Australian coast. The current moves along the west Australian coast and flows into the Great Australian Bight. The Leeuwin current is weakest over the summer months and strongest over autumn and winter (Godfrey and Ridgway, 1985). Given that Yellowtail Kingfish likely breed in the summer months (Poortenaar et al., 2001); it is possible that the weakening of this current reduces the passive dispersal of juvenile *S. lalandi* that might be spawned in the west.

A number of marine species display natal homing, the most iconic being salmon (Salmonidae) and sea turtles. It has been suggested that selective processes, such as active homing or other behavioural traits may limit dispersal. This could explain why fish that are capable of migration over large distances do nevertheless show genetic structuring. Similar to the Yellowtail Kingfish, the sea bass (*Dicentrarchus labrax*) found throughout the Mediterranean ocean, migrate large distances and thus have high dispersal potential, however, genetic structuring of the sea bass exists within the eastern and western Mediterranean basins (Bahri-Sfar et al., 2000). The authors suggest that behavioural traits that isolate populations over time may have resulted in these observed genetic differences. Currently not enough is known of the ecology, behaviour and reproductive biology of *S. lalandi* to determine if they show active homing or other selective traits that could account for the genetic divergence of this species. Observation and tag recapture studies suggest Yellowtail Kingfish return annually to northern Spencer Gulf, South Australia, where they presumably aggregate to spawn (Burlinson, 1947; Hutson et al., 2007b).

Principal Component Analysis and examination of allele frequencies suggested that Victorian samples might show a slight genetic variation from the other central/eastern localities; however, this difference was not observed in any of the other analyses performed. The power analysis performed suggested that this study had adequate

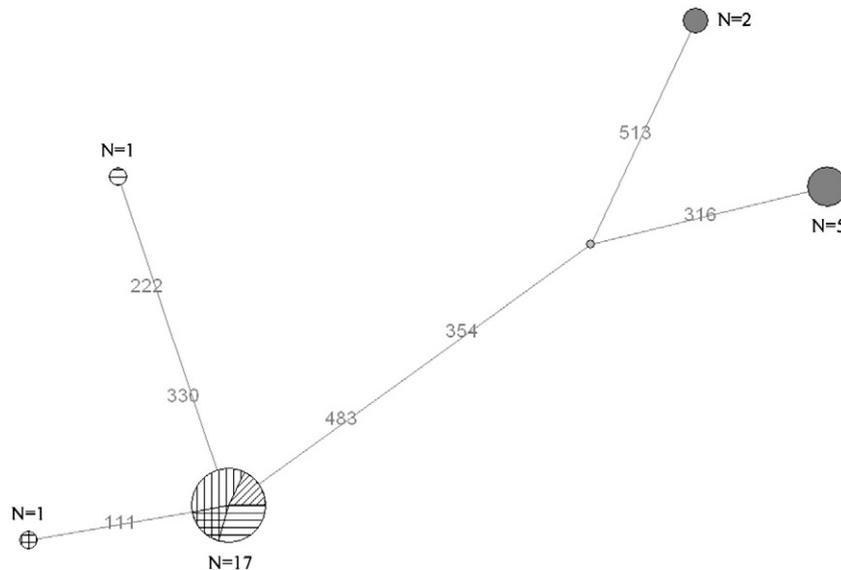


Fig. 5. Median-joining network based on the mitochondrial sequence alignment of 26 *Seriola lalandi* samples. Vertical lines represent samples from New South Wales, horizontal are from New Zealand, cross hatching represents South Australia, diagonal lines from Victoria, and solid colour represents samples from Western Australia. Numbers along lines refer to nucleotide mutations separating haplotypes (numbering according to Genbank Accession nos. JF345183–JF345208).

power to detect the population differentiation observed between the eastern/central and western samples but was not strong enough to detect fine scale structuring within the eastern/central localities. Given that the mtDNA analysis did not detect any differences in the Victorian samples, it is unlikely that divergences at this locality are large and the small differences detected may be an artefact of limited sampling.

Bayesian analysis showed that within the western samples there was one individual in the BAPS results and two individuals in the BAYESASS results that appeared to come from the eastern/central population. Additionally, in the BAYESASS results, a single individual from New South Wales was assigned to the western cluster. These findings support data from tagging studies that show that Yellowtail Kingfish are able to migrate long distances (Gillanders et al., 2001). Indeed, a single individual tagged with an artificial dart tag at Cape Leveque (Western Australia) was recaptured in the Solitary Islands, NSW (New South Wales Fisheries, unpublished data). Given that the populations identified by Bayesian analysis appear to be relatively homogenous, it is suggested that individuals that migrate large distances might return to a particular place to breed and thus presence of an eastern fish in the west would not necessarily imply gene flow associated with interbreeding. Alternatively, the BAPS analysis found two individuals sampled from New South Wales were equally likely to be grouped with cluster one or cluster two. This could indicate that these two individuals are hybrids between the two populations found within this study. Given that only two out of 272 individuals showed this putative hybrid genotype any hybridisation would be a rare event and has not contributed adequate gene flow to break down population differentiation.

This study concurs with tagging studies that suggest Yellowtail Kingfish migrate between Australia and New Zealand. Gillanders et al. (2001) suggested that large Yellowtail Kingfish over 75 cm in length are more likely to move long distances than smaller fish. The current study also confirms the findings of Nugroho et al. (2001) who found no evidence of genetic differentiation between fish sampled from New Zealand and New South Wales. Furthermore, Hutson et al. (2007a) found similarities between *S. lalandi* ectoparasite assemblages in eastern Australia and New Zealand.

The Tasman Front, a strong current flowing from Australia to New Zealand, could contribute to mixing of the southern (New Zealand) and central/eastern Australian populations given that juvenile Yellowtail Kingfish (<30 cm in length) are thought to inhabit the epipelagic zone, far offshore, for around one year and are likely to associate and drift with flotsam and floating seaweed in this zone (Diggle, 2002). The recent migration rates, calculated in BAYESASS, support this theory by suggesting that migration from New South Wales to New Zealand is larger than migration from New Zealand to New South Wales. Limited tag recapture data indicates Yellowtail Kingfish travel in both directions across the Tasman Sea (Bolton, 2009), although these movements have not been quantified.

For fisheries stock assessment, an ideal commercial fisheries stock is defined as being well mixed and having no gene flow with other stocks (Moran et al., 2003). Most fisheries stocks, however, are not ideal. Taylor and Dizon (1999) describe a management unit as 'geographical areas with restricted interchange of the individuals of interest with adjacent areas'. Given that this study found two distinct populations of *S. lalandi* in temperate Australasian waters that showed very limited, if any, mixing, it is recommended that this species be considered and managed for now as two separate, genetically distinct stocks or management units.

Maintaining the genetic integrity of wild fish populations is important for the conservation and management of fisheries (Farrington et al., 2000). Translocation is considered a problem when it leads to interbreeding of different stocks (Johnson, 2000). Outbreeding depression is a term used when hybridization of two genetically distinct populations results in reduced fitness (Ward, 2006). Human induced mixing of populations, for example through fish escaping from farms,

can lead to genetic degradation of local gene pools and outbreeding depression, although this depends to a large extent on the size of the receiving population compared to the number of escapees and on the degree of genetic differentiation of the cultured stock (Johnson, 2000). A reduction in fitness or viability of a species after crossbreeding can occur when fish genetically different from local populations escape from aquaculture farms and interbreed with wild fish (Keenan, 2000). A loss of genetic variation can lead to a reduction in a species' ability to adapt to a changing environment, thus potentially increasing its vulnerability to extinction over time (Chauhan et al., 2007). This may be particularly relevant in Western Australia, as low catch rates of Yellowtail Kingfish within this locality could suggest that western populations are small and hence more vulnerable to genetic degradation. However, low catch rates in Western Australia may merely reflect a lower fishing effort.

On the other hand, the mixing of two genetically distinct populations may not always result in outbreeding depression; it can have positive effects (Ward, 2006). Indeed recent analysis of outbreeding depression in wild populations suggests the risks are often overstated (Frankham et al., 2011). Hybrid vigour occurs when the hybridisation of two genetically distinct populations creates new variation that improves local adaptation (McClelland and Naish, 2007) although this phenomenon will tend to decrease in subsequent generations (Edmands, 1999; Falconer and Mackay, 1996). Populations that have undergone a bottleneck generally display the most positive response to hybridisation (McClelland and Naish, 2007). The Western Australian samples did not differ significantly in allelic richness and the mtDNA analysis suggested a historical evolutionary divergence as opposed to recent separation due to drift and/or inbreeding. This indicates that a bottleneck or inbreeding scenario is unlikely within this locality; hence hybrid vigour would be minimal. It is recommended that until more information on hybridisation between eastern and western Yellowtail Kingfish is obtained, a conservative approach be undertaken that limits translocation of this species to Western Australia, thus reducing the possibility of outbreeding depression.

The implications of this study are very significant to the Yellowtail Kingfish aquaculture industry. With industry expansion, it is likely that increased collaborations will occur between *S. lalandi* hatcheries nationally and internationally. This may involve translocation of broodstock and their progeny which differ in genetic makeup to wild fish in the receiving region and indeed some translocations of fish between land based facilities have already occurred. Translocations may also arise as part of a genetic programme, particularly if this is carried out on a national or regional basis. Translocations are particularly likely in Western Australia as Kingfish are more rarely caught in this state than in the eastern/central locations. Given the results of this study, key stakeholders and policy makers should consider the regulation of translocation to take into account the protection of the genetic diversity and population structure now apparent in the species. From an aquaculture perspective it will also be of interest to determine if there is any culture performance related differences between fish derived from the western locality compared to those from the other localities.

Although our findings are quite conclusive on the population structuring between western stocks and the eastern/central stocks, further work could be conducted to define any finer scale population structure within Australasian waters and beyond. The large distance that separates the South Australian and Western Australian sample sites could have potentially impacted on the results. It would be beneficial to sample one or two extra locations between the South Australian and Western Australian sampling sites to determine if there is a sharp boundary between the two genetic populations found or a gradual shift in allele frequencies over the geographical range. Gaps in sampling locations can potentially reduce the power of inferences that can be taken from the results of studies such as this (Anderson et al., 2010). We did attempt to sample from locations

between western WA and South Australia, however there is no commercial harvest of this species within the Australian Bight or southern Western Australia and reliance solely on recreational fishers and charter boats did not yield any samples.

It would also be beneficial to undertake temporal sampling as this has been shown to influence population results in some species (Olsen et al., 2002). An earlier study by Smith (1987) using allozymes, suggested that there could be temporally separated subpopulations of *S. lalandi* in New South Wales. No sub-structuring of the New South Wales population was found in the current study from fish sampled from three sites along the east coast; however, this might be due to a lack of temporal sampling. It would also be valuable to have larger sample sizes collected from more sites, particularly from Western Australia as only 15 samples were obtained for this study from only one site. It has been suggested that sample sizes of more than 50 are best for population analysis (Chauhan et al., 2007). Larger sample sizes would enable better analysis of the frequency of exchange between the two populations. Notwithstanding the small sample size from Western Australia, the high level of differentiation observed in the current study, analysed using sample size independent tests, leaves little doubt that there are two genetically distinct populations of *S. lalandi* in temperate Australasia. Additionally, the microsatellite findings were supported by the mtDNA analysis. MtDNA has been shown to be effective at detecting fine population structure and is capable of detecting genetic drift and founder effects (Barroso et al., 2005). Within the last couple of decades there has been much debate over what constitutes a unit of management, 'evolutionary significance' and at what level genetic conservation should be conserved (e.g. population, subspecies, species; Taylor and Dizon, 1999). When implementing a management strategy to help protect a species it is important that the decision is not solely based on population genetic data, but rather on an integration of genetic, demographic and ecological information (Paetkau, 1999; Taylor and Dizon, 1999). It is recommended that further analysis, both genetic and ecological, be performed on this species in the near future. In particular there is a need to determine the fitness of possible east–west hybrids, identify spawning grounds and discover if Yellowtail Kingfish display natal homing and try to ascertain if there is a distinct boundary between east and west genetic population or gradual shift in allele frequencies along a geographical range.

The clear differentiation of *S. lalandi* sampled from Western Australia suggests, at least, two genetically distinct populations of this species in temperate Australasia. This new information indicates the need for a review of translocation policies and to consider genetic diversity as a factor in the development of Yellowtail Kingfish aquaculture.

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