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RESEARCH ARTICLE

Genetic structuring of *Latris lineata* at localized and transoceanic scales

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Abstract Striped trumpeter (*Latris lineata*) is a demersal teleost distributed around the temperate clines of all the major oceans in the southern hemisphere. Within Tasmanian waters the species is managed as a single stock, although no studies have been performed to confirm genetic panmixia. A protracted pelagic larval phase and a recent transoceanic tag recapture of an adult fish suggest significant potential for genetic mixing between widely separated populations. Phylogenetic analysis of mitochondrial DNA control region sequences suggested no genetic mixing between Tasmania, New Zealand and St Paul/Amsterdam Islands, evidence for the first time that there is population structure at a transoceanic scale for this species. In addition, an analysis of molecular variance coupled with phylogenetic analyses suggested no significant structuring of striped trumpeter from three locations around Tasmania. The information provided in this study is useful for the design of modern fisheries management techniques such as spatially implemented marine reserves. In addition, species-by-species knowledge about population structures of marine species facilitates ecologically useful generalizations concerning their population dynamics and key issues on the broader ecology of the oceans.

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Introduction

Striped trumpeter (*Latris lineata* Forster in Bloch and Schneider 1801) are widely distributed around the temperate clines of the southern hemisphere. The species has been identified in Australia, New Zealand (Last et al. 1983), including the sub-Antarctic Auckland Island (Kingsford et al. 1989), the Gough and Tristan Da Cunha Island groups in the southern Atlantic Ocean (Andrew et al. 1995), the Amsterdam and St Paul Island groups in the southern Indian Ocean (Duhamel 1989) and more recently the Foundation seamount in the southern Pacific Ocean (Roberts 2003). Their distribution in Australia extends from the mid-coast of New South Wales to Kangaroo Island in South Australia as well as Tasmania (Kailola et al. 1993). From these accounts their distribution is limited to a latitudinal belt spanning from 35°S to 51°S (Fig. 1). At present the Australian population is assumed to consist of a single stock although no studies, genetic or otherwise, have been performed to corroborate this. For management purposes striped trumpeter populations from New South Wales, Victoria, South Australia and Tasmania are considered separate management units and are controlled independently by each state.

There are two main conduits for genetic mixing of marine organisms, larval dispersal and adult migration. Many demersal fish species have an extensive larval phase, a trait that may lead to high levels of dispersal and result in a lack of stock structure at various spatial scales. The extent of spatial structuring arising from larval dispersal is dependent on the pelagic larval duration (Cowen et al. 2006). Striped trumpeter are known to exhibit an extended offshore neustonic larval phase believed to be approximately 9 months in duration based on aquaculture studies (Furlani and Ruwald 1999). This extended pelagic larval

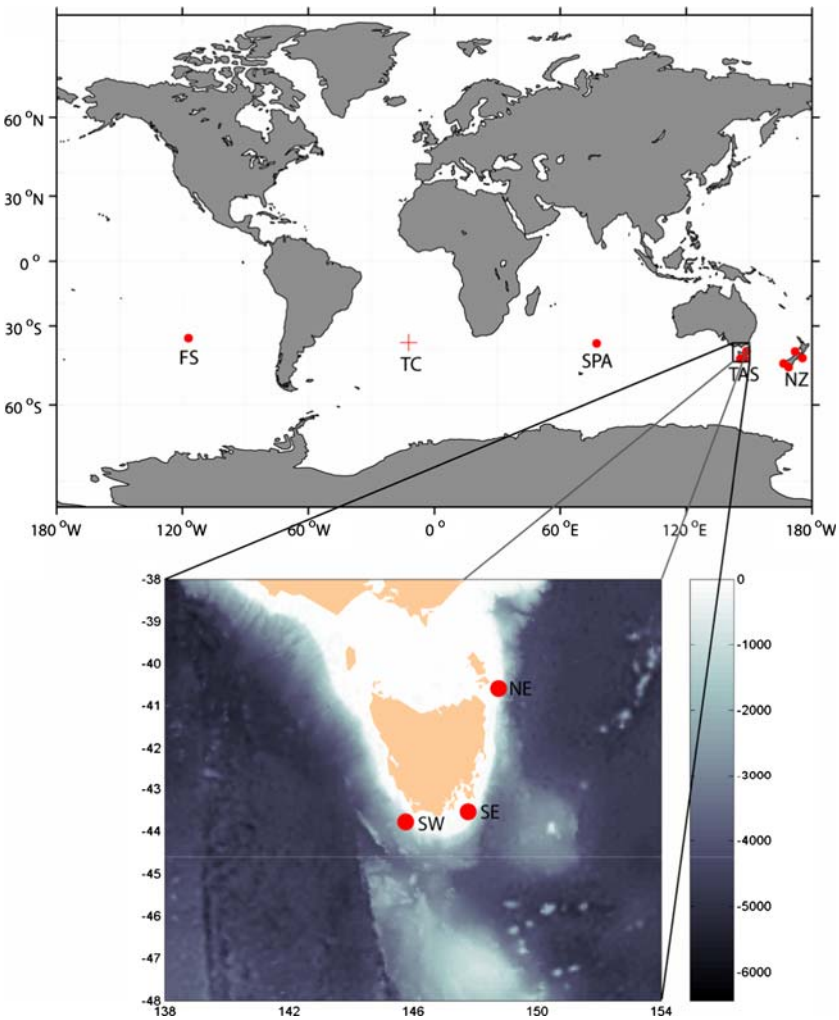

Fig. 1 Current known distribution of *Latris lineata*. This map has been adapted from Roberts (2003). *Filled circles* indicate sample sites for this study

phase combined with the mesoscale current systems flowing, generally, west to east in the southern hemisphere suggests potential for transoceanic mixing between striped trumpeter populations.

Active migration between reproductive populations of mature individuals is another source of population mixing. This mechanism is reasonably common for pelagic species but active migration over large distances particularly at an oceanic scale is not considered a common trait of demersal fish. However, the recapture of a striped trumpeter 3 years after tagging adjacent to the southeast coast of Tasmania approximately 5,800 km to the west at the Amsterdam Island group represents an obvious anomaly (Tracey et al. 2006). This finding not only revealed that they are capable of transoceanic journeys but also provided another possible mechanism for the wide dispersal and genetic mixing of this species. Of particular interest was the counter current direction of this migration, assuming the migratory path followed the shortest route. If this tag recapture is evidence of a migratory ability previously unobserved for this species, it provides an alternative potential source of mixing.

The mitochondrial genome is particularly suited to genetic studies of intraspecific population structure as it has a rapid rate of evolution and is predominately maternally inherited (Alvarado Bremer et al. 1995). The degree of geographic structuring of mitochondrial DNA (mtDNA) polymorphism in highly mobile vertebrate species reflects both historical and current levels of gene flow among intraspecific populations (Avise et al. 1992; Alvarado Bremer et al. 1995). The d-loop control region is of particular use in phylogenetic studies due to its hypervariability (Wenink et al. 1994).

In this study we have presented the analysis of striped trumpeter mtDNA control region sequences. Firstly, to determine whether striped trumpeter from Tasmania, New Zealand and the St Paul/Amsterdam Island regions are a panmictic unit or structured into distinct phylogeographic populations. Secondly, to test for genetic homogeneity of the Tasmanian population.

Materials and methods

Sampling

Skeletal muscle tissue was collected from 104 striped trumpeter between 1995 and 2004. Thirty individuals were collected from the St Paul and Amsterdam Islands (SPA) and stored in formalin. Twelve were collected from New Zealand (NZ), 62 individuals from around Tasmania (TAS) and one from the Foundation seamount. These were stored in 70% ethanol. As there was only one sample available from the Foundation seamount it was excluded from most analyses with the exception of the neighbor-joining and maximum likelihood phylogenetic trees. The TAS samples were further divided into three specific areas: northeast, southeast and southwest (Table 1).

DNA extraction and amplification

Approximately 50 mg of muscle tissue from each individual was digested for 2 h at 65°C in a 1.5 ml micro centrifuge tube containing 500 µl of CTAB and 5 µl of 20 mg/ml Proteinase K. The homogenate was extracted with 500 µl of chloroform-isoamyl alcohol 24:1 v/v followed by extraction with phenol/chloroform-isoamyl alcohol 25:24:1 v/v/v, before a final extraction with chloroform-isoamyl alcohol to remove traces of phenol prior to precipitation in isopropanol. Following centrifugation at 3,100 *g* for 15 min, DNA pellets were washed with 500 µl of 70% ethanol, before being dried and resuspended in 100 µl of deionized water.

PCR and automated sequencing

Polymerase chain reaction (PCR) was used to amplify a section of the mtDNA control region. PCRs were conducted in 50 µl volumes, each containing 1 unit of *Taq* DNA polymerase (Promega, Madison), 5 µl of 10× reaction buffer (67 mM Tris–HCL (pH 8.8), 16.6 mM $(NH_4)_2SO_4$, 0.4% Triton X-100 and 0.2 mg/ml Gelatin), 200 µM dNTPs, 0.5 µM of each oligonucleotide primer, 1.5 mM $MgCl_2$, and 20–100 ng of suspended genomic DNA. The primer pair L15995 (5′AAC TCT CAC CCC TAR CTC CCA AAG 3′) and 16498H (3′CCT GAA GTA GGA ACC AGA TG 5′) (Kocher et al. 1989) was used to amplify a 403 base pair region of the d-loop. Thermal cycling conditions for the amplification of the control region consisted of an initial denaturation period of 94°C/3 min, followed by 35 cycles of 94°C/30 s, 52°C/30 s and 72°C/60 s, and a final extension of 72°C/5 min. To determine successful amplification, the PCR products were separated by electrophoresis in a 1.0% agarose gel with 0.5 µg/ml ethidium bromide, and viewed under ultraviolet light. Prior to sequencing the target PCR products were purified using an UltraClean PCR Clean-up kit (MO BIO Laboratories, Inc.).

Sequencing reactions were performed using the CEQ Dye Terminator Cycle Sequencing Kit (Beckman Coulter)

Table 1 *Latris lineata.* Collection details of samples and the number of haplotypes within each sample

Geographic region	Latitude[a]	Longitude[a]	(*n*)	Collection year	No. of haplotypes
Pacific Ocean					
Northeast Tasmania	40°36′S	148°47′E	15	2003–2004	15
Southeast Tasmania	43°32′S	147°55′E	23	2003–2004	20
Southwest Tasmania	43°33′S	145°56′E	23	2003–2004	20
Sub-total			61		55
Indian Ocean					
St Paul Island	37°50′S	77°30′E	30	2003	29
Sub-total			30		29
Tasman Sea					
Fiordland, New Zealand	45°46′S	166°38′E	5	1995–1996	5
Stewart Island, New Zealand	46°53′S	168°06′E	4	1995–1996	4
Tolaga Bay, New Zealand	38°17′S	177°30′E	1	1996	1
Kapiti Island, New Zealand			1	1996	1
Mernoo Bank, New Zealand	43°16′S	175°26′E	1	1996	1
Sub-total			12		12
Pacific Ocean					
Foundation seamount	35°27′S	117°20′W	1	1995	1
Sub-total			1		1
Total			104		96

[a] Approximate latitudes and longitudes

by following the manufacturer's instructions, and sequencing extension products were separated on a Beckman Coulter CEQ 8000 DNA analysis system.

Phylogenetic analysis and population structure

All sequences were aligned using ClustalW (Higgins et al. 1994) within BIOEDIT version 5.0.9 (Hall 1999). The vertebrate mtDNA control region is known to have a high rate of nucleotide substitution that can be modeled by a gamma distribution specified by the parameter α (Wakeley 1993). The parameter α was empirically estimated from the sequence data using DAMBE version 4.0.98 (Xia and Xie 2001). Values of haplotypic diversity (h) (Nei and Tajima 1981) and nucleotide diversity (π) (Nei 1987) based on the Tamura–Nei distances (Tamura and Nei 1993) were computed with ARLEQUIN version 2.0 (Schneider et al. 2000). The 104 samples were used to calculate a mean transition: transversion ratio in MEGA version 2.1 (Kumar et al. 2001). Geographical structuring within TAS samples and between TAS and SPA samples was tested using a hierarchical analysis of the molecular variance (AMOVA), based on the gamma corrected Tamura–Nei distances. The significance of the tests was determined by a nonparametric permutation procedure (Excoffier et al. 1992) conducted in ARLEQUIN. The pairwise matrix of fixation index values was also conducted in ARLEQUIN.

The phylogenetic relationship among haplotypes was reconstructed using two methods: neighbor-joining (Saitou and Nei 1987), using the gamma corrected Tamura–Nei distance matrix reconstructed in MEGA version 2.1, and maximum likelihood analysis performed using the heuristic search algorithm of PAUP version*4.0b10 (Swofford 2002). Pairwise distances for the maximum likelihood analysis were calculated under the general time reversible model GTR + I + G (Lanave et al. 1984) as calculated by MrModeltest version 2.1 (Nylander 2004), with resulting trees being unrooted. Nonparametric bootstrap analysis was performed based on 35,000 replicate data sets using the fast stepwise addition in PAUP* retaining groups compatible with the 50% majority-rule consensus.

Results

Sequence variation

Analysis of 104 striped trumpeter control region sequences identified 115 polymorphic sites within a 403 bp fragment. These polymorphisms yielded 96 haplotypes from the five sample areas. This large number of haplotypes gave a high global value of haplotypic diversity ($h = 0.9970 \pm 0.0020$), therefore the probability that two specimens drawn at random will have differences in this particular section of the control region is greater than 99%. Such a high rate of diversity agrees with other studies of teleost fish (Dudgeon et al. 2000; Aboim et al. 2005). The sequence from the most common haplotype was registered in GenBank–accession reference: DQ845246. Nucleotide frequencies were $T = 33.7\%$, $C = 18.3\%$, $A = 34.7\%$ and $G = 13.2\%$, revealing a clear A–T bias in base composition (68%). The observed transition:transversion ratio was 2.9:1.0. These mutations were heterogeneously distributed through the selected mtDNA segment resulting in a low alpha parameter estimate ($\alpha = 0.227$). The estimated global mean nucleotide diversity was 0.029 ± 0.004.

Population variability

Within the NE-TAS sample no haplotype occurred more than once resulting in the highest possible haplotypic diversity estimate ($h = 1.000 \pm 0.024$). This may be due to the low sample size from this area. Within both the SE and SW-TAS samples 20 different haplotypes were identified yielding the lowest haplotypic diversity ($h = 0.988 \pm 0.016$). The NZ samples also yielded the highest possible value of haplotypic diversity ($h = 1.000 \pm 0.03$) with each of the sampled individuals having a unique haplotype. From the SPA sample, 29 haplotypes were identified ($h = 0.998 \pm 0.09$).

Phylogenetic analysis

From the neighbor-joining tree (Fig. 2), it is clear that Tasmanian striped trumpeter dominate clade I (81%). By removing clade Ia, which includes several of the SPA samples present in clade I, the percentage of Tasmanian samples was further increased to 88%. The St Paul/Amsterdam Island samples dominate clade II (61%). Again the removal of clade IIa increased the uniqueness of clade II to the SPA region (76%).

Within both clades I and II there was no significant structuring of the Tasmanian samples, supporting the theory that the Tasmanian population is homogenous. Interestingly, of the 11 Tasmanian striped trumpeter occurring in clade II, 10 were from the southern regions of Tasmania.

The model of best fit calculated by MrModeltest version 2.1 was the GTR + I + G with a log likelihood score of 2,076.99. The maximum likelihood tree derived from this substitution model (tree score 2,040.88) suggested trans-oceanic structuring, with greater than 50% bootstrap support for clade II which represented the majority of the St Paul/Amsterdam Islands sample (Fig. 3).

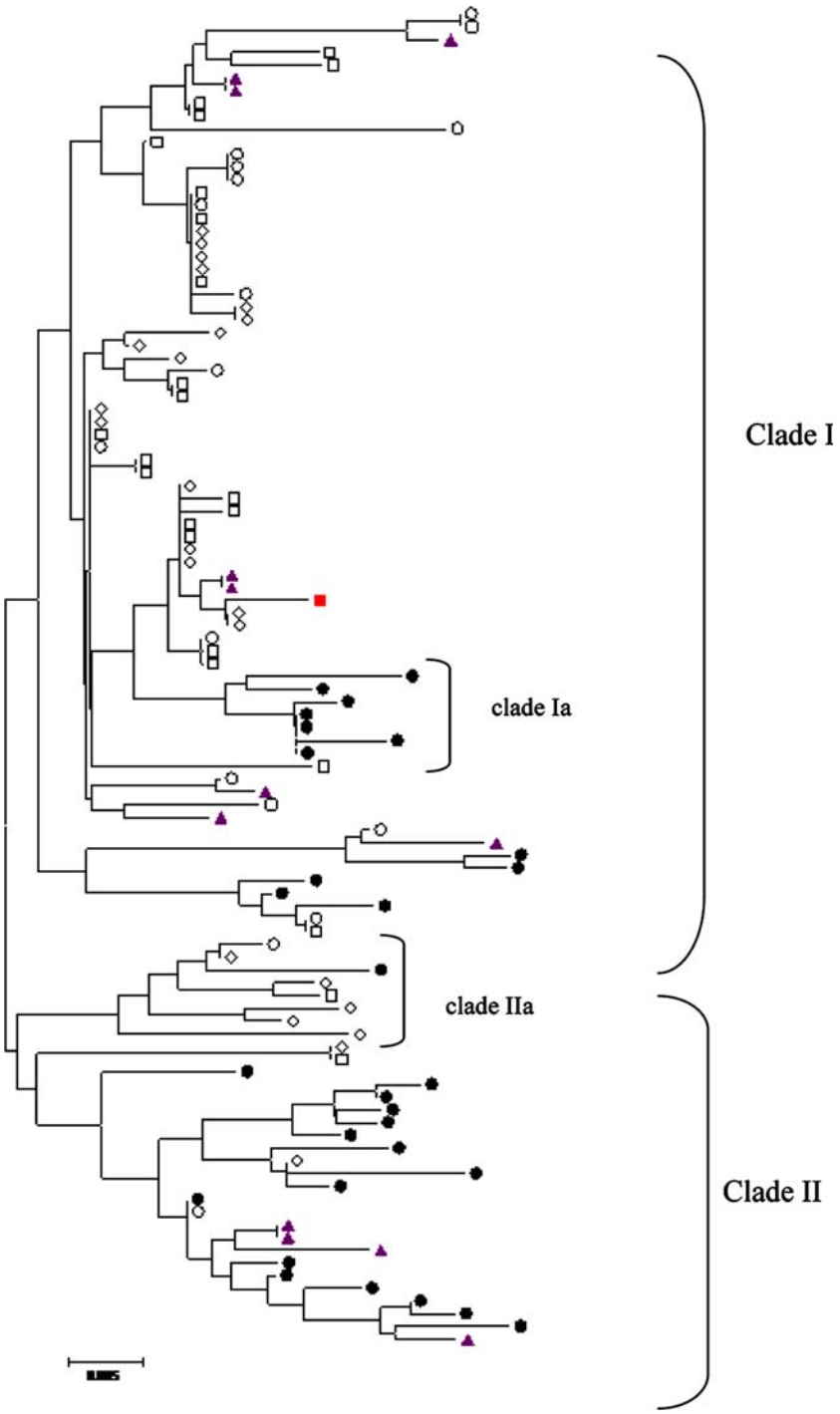

Fig. 2 *Latris lineata.* Unrooted neighbor-joining tree of the 104 samples based on the gamma corrected Tamura–Nei distance matrix of mtDNA control region sequences. Symbols refer to the geographical origin of the haplotypes: northeast (*open circle*), southeast (*open diamond*) and southwest Tasmania (*open square*), St Paul/Amsterdam Islands (*dark filled circle*), New Zealand (*dark filled triangle*) and the Foundation seamount (*dark filled square*)

Phylogeographical relationships of populations

The pairwise matrix of Φ_{ST} values and their corresponding *P*-values, shows a low level of genetic differentiation between all of the TAS samples and a highly significant level between all three TAS samples and the SPA sample (Table 2). This absence of genetic heterogeneity between the three TAS sites was confirmed by AMOVAs (Table 3) with no significant difference detected ($P < 0.05$). The Tasmanian sites were pooled for further analysis. The subsequent AMOVA performed on the TAS, NZ and SPA data again identified a highly significant divergence between these three populations (Table 4).

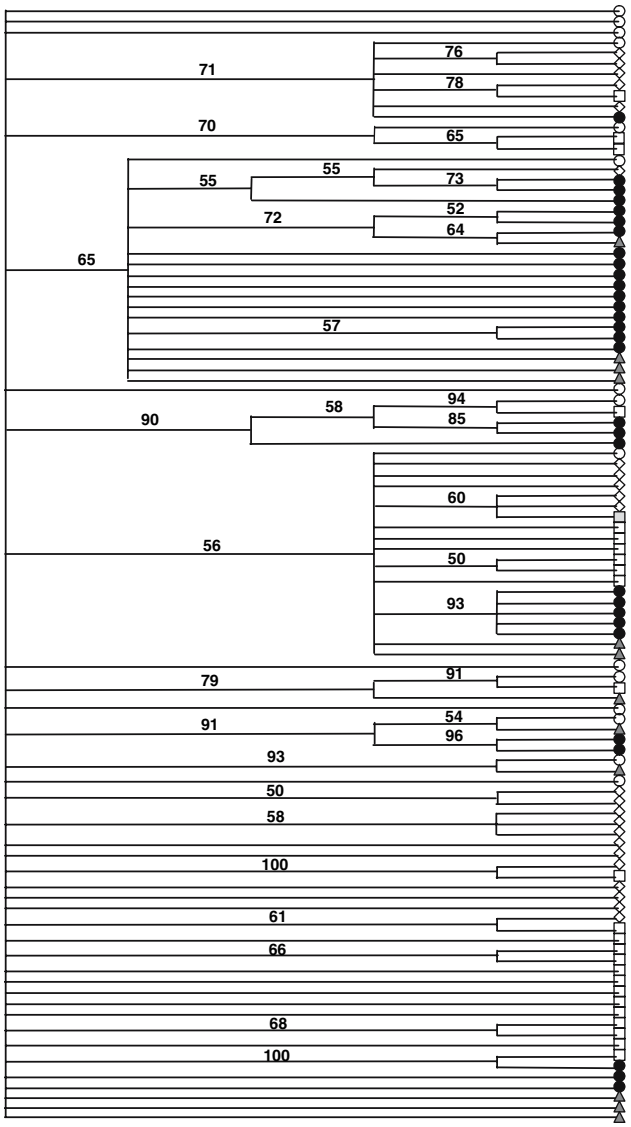

Fig. 3 *Latris lineata.* Maximum likelihood tree of the 104 samples with bootstrap values corresponding to 50% majority rule consensus. Symbols refer to the geographical origin of the haplotypes: northeast (*open circle*), southeast (*open diamond*) and southwest Tasmania (*open square*), St Paul/Amsterdam Islands (*dark filled circle*), New Zealand (*dark filled triangle*) and the Foundation seamount (*dark filled square*)

Discussion

Transoceanic mixing of striped trumpeter

There are many studies with contrasting findings related to genetic mixing of demersal species associated with seamount and oceanic islands. Some suggest that populations exhibit panmixia across large geographical distances on oceanic scales. These include: slender armourhead *Pseudopentaceros wheeleri* and wreckfish *Polyprion americanus*, while others demonstrate evidence of gene divergence among populations at the transoceanic, oceanic and regional scales. These include: roundnose grenadier *Coryphaenoides rupestris*, ling *Genypterus blacodes*, hoki *Macruronus novaezealandiae* and oreos *Allocyttus niger* (reviewed in Creasey and Rogers 1999; Rogers 2003). The concept that the temperate latitudes of the southern hemisphere may be a broad zoogeographic province for ichthyofauna has also been presented in several studies (Collette and Parin 1991; Duhamel 1997; Burridge and White 2000).

Striped trumpeter are distributed widely around the temperate latitudes of the southern hemisphere. They are found as far north as 35°S at the Foundation seamount and as far south as 51°S at Stewart Island, located below the southern island of New Zealand. If the striped trumpeter populations are linked genetically there are two conduits that would facilitate such a state, adult migration and larval advection. Based on its life history traits larval advection would be the most obvious for striped trumpeter. However, because there was a tag recapture at Amsterdam Island of a fish tagged near Tasmania, adult migration cannot be discounted. Although this was only one individual the exchange of ecologically insignificant numbers of migrants between populations can maintain apparent panmixia (Utter 1991; Dudgeon et al. 2000). This migration was particularly unusual as the maximum depth that striped trumpeter has been recorded at is 350 m (Last et al. 1983). As the species is demersal it would be reasonable to assume that the depths of the southern ocean basins would constitute barriers for adult migration.

Table 2 *Latris lineata.* Genetic differentiation matrix of sampled striped trumpeter populations

Population	TAS_{NE}	TAS_{SE}	TAS_{SW}	NZ	SPA
TAS_{NE}	–	0.334 ± 0.008	0.171 ± 0.007	0.000 ± 0.000	0.000 ± 0.000
TAS_{SE}	0.004	–	0.090 ± 0.005	0.000 ± 0.000	0.000 ± 0.000
TAS_{SW}	0.017	0.024	–	0.000 ± 0.000	0.000 ± 0.000
NZ	0.194	0.201	0.222	–	0.002 ± 0.000
SPA	0.195	0.216	0.248	0.143	–

Φ_{ST} below diagonal line, *P*-values above line; number of permutations = 3,024

Table 3 *Latris lineata.* Tests of genetic diversity between striped trumpeter populations from different locations around Tasmania (NE = northeast, SE = southeast, SW = southwest) using hierarchical analysis of molecular variance (AMOVA) on mtDNA control region sequences

Test	Source of variation	*df*	Variance component	Percentage variation	Fixation index	*P*-value[a]
NE versus SW	Among populations	1	0.0973	1.66	$\Phi_{ST} = 0.0166$	0.167 ± 0.011
	Within populations	36	5.7680	98.34		
NE versus SE	Among populations	1	0.0228	0.38	$\Phi_{ST} = 0.0038$	0.355 ± 0.015
	Within populations	36	5.9504	99.62		
SE versus SW	Among populations	1	0.1422	2.44	$\Phi_{ST} = 0.0244$	0.121 ± 0.009
	Within populations	44	5.6848	97.56		

[a] 10,000 permutations

Table 4 *Latris lineata.* Test of genetic diversity between striped trumpeter populations from Tasmania (TAS), New Zealand (NZ) and the St Paul/Amsterdam Island group using hierarchical analysis of molecular variance (AMOVA) on mtDNA control region sequences

Source of variation	*df*	Variance component	Percentage variation	Fixation index	*P*-value[a]
Among regions	2	1.85	21.87	$\Phi_{ST} = 0.219$	$\ll 0.0001$
Within regions	100	6.60	78.13		

[a] 10,000 permutations

Adjacent to Tasmania, female striped trumpeter are highly fecund with a relatively protracted spawning period (Tracey et al. 2007). The larvae are also characterized by a pelagic larval duration of approximately 7–9 months. These characteristics combined with the predominant westerly wind drift that occurs in the southern hemisphere provide the most likely mechanism for transoceanic population connectivity.

If larval migration were to occur between the landmasses and seamounts which striped trumpeter inhabit, the most likely location would be between Australia and New Zealand as this is the shortest stretch of ocean between two populations at approximately 1,700 km. This is compared with approximately 5,600km between St Paul/Amsterdam Island and Tasmania and 6,000 km between the Foundation seamount and New Zealand.

An oceanographic transport mechanism between Australia and New Zealand exists in the form of the Tasman Front which meanders west to east, diverging off the north–south flowing East Australian Current as it reaches about 35°S (Chiswell et al. 2003). However, the time frame for passive drifters deployed off the coast of Australia to reach New Zealand is approximately 15–24 months (Cresswell et al. 1994), much longer than the 9-month pelagic larval phase of striped trumpeter.

F-statistics, AMOVA and phylogenetic analyses all indicated genetic structuring of striped trumpeter populations at the transoceanic scale. This suggests little recent gene flow between the SPA, NZ and TAS populations arising from either larval dispersal or active migration of adult fish. The sample from the Foundation seamount was allocated to clade I of the neighbor-joining tree which contained the majority of the Tasmanian samples. Although, as there was only one sample from the Foundation seamount it was impossible to draw any conclusions as to the relationship of the Foundation seamount with the other sampled populations. The fixation index was relatively consistent and highly significant between the three transoceanic populations. Surprisingly, the lowest F_{ST} value was recorded between the NZ and SPA populations, the locations with the greatest geographic separation. It is quite likely that the low sample size from New Zealand has contributed to this apparent homoplasy. The phylogenetic trees do not give any indication of the New Zealand population forming a cohesive unit; again, the low sample size is assumed to have contributed to this outcome. Another potential source of error arising from the New Zealand sample is the issue of temporal genetic stability as the New Zealand sample was collected 8 years prior to the other samples. A collection of both temporal and spatial replicates allows a quantitative evaluation of the importance of sampling error and signal:noise ratio in gene diversity analysis (Waples 1998), although this was beyond the scope of this study.

The structuring between the TAS and SPA samples concurs with a previous study based on otolith morphometrics which found otolith form differences between striped trumpeter collected from TAS and SPA were indicative of two distinct populations (Tracey et al. 2006).

The genetic differences between the Tasmanian and New Zealand populations of striped trumpeter indicated in

this study also concur with other studies exploring the genetic divergence of marine species between Australian and New Zealand populations. Jackass morwong *Nemadactylus macropterus*, a demersal perciform with an extended larval phase, showed distinct separation between Australian and New Zealand populations (Grewe et al. 1994). The lobster species *Sagmariasus verreauxi* also was shown to have populations genetically different between the two countries (Brasher et al. 1992). *S. verreauxi* also has an extended pelagic phyllosoma phase estimated to be between 8 and 12 months (Booth 1986). In contrast to these studies the southern rock lobster *Jasus edwardsii* is genetically indistinguishable between Australia and New Zealand (Ovenden et al. 1992). It has a larval phase estimated to be between 12 to 24 months (Booth and Phillips 1994), concurring with the time taken for the remote drifters to advect from one country to the other. This synthesis would suggest that pelagic larval duration is a major determinant in transoceanic gene mixing. Although the consideration of active versus passive migration cannot be discounted, for example, the lobster species use passive migration for the duration of their larval phase with the exception of diurnal vertical migration (Bradford et al. 2005), while the fish species are capable of extensive active migration once they are post-flexion, which occurs after approximately 1 month for striped trumpeter (Furlani and Ruwald 1999).

In terms of fishery stock assessment, identifying the lack of significant migration to or from the Tasmanian stock is of significant benefit, satisfying the assumption of a ''closed'' population, common to many fishery stock assessment models.

Structuring of the Tasmanian striped trumpeter population

The results from this study indicate that adjacent to Tasmania, striped trumpeter constitute a single homogenous stock. Although the F_{ST} values between the Tasmanian samples are large enough to represent isolation in an ecological if not evolutionary sense, considering the scale of the fixation index is from 0 to 1, with the lower the value the less the genetic difference, therefore it is possible that if the sample sizes were increased these values could become significant and the finding of a homogenous stock would be compromised. Data from striped trumpeter larval dispersal modeling (S.R. Tracey and A. Hobday, unpublished data) indicate that the extended larval dispersal coupled with the oceanographic features common to Tasmania create a situation where there is a high probability of significant mixing of larvae from isolated spawning grounds adjacent to Tasmania. This supports the case for homogeneity of the Tasmania population.

A similar finding indicating the absence of sub-structuring across southern Australia based on genetic analysis has been reported for *N. macropterus* (Grewe et al. 1994), although there is conjecture as to this finding. An otolith microchemistry study suggested a more complex population structure around the same area (Thresher et al. 1994). The discrepancy between these two findings has been ascribed to the relative sensitivities of the two techniques to the rates of exchange between the two populations (Thresher et al. 1994).

Identifying stock structure is an essential component to understanding a population's ability to maintain viability under fishing pressure. The apparent homogenous structure of the population adjacent to Tasmania would indicate that a single stock management strategy is appropriate for this species. However, the caveat as to the robustness of the findings based solely on genetic analysis would warrant further study to confirm this finding. This could include analysis of: sequence data from the entire control region, sequence data from another coding region of the mitochondrial genome, a nuclear marker or even a divergent technique such as otolith microchemistry. All these techniques have potential to further resolve the phylogenetic relationship between the Tasmanian sample locations. However, given the small-scale of the striped trumpeter fishery adjacent to Tasmania it would be difficult to warrant management in the traditional sense as anything other than a single stock based on genetic divergence alone. If it were shown that the life history parameters of the discrete sub-populations were different, then separate stock assessments would be warranted and potentially, alternate size limits, etc could be imposed to regulate exploitation of the sub-populations.

Genetic data relating to the structure of marine population on a species-by-species basis are important from both an ecological and a conservation perspective. This information enhances the design of modern fisheries management techniques such as spatially implemented marine reserves. In addition, only by gaining knowledge about the population structures of a greater number of marine species can we make ecologically useful generalizations concerning their population dynamics and key issues such as the impact of pelagic larval duration on the broader ecology of the oceans.

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