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ORIGINAL PAPER

Connectivity between marine reserves and exploited areas in the philopatric reef fish *Chrysoblephus laticeps* (Teleostei: Sparidae)

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Abstract 'No-take' marine protected areas (MPAs) are successful in protecting populations of many exploited fish species, but it is often unclear whether networks of MPAs are adequately spaced to ensure connectivity among reserves, and whether there is spillover into adjacent exploited areas. Such issues are particularly important in species with low dispersal potential, many of which exist as genetically distinct regional stocks. The roman, *Chrysoblephus laticeps*, is an overexploited, commercially important sparid endemic to South Africa. Post-recruits display resident behavior and occupy small home ranges, making *C. laticeps* a suitable model species to study genetic structure in marine teleosts with potentially low dispersal ability. We used multilocus data from two types of highly variable genetic markers (mitochondrial DNA control region and seven microsatellite markers) to clarify patterns of genetic connectivity and population structure in *C. laticeps* using samples from two MPAs and several moderately or severely exploited regions. Despite using analytical tools that are sensitive to detect even subtle genetic structure, we found that this species exists as a single, well-mixed stock throughout its core distribution. The high levels of connectivity identified among sites support the findings of previous studies that have indicated that inshore MPAs are an adequate tool for managing overexploited temperate reef fishes. Even though dispersal of adult *C. laticeps* out of MPAs is limited, the fact that the large adults in these reserves produce exponentially more offspring than their smaller counterparts in exploited areas makes MPAs a rich source of recruits. We nonetheless caution against concluding that the lack of structure identified in *C. laticeps* and several other southern African teleosts can be considered to be representative of marine teleosts in this region in general. Many such species are represented in more than one marine biogeographic province and may be comprised of regionally adapted stocks that require individual management.

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Introduction

'No-take' marine protected areas (MPAs) are an important tool to manage coastal fisheries and prevent the collapse of fish stocks (Sale et al. 2005). Primary considerations when

designating MPAs are the conservation of biodiversity and the maintenance of ecosystem functioning (e.g., Leslie 2005). Although connectivity among populations residing in different MPAs and maintenance of genetic diversity are recognized as important aspects of reserve design (e.g., Roberts et al. 2003), they have rarely been considered when designating marine reserves. The possibility that cryptic biodiversity exists within the ranges of widely distributed species is considered even less frequently (von der Heyden 2009). In South Africa, recent genetic studies have indicated that many coastal species are subdivided into distinct genetic units that are often associated with two or more of the region's four major marine biogeographic provinces (the cool-temperate west coast, the warm-temperate south coast, the subtropical south-east coast and the tropical north-east coast; Teske et al. 2009a). In several cases, these units are so distinct from each other on the basis of genetic data (Teske et al. 2009a, b), physiological data (Teske et al. 2008, 2009a; Zardi et al. 2010) and morphological data (Edkins et al. 2007; Teske et al. 2008, 2009b) that they can be considered to be distinct stocks or even distinct species. Information on genetic structure is thus of great importance when designating MPAs to ensure adequate management of each of a species' stocks (von der Heyden 2009).

Whether or not a species is demographically structured depends largely on its dispersal potential (Palumbi 1994). Southern African coastal marine animals that disperse passively (e.g., by means of planktonic larvae) are often subdivided into distinct genetic units (e.g., Teske et al. 2007a; Zardi et al. 2007), whereas actively dispersing species are not (e.g., Klopper 2005; Tolley et al. 2005; Oosthuizen 2007; Teske et al. 2007b), but there are exceptions (e.g., Teske et al. 2007c; Neethling et al. 2008). Studies showing that larvae of many species do not simply disperse like passive particles (e.g., Stobutzki 2001), and that species with high dispersal potential may nonetheless be highly structured (e.g., Möller et al. 2007), suggest that genetic structure needs to be assessed on a case by case basis.

An important function of South African MPAs is to manage temperate reef fishes, many of which are heavily exploited and whose stocks are considered to have collapsed (Griffiths 2000; Sauer et al. 2006). Particularly vulnerable are the seabreams (family Sparidae) of which over 40 species are targeted by both recreational and commercial fisheries on South Africa's south coast (Tilney et al. 1996). Seabreams are typically long-lived and may attain maximum ages of approximately 30 years (Griffiths and Wilke 2002). They grow slowly and mature late, and as some species undergo an age-related sex change, traditional management strategies based on bag limits and size restrictions appear to be ineffective in aiding their stock recovery because selective removal of larger specimens will result in a skewed sex ratio and reduced reproductive potential (Buxton 1992; Griffiths 2000). By protecting spawner biomass, MPAs are considered to not only protect the remaining populations, but also to facilitate reseeding of surrounding areas and in that way improve fishery production in exploited areas (Roberts et al. 2005). South African MPAs are generally considered successful in protecting local populations of overexploited fishery species, as population densities and maximum reported body sizes are significantly greater than in non-protected areas (Buxton and Smale 1989; Kerwath 2005; Kerwath et al. 2007; Götz et al. 2008a, 2009). However, little is known about spillover into adjacent exploited areas and levels of gene flow between MPAs.

The roman, *Chrysoblephus laticeps* (Valenciennes, 1830), is a sparid endemic to South Africa whose core distribution extends from False Bay in the west to the Kei River in the southeast (Griffiths and Wilke 2002) (Fig. 1). The species is mostly associated with inshore reefs and offshore pinnacles, but has also been found at depths of up to 100 m (Buxton and Smale 1984; Buxton 1987; Mann 2000). *Chrysoblephus laticeps* is severely overexploited throughout its range (Griffiths 2000) but still occurs at high densities in several MPAs, most notably in the Tsitsikamma National Park (Tsitsikamma NP) (Götz et al. 2008b), which was established in 1964 and is one of the oldest marine reserves in the world (Buxton and Smale 1989). The roman can be considered to be a suitable model organism to study the effects of environmental discontinuities and large geographic distances between MPAs on exploited reef fish species with potentially low dispersal ability. Most dispersal in this species is expected to occur early during the species' life history by means of larvae that remain pelagic for up to 30 days (Davis 1996). Active adult dispersal is likely to be extremely low, as post-recruits reside within home ranges less than 100 m^2 in size (Kerwath et al. 2007), and dispersal over greater distances (>2 km) is rare (Buxton and Allen 1989). Maximum dispersal distances of 39–54 km have been reported in individual cases (Griffiths and Wilke 2002; ORI tagging program, unpublished data), but concerns have been expressed about the accuracy of these estimates (Kerwath et al. 2007). Spillover of adults out of MPAs is negligible (Kerwath et al. 2008), suggesting that gene flow between MPAs may also be low. In addition to the species' potentially low dispersal ability, its protogynous hermaphroditism (sex change from female to male at an age of approximately 7 years) (Buxton 1992) may theoretically drive genetic structuring in this species because of a reduced effective population size (Hartl and Clark 1997) and increased genetic drift (Hauser and Carvalho 2008). In the long term, a combination of these factors may result in loss of genetic diversity in populations residing in many of the smaller MPAs.

Given that most of the southern African marine animals that disperse primarily by means of planktonic larvae are

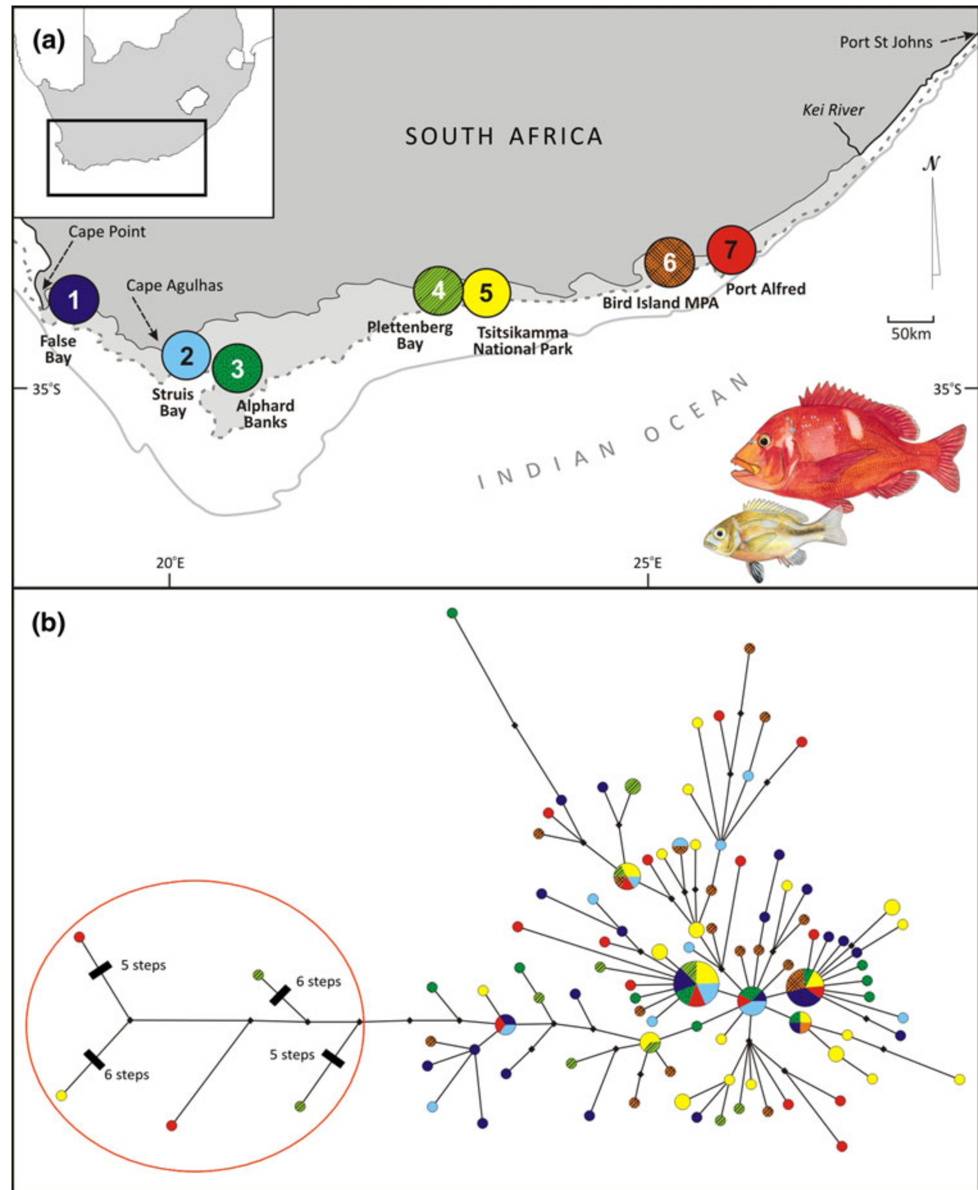

Fig. 1 *Chrysoblephus laticeps*. **a** A map of the temperate south coast of South Africa showing sampling sites. The *light grey* area indicates the species' core distribution. Hundred and 200 m contour depths are indicated by *dotted and light grey lines*, respectively. Cape Agulhas (which separates False Bay from the other sampling locations) and Cape Point are the approximate boundaries of a transition zone between warm- and cool-temperate biotas. Genetic breaks have been identified across both localities. "False Bay" (Site 1) is a composite of three distinct sampling sites that are in close proximity to each other: Seal Island, Wolfgat and Rooiels (Table 1); **b** a median-reducing haplotype network (with maximum parsimony) showing genealogical relationships among mtDNA control region haplotypes of *C. laticeps*. The sizes of the circles are proportional to haplotype frequencies, and the lengths of *connecting lines* indicate the number of mutation steps between them, with the *shortest lines* representing a single step. The *small black nodes* represent hypothetical vector haplotypes not present in the samples. The group of 'outliers' is encircled. In several cases, long branches have been reduced; the number of mutational steps is indicated for these

genetically structured, we hypothesized that *C. laticeps* is subdivided into two or more distinct regional stocks. Genetic differentiation may exist between False Bay (a site often considered to be located in a transition area between warm- and cool-temperate provinces, e.g., Bolton and Anderson 1997) and sites on the warm-temperate south coast, between coastal and offshore sites, or even among coastal sites along the south coast. We tested this hypothesis by analysing multilocus data from highly resolving genetic markers using a range of methods capable of identifying both large- and fine-scale patterns of population genetic structure and connectivity. Our results are discussed within the context of the species' biology and focus on the usefulness of MPAs in protecting the remaining populations of overexploited South African marine fishes.

Materials and methods

Sampling

Chrysoblephus laticeps was sampled at seven sites spanning the species' core distribution (Fig. 1a; Table 1). Two of these sites are located in MPAs (Tsitsikamma NP and Bird Island), three are in heavily exploited areas (False Bay, Struis Bay and Plettenberg Bay) (Buxton 1992; Smith 2005), and two are located in regions with moderate fishing pressure (Alphard Banks and Port Alfred). With the exception of Alphard Banks, all sites are coastal. The population in False Bay is separated from the other populations by a marine biogeographic disjunction near Cape Agulhas where genetic breaks have been identified in several coastal

Table 1 Sampling sites, coordinates, and number of samples used per site to generate genetic data

Site no.	Site name	Sub-site	Coordinates	*N*	
				mtDNA	Microsatellites
1	False Bay	Seal Island	34°05′69″S, 18°58′33″E	3	3
		Wolfgat	34°08′28″S, 18°64′72″E	11	11
		Rooiels	34°29′73″S, 18°81′24″E	13	13
2	Struis Bay		34°47′46″S, 20°04′19″E	16	0
3	Alphard Banks		35°02′00″S, 20°51′60″E	9	9
4	Plettenberg Bay		34°00′72″S, 23°49′20″E	17	45
5	Tsitsikamma NP		34°01′76″S, 23°55′38″E	33	53
6	Bird Island MPA		33°50′00″S, 26°18′00″E	21	45
7	Port Alfred		33°36′15″S, 26°54′12″E	20	0

In the case of samples that originated from a larger area (e.g., False Bay, Plettenberg Bay and Tsitsikamma NP), a central point was used in analyses that investigated spatial genetic structure at a scale that encompassed the species' core distribution (Wolfgat in the case of False Bay). In analyses used to investigate structure at a smaller scale, coordinates from sub-sites (False Bay) or GPS coordinates for each individual were specified, whenever available (Plettenberg Bay and Tsitsikamma NP). Site numbers correspond to those in Fig. 1

invertebrates (Evans et al. 2004; Teske et al. 2007a, c, 2009a) and teleosts (von der Heyden et al. 2008).

A total of 254 specimens were caught using either conventional hook and line fishing or spearfishing. Fin clips approximately 1–2 cm^2 in size were collected at all sites and stored in 80% ethanol. Genomic DNA was extracted from the fin tissue using the Wizard® Genomic DNA purification kit (Promega, USA) and was stored in 100 µl DNA rehydration solution. GPS coordinates were recorded to an accuracy of at least five geographical minutes for approximately 75% of the samples.

MtDNA control region sequencing and microsatellite scoring

Primers were designed that amplify the mitochondrial control region in *Chrysoblephus laticeps* (forward primer: *ChrysoCytbF* 5′-GCA GCA GCA YTA GCA GAG AAC-3′; reverse primer: *Sparid12SR1* 5′-TGC TSR CGG RGC TTT TTA GGG-3′). The forward primer anneals to the 3′ end of the mitochondrial cytochrome *b* gene (positions 1,102–1,122) in *Chrysoblephus cristiceps* (GenBank accession AF240719; Orrell et al. 2002) and the reverse primer to the 5′ end of the 12S rRNA in a region that is relatively conserved among published mtDNA sequences of two sparids from other genera (AB124801: *Pagrus auriga*, Ponce et al., unpublished data; AF381106: *Acanthopagrus schlegelii*, Jean and Lee, unpublished data). In both cases, we compared the primer annealing regions with corresponding positions in various other genetically similar sequences of percomorphs available on GenBank and specified ambiguity characters at positions that differed among species to make the primers as universal as possible. Because of this, they should be suitable to amplify the control region in all members of the genus *Chrysoblephus* and possibly also some other sparid genera. Tests for cross-amplification have so far indicated that they work well for steenbras (*Lithognathus lithognathus*) and, with variable success, for bronze bream (*Pachymetopon grande*) and poenskop (*Cymatoceps nasutus*) (G. Gouws, SAIAB, personal communication).

Amplifications were performed in a 50 µl solution containing 2–5 µl of DNA (~10–20 ng/µl), 0.2 mM of each primer, 2.5 mM of $MgCl_2$, 10 µl of 10× PCR buffer, 0.2 mM of each dNTP and 0.5 units of DNA Super-Therm Taq Polymerase (ABgene). The polymerase chain reaction (PCR) cycling profile comprised an initial denaturing step at 94°C for 4 min, 35 cycles of denaturation (94°C for 30 s), annealing (60°C for 45 s) and extension (72°C for 45 s), and final extension at 72°C for 10 min. PCR products were purified using the Qiaquick PCR purification kit (Qiagen) and sequenced at Macrogen Inc. (Seoul, Korea). Sequences were then checked using SEQMAN (Dnastar, Madison, USA) and aligned by eye. Reverse sequences were obtained for 10% of samples to rule out the possibility of sequencing errors. In all cases, these were identical to the forward sequences.

We selected seven microsatellite loci designed for *Chrysoblephus laticeps* (Teske et al. 2009c) on the basis of the following criteria: high variability, ease of scoring, no departure from Hardy–Weinberg equilibrium in a test sample of 40 individuals collected in the Tsitsikamma NP, and no linkage disequilibrium among pairs of loci. The following loci were selected: *Clat1*, *Clat2*, *Clat3*, *Clat4*, *Clat6*, *Clat7* and *Clat9*. PCR conditions and electrophoresis followed Teske et al. (2009c). Microsatellite profiles were examined using GENEMAPPER 4.0 (Applied Biosystems) and peaks were scored manually. To ensure consistent scoring among runs, eight control individuals were used in all runs. Tests for departures from Hardy–Weinberg equilibrium and

linkage disequilibrium were performed in ARLEQUIN 3.1 (Excoffier et al. 2005) using default settings. Bonferroni corrections (Rice 1989) were applied when conducting multiple statistical tests.

The data sets used for mtDNA and microsatellite analyses were not identical (Table 1). We sequenced the mtDNA control region of a moderate number of samples (~20) from all seven sites. No GPS coordinates were available for individuals collected at two sites (Struis Bay and Port Alfred) and approximately 20% of individuals from two other sites (Tsitsikamma NP and Plettenberg Bay) also lacked detailed sampling information. The mtDNA data were thus primarily used to explore large-scale genetic structure. Five sites for which samples with detailed sampling coordinates were available were analysed using the microsatellite data. In several cases, this required the exclusion of individuals from Tsitsikamma NP (24 individuals) and Plettenberg Bay (15 individuals) for which mtDNA data had been generated but that lacked GPS coordinates. For several sites, we increased the number of individuals for which microsatellite data were generated to more than twice the number of samples used for sequencing (≥45, Table 1), a strategy aimed at investigating both smaller-scale genetic structure and exploring whether the increased precision associated with this number of samples (as reported by Ruzzante 1998) changed the results.

Genetic diversity

Genetic diversity at individual sampling sites was investigated by estimating haplotype diversity h and nucleotide diversity π (Nei and Tajima 1981) for the mtDNA data, as well as observed and expected heterozygosity averaged over microsatellite loci using ARLEQUIN 3.1 (Excoffier et al. 2005). We also calculated mean allelic richness of microsatellites at each site using FSTAT 2.9.3 (Goudet 2001). For the sequence data, the Tamura model of nucleotide substitution (Tamura 1992) was specified, as it fitted our data best as determined using a likelihood-ratio test in MODELTEST 3.6 (Posada and Crandall 1998).

Genetic differentiation and spatial genetic structure

For the study of genetic structure and spatial patterns, we employed a suite of complementary techniques, some of which are sensitive to detect even subtle genetic patterns. The three False Bay sites (Table 1) were pooled unless stated otherwise. To determine whether mtDNA haplotypes of *Chrysoblephus laticeps* comprise distinct clusters suggestive of stock structure, a median-joining haplotype network was constructed using NETWORK 4.2.0.1 (Bandelt et al. 1999).

Pairwise genetic differentiation among sampling sites was estimated using fixation indices and related statistics, as well as exact tests for population differentiation. For the mtDNA data, pairwise Φ_{ST} values (Excoffier et al. 1992) were calculated using Tamura distances, and F_{ST} (Weir and Cockerham 1984) was reported for the microsatellite data, both calculated in ARLEQUIN. In addition, we calculated the harmonic mean of the estimated D statistic (Jost 2008) from the microsatellite data for each population pair using SMOGD 1.2.5 (Crawford 2010). Jost's D is considered to be more suitable to estimate genetic differentiation from high diversity loci such as microsatellites than measures such as F_{ST} or G_{ST}, as the latter may underestimate genetic divergence. Exact tests of population differentiation (Raymond and Rousset 1995) for pairs of samples were conducted in ARLEQUIN using both mtDNA and microsatellite data. The number of steps in the Markov chain was set to 100,000, and 10,000 dememorization steps were specified.

Measures of genetic differentiation calculated for each of seven microsatellite loci averaged over five sampling sites included G_{ST} (relative differentiation; Nei and Chesser 1983) and D (actual differentiation, Jost 2008). These were calculated in SMOGD, and 1,000 bootstrap replications were specified to estimate 95% confidence intervals about mean measures of differentiation.

A spatial analysis of molecular variance (SAMOVA) was performed to identify groups of sampling sites with maximum genetic differentiation. SAMOVA uses a simulated annealing procedure that aims to maximize the proportion of total genetic variance due to differences between groups of sites (Dupanloup et al. 2002). We ran the program for K (the user-defined number of groups) $= 2$ and $K = 3$ and specified 100 random initial conditions. Pairwise differences among haplotypes were specified as the molecular distance measure for mtDNA data, and the sum of squared size differences (Slatkin 1995) was specified for microsatellite data. If a genetic break was associated with Cape Agulhas or if *C. laticeps* at offshore sites were genetically distinct from coastal individuals, then one would expect False Bay and Alphard Banks to be recovered as distinct groups, respectively.

When a species' average dispersal distance per generation is smaller than the species' range, a correlation between genetic distance among individuals with geographic distances between sampling sites is commonly identified, a pattern known as isolation by distance (IBD; Slatkin 1993). We used a Mantel test (Mantel 1967) to test for correlations between distance matrices containing Slatkin's linearized F_{ST} transformation ($F_{ST} / (1 - F_{ST})$ (Slatkin 1995) and a geographic distance matrix containing shortest distances between pairs of sampling sites in km measured using the path tool in GOOGLE EARTH 5.1 (available at http://earth.google.com). Mantel tests were performed in ARLEQUIN, and 10,000 random permutations of matrices were specified to test for significance. Genetic distances

among mtDNA sequences were corrected using the Tamura model. The three False Bay sites were treated separately.

Additional analyses were performed using the microsatellite data only. The Bayesian clustering procedure implemented in STRUCTURE 2.3.3 (Pritchard et al. 2000) was used to estimate assignments of individuals to sampling sites. These were calculated using an admixture model that incorporates information on sample groups (Hubisz et al. 2009), an approach that is more sensitive to detect genetic structure than the standard STRUCTURE models when there is little genetic divergence among samples. For each value of K (the specified number of genetic clusters of individuals), we specified 10 runs with 10^6 iterations each, following a burn-in of 2.5×10^5 iterations. Values of K ranged from 1 (panmixia) to 5 (each sampling site distinct). Mean likelihoods of K from ten runs were plotted using STRUCTURE HARVESTER 0.56.3 (available at http://taylor0.biology.ucla.edu/struct_harvest/).

Assigning individuals to pre-defined groups may be problematic when individuals are genetically structured as a cline. In such cases, analyses of spatial autocorrelation that investigate relatedness of individuals at different spatial scales are more appropriate. Also, unlike the models implemented in STRUCTURE, spatial autocorrelation methods do not assume that the populations meet the expectations of Hardy–Weinberg and linkage equilibrium. We tested for positive correlation among individuals by estimating the coefficient r among genotypes for various distance classes using the program GENALEX 6 (Peakall and Smouse 2006). 95% confidence intervals about r were estimated by specifying 1,000 bootstrap replications per distance class, and 95% confidence intervals about the null hypothesis of no autocorrelation were determined by specifying 1,000 random permutations. As the program cannot handle missing data, five individuals from the Tsitsikamma NP for which data from only six loci were available were excluded from the analyses. Analyses were conducted using two data sets that provided information at different scales. Large-scale spatial structure (in hundreds of km) was investigated by including data from all five sampling sites, with the three False Bay sites treated separately. Small-scale structure (in tens of km) was investigated by including samples from two areas that are within close proximity to each other, namely the Tsitsikamma NP and Plettenberg Bay. Results were visualized as correlograms displaying the autocorrelation coefficient r and associated confidence intervals at various geographic distance classes.

Results

Genetic variability

A portion of the mtDNA control region 549 nucleotides in length was obtained from 143 samples. These sequences were submitted to GenBank (Accession numbers HM043424-HM043569). A total of 86 variable sites were observed and 97 unique haplotypes were identified. No length differences were found and the samples could thus be readily aligned by eye.

The mean number of microsatellite alleles recovered per locus ranged from 8.6 (*Clat6*) to 20.2 (*Clat1*), and mean genetic diversity was almost identical among the five sampling sites. Departure from Hardy–Weinberg equilibrium was identified at three sites, but only a single locus (*Clat3*) was identified more than once (False Bay: $P = 0.007$ and Bird Island: $P = 0.003$). In both cases, P-values remained significant after Bonferroni correction. Significant linkage disequilibrium after applying Bonferroni correction among pairs of loci was identified only in the Tsitsikamma NP (among loci *Clat1* vs. *Clat9* and among loci *Clat3* vs. *Clat9*), even though the data set used here differed from the non-significant one used previously (Teske et al. 2009c) by only 13 additional samples. A small proportion of tests for Hardy–Weinberg and linkage disequilibrium tend to be significant when analysing highly variable loci from populations of marine organisms, which may be expected by chance alone (Norris et al. 1999). As we found no consistent trends in these test results among loci and sites, we did not consider it necessary to exclude any loci from subsequent analyses.

Genetic diversity

Genetic diversity indices of mtDNA sequence data among sampling sites were similar in most cases, except that nucleotide diversity indices were comparatively high at sites 4 (Plettenberg Bay) and 7 (Port Alfred) (Table 2). Exclusion of 'outlier' samples (see next paragraph) resulted in lower values of π at all sites where these were present (Plettenberg Bay: 0.007 ± 0.004, Tsitsikamma NP: 0.007 ± 0.004, Port Alfred: 0.009 ± 0.005). Allelic richness estimates of the microsatellite data generated using FSTAT are standardized on the basis of the population with the smallest number of samples ($N = 9$, Alphard Banks) and thus particularly powerful to detect differences in genetic variation (Leberg 2002). Estimates of allelic richness were of similar magnitude at the five sites for which microsatellite data were generated, indicating that these do not differ in terms of genetic diversity. No geographic trend was identified in the magnitude of genetic diversity estimates.

Although values of D calculated for each microsatellite locus were generally larger than those of G_{ST} when assuming that allele frequencies are known, estimated parameters that accounted for small sample sizes were considerably lower and of similar magnitude (Table 3). Lower 95% confidence intervals were in many cases larger than the estimated measures of genetic differentiation, which is

Table 2 Genetic diversity of mtDNA sequence data and microsatellite data from seven (mtDNA data) and five (microsatellite data) sampling sites spanning the core distribution of *Chrysoblephus laticeps*

Population		mtDNA data		Microsatellite data			
No.	Name	*h*	π	N_A	H_O	H_E	A_R
1	False Bay	1.00 (±0.01)	0.007 (±0.004)	13.42 (±4.53)	0.78 (±0.16)	0.84 (±0.11)	8.63 (±2.38)
2	Struis Bay	1.00 (±0.02)	0.005 (±0.003)				
3	Alphard Banks	1.00 (±0.05)	0.006 (±0.004)	8.29 (±2.12)	0.78 (±0.17)	0.85 (±0.08)	8.29 (±2.29)
4	Plettenberg Bay	1.00 (±0.02)	0.011 (±0.006)	15.00 (±5.00)	0.86 (±0.07)	0.86 (±0.08)	8.65 (±2.18)
5	Tsitsikamma NP	1.00 (±0.01)	0.008 (±0.004)	14.86 (±2.80)	0.89 (±0.03)	0.87 (±0.05)	8.65 (±1.47)
6	Bird Island	1.00 (±0.02)	0.006 (±0.004)	14.71 (±3.84)	0.80 (±0.12)	0.84 (±0.09)	8.20 (±2.25)
7	Port Alfred	1.00 (±0.02)	0.013 (±0.007)				

Diversity statistics include haplotype diversity (*h*), nucleotide diversity (π) calculated for the mtDNA, and mean number of microsatellite alleles (N_A), observed and expected heterozygosity (H_O and H_E), as well as allelic richness (A_R) averaged over seven microsatellite loci. Standard deviations are indicated in brackets

Table 3 Measures of genetic differentiation averaged over populations for seven microsatellite loci, including G_{ST} (relative differentiation; Nei and Chesser 1983) and *D* (actual differentiation, Jost 2008)

Locus	G_{ST}	$G_{ST\ est}$ (±SE)	$G_{ST\ est}$ 95% C.I.	*D*	D_{est} (±SE)	D_{est} 95% C.I.
Clat1	0.017	0.000 (±0.000)	0.006–0.031	0.262	0.008 (±0.003)	0.101–0.404
Clat2	0.013	0.000 (±0.000)	0.000–0.038	0.068	0.000 (±0.002)	0.000–0.194
Clat3	0.020	0.003 (±0.000)	0.006–0.040	0.196	0.035 (±0.002)	0.069–0.627
Clat4	0.011	0.000 (±0.000)	0.001–0.027	0.098	0.000 (±0.002)	0.005–0.218
Clat6	0.032	0.015 (±0.001)	0.010–0.066	0.083	0.041 (±0.001)	0.028–0.164
Clat7	0.013	0.000 (±0.000)	0.002–0.034	0.075	0.000 (±0.001)	0.013–0.174
Clat9	0.014	0.000 (±0.000)	0.001–0.029	0.127	0.000 (±0.002)	0.007–0.243

Each measure is reported as a basic parameter which assumes that actual allele frequencies are known (G_{ST} and *D*) and as an estimated parameter that accounts for small sample sizes ($G_{ST\ est}$ and D_{est}; harmonic mean $\tilde{N} = 23.56$). 95% confidence intervals of mean estimated measures were calculated by performing 1,000 bootstrap replications

common in loci that have small standard deviations (Crawford 2010). To explore the effect of differences in genetic diversity of microsatellite loci, some analyses were repeated by excluding loci that had zero estimates of D_{est} and/or whose 95% confidence intervals included zero ($D_{est} > 0$ and 95% C.I. does not include zero: *Clat1*, *Clat3*, *Clat6*; 95% C.I. for D_{est} does not include zero: all except *Clat2*).

Spatial genetic structure

The haplotype network showed no relationship between haplotype genealogy and geographic location (Fig. 1b). However, whereas most haplotypes within the main network differed by no more than five steps, five haplotypes differed from the main group by between 10 and 15 steps. The five specimens having these distinctly different haplotypes are hereafter referred to as 'outliers' and subsequent analyses were performed by either including or excluding them. The outliers did not exhibit any clear geographical pattern and were found at only three sites.

Pairwise fixation indices among most sampling sites were low, and most were non-significant (Table 4). Exceptions were a significant Φ_{ST} value between False Bay and Port Alfred (Table 4a, this value remained significant when outliers were excluded) and a significant F_{ST} value between False Bay and the Tsitsikamma NP (Table 4b). Although F_{ST} is considered to underestimate genetic structure, harmonic means of D_{est} values were even lower. The highest value of D_{est} was also found between False Bay and the Tsitsikamma NP. No differentiation among sampling sites was identified using exact tests for either mtDNA or microsatellite data (all *P*-values were equal to 1.0).

No significant isolation by distance was identified for mtDNA sequence data ($Z = 16.97$, *r* (correlation coefficient) = 0.11, $P = 0.30$) and microsatellite data ($Z = 0.52$, $r = 0.28$, $P = 0.25$). These results did not change when outliers were excluded from the mtDNA data ($Z = 1.71$, $r = 0.17$, $P = 0.21$) or when certain loci were excluded from the microsatellite data because of zero estimates of D_{est} and/or whose 95% confidence intervals included zero (*Clat2*

Table 4 Measures of genetic differentiation among pairs of populations; a, Pairwise Φ_{ST} values based on mtDNA control region sequence data (below diagonal); b, F_{ST} values (below diagonal) and harmonic means of pairwise D_{est} values (above diagonal) based on seven microsatellite loci

	1	2	3	4	5	6
a						
1—False Bay						
2—Struis Bay	0.008					
3—Alphard Banks	0.000	0.000				
4—Plettenberg Bay	0.010	0.009	0.000			
5—Tsitsikamma NP	0.018	0.000	0.000	0.011		
6—Bird Island	0.004	0.010	0.000	0.021	0.008	
7—Port Alfred	0.032*	0.003	0.000	0.000	0.000	0.023
b						
1—False Bay		0.000	0.000	0.005	0.000	
2—Alphard Banks	0.000		0.000	0.000	0.000	
3—Plettenberg Bay	0.003	0.000		0.000	0.000	
4—Tsitsikamma NP	0.006*	0.000	0.002		0.000	
5—Bird Island	0.003	0.000	0.000	0.003		

Values significantly different from zero at $\alpha = 0.05$ are indicated with asterisks

excluded: $Z = 4.26$, $r = 0.37$, $P = 0.18$; only *Clat1*, *Clat 3*, and *Clat6* included: $Z = 27.98$, $r = 0.29$, $P = 0.27$).

SAMOVA analyses did not recover samples collected on either side of Cape Agulhas as distinct groups, and neither were samples from the offshore site (Alphard Banks) recovered as a distinct group (Table 5). Moreover, none of the groupings identified were geographically contiguous, suggesting that there are no regional clusters of haplotypes along the species' core distribution.

The highest likelihood of the STRUCTURE analysis was found when all sampling sites were combined ($K = 1$, i.e., panmixia) (Fig. 2). In addition, no significant spatial autocorrelation was identified for any distance classes at scales of tens (Fig. 3a) or hundreds of km (Fig. 3b). When loci with low levels of differentiation ($D_{est} = 0$ or 95% confidence intervals about the mean of D_{est} included zero) were excluded, the null hypothesis of no autocorrelation could not be rejected either (correlograms not shown). This indicates that individuals collected at same sites are not more closely related to each other than they are to individuals from different sites.

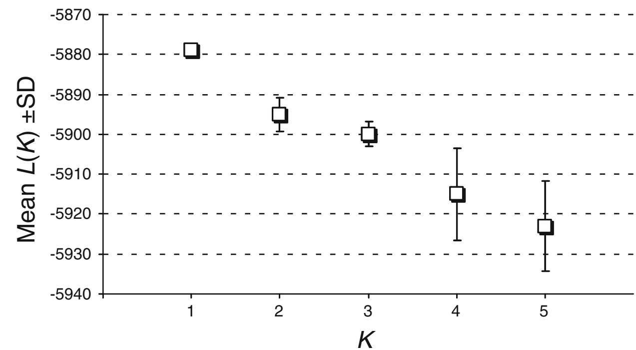

Fig. 2 *Chrysoblephus laticeps*. Mean likelihoods (L) of the number of genetic clusters of individuals (K) ± SD along the species' South African core distribution. Values were calculated using an admixture model that incorporates information on sample groups based on genetic data for seven microsatellite loci from 179 individuals

Discussion

Chrysoblephus laticeps is one of the most extensively studied fish species in southern Africa. Most aspects of the species' biology are well understood, including feeding (Buxton 1984), reproduction (Buxton 1990), age and growth (Buxton 1992). Furthermore, the movement behavior of adult fish and the role of MPAs in the management of this species have received much attention (Kerwath et al. 2007; Götz et al. 2009). Given the adults' highly philopatric behavior and the fact that many species that disperse primarily by means of planktonic larvae are genetically structured, genetic studies that reveal information about long-term dispersal patterns and potential stock structure constitute an important addition to the information required to successfully manage South Africa's overexploited fishery species.

Table 5 Results of SAMOVA analyses for three different data sets

Data set	K	Grouping	% variation	Φ_{CT}/F_{CT}	P
mtDNA	2	1, 2, 3, 5, 6/4, 7	2.01	0.020	0.041 ± 0.006
	3	1, 2, 3, 5, 6/4/7	2.19	0.021	0.061 ± 0.008
mtDNA (excl. outliers)	2	1, 2, 5, 6, 7/3, 4	0.00	0.000	0.291 ± 0.016
	3	1, 6/3, 5, 7/2, 4	0.61	0.006	0.245 ± 0.012
Microsatellites	2	1, 3, 4, 6/5	0.00	0.000	0.799 ± 0.012
	3	1, 3, 6/4/5	0.14	0.001	0.513 ± 0.013

Two or three groups of sampling sites (K) were specified. Numbers representing sites are the same as those in Fig. 1

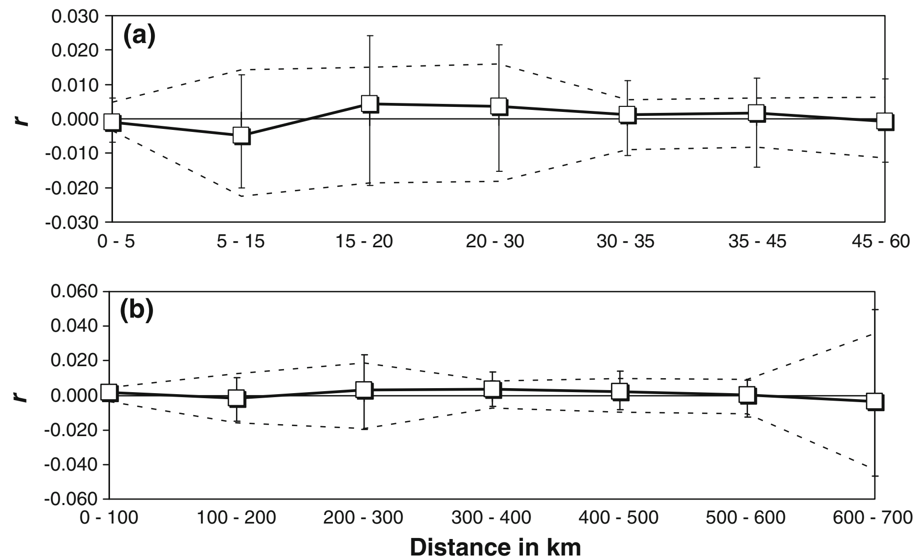

Fig. 3 *Chrysoblephus laticeps*. Correlograms depicting the autocorrelation coefficient *r* over a range of geographic distance classes based on genetic data from seven microsatellite loci; **a** 93 individuals from two South African populations in close proximity to each other (Tsitsikamma NP and Plettenberg Bay); **b** 174 individuals from five populations spanning the species' core distribution (Fig. 1). Whiskers represent 95% confidence intervals about *r*, and *dashed lines* are 95% confidence intervals about the zero autocorrelation value beyond which the null hypothesis of no genetic structure is rejected

Although the genetic data sets generated in this study were highly informative in terms of the number of polymorphic sites (control region data) and allelic variation (microsatellite data), there was no strong support for the hypothesis that the species is genetically structured along its core distribution. Although we identified genetic structure between two pairs of sites using fixation indices, the fact that different pairwise comparisons were identified as being significant using different markers and that fixation indices were generally low, indicates that these results are probably random artifacts of fairly low sample sizes. We consider particularly the results from the autocorrelation analysis to be of great importance, as the lack of positive autocorrelation at the lowest distance classes indicates that individuals from the same sampling site are not more closely related to each other than they are to individuals from different sampling sites. This supports the idea that despite limited adult dispersal, *C. laticeps* constitutes a single, well-mixed stock. This result is similar to findings for other commercially important South African teleosts in which adult dispersal potential is much greater, including the spotted grunter (*Pomadasys commersonnii*) (Klopper 2005), dusky kob (*Argryrosomus japonicus*) (Klopper 2005) and Cape stumpnose (*Rhabdosargus holubi*) (Oosthuizen 2007).

Connectivity among MPAs

Recent genetic studies have indicated that populations of marine organisms are more closed than previously thought and that the potential for long-distance dispersal in the sea may have been overestimated (e.g., Cowen et al. 2000; Levin 2006). However, a disproportionate number of studies on marine teleosts have focused either on tropical reef species in which larval retention is of great importance or on temperate species in which natal homing drives genetic structuring (Bradbury et al. 2008). The dispersal potential of temperate species with high fecundity and an extended passive dispersal phase may thus be considerably greater.

Most dispersal in *Chrysoblephus laticeps* likely occurs early during the species' life history. This species produces small pelagic eggs with a relatively large oil globule that provides buoyancy (Davis 1996; Mann 2000). The oil globule continues to provide buoyancy for four to six days after hatching, and then this function is taken over by the swim bladder until settling, which occurs approximately 17–30 days after hatching (Davis 1996). Although the post-flexion larvae can influence their vertical position in the water column (Davis 1996), they are nonetheless highly dispersive. Tilney et al. (1996) suggested that sparid larvae in South Africa do not pursue a behavioral strategy aimed at position retention, because they tend to be distributed homogenously relative to the type of substratum, water depth, and distance from the shore.

In terms of the dispersal potential of its early life history stages, *C. laticeps* is likely to be similar to the goby *Caffrogobius caffer*, another coastal fish species with low adult dispersal potential that is panmictic throughout much of its range (Neethling et al. 2008). In this species, lack of genetic structure between most sampling locations, and the absence of a phylogeographic break across Cape Agulhas, were attributed to a long larval duration, the ability of larvae to disperse actively and the release of large numbers of eggs. The fact that adult dispersal in this species is limited to movement among adjacent rock pools (Butler 1980) supports the idea that the observed panmixia in *C. laticeps* is also the result of passive larval dispersal rather than active long-distance dispersal of adults.

Whether or not the oceanography of the south coast of South Africa is conducive to large-scale passive dispersal is

a matter of debate. Measurements of surface currents have indicated that larvae released in the Tsitsikamma NP can theoretically disperse up to 583 km in 30 days (Brouwer et al. 2003). However, near-shore currents are believed to be largely wind driven (Tilney et al. 1996) and the direction of the wind changes frequently, which may reduce dispersal potential (McQuaid and Phillips 2000; Götz et al. 2009).

Our findings that individuals collected at the same sites are not more closely related to each other than they are to individuals from different sites and that genetic differentiation does not increase with geographic distance indicates that the dispersal potential of the larvae of *C. laticeps* is very high. The rejection of a model of IBD in fact suggests that the realized mean dispersal distance per generation may not be lower than the species' range, and that a considerable amount of gene flow takes place even among MPAs that are at a great distance from each other. Although sample size at some sites are low, tests for IBD tend to be robust when samples at individual sites are comprised of fewer than 50 individuals (Gomez-Uchida and Banks 2005).

Spillover into exploited areas

Exploited areas adjoining marine reserves are often preferably targeted by fishers because spillover out of the protected areas improves fishing (Gell and Roberts 2003). In species whose adults are highly mobile and are likely to stray out of the reserves, this can counter the positive effects of MPAs on local stocks (Kramer and Chapman 1999). In philopatric species such as *Chrysoblephus laticeps*, spillover of adults is considered negligible. For example, improvement of catches in exploited areas adjoining the Goukamma MPA (a small reserve west of Plettenberg Bay) was only 1% (Kerwath et al. 2008). The lack of genetic structure identified in the present study suggests that MPAs nonetheless play an important role in improving fishing outside the reserves, but that the benefits are only tangible at a much larger scale. This was illustrated by Buxton (1992), who identified a discrepancy between population structure and stability of the roman fishery near Port Elizabeth. Although the population structure was severely skewed towards females as the larger males had been selectively removed, there was no indication of reduced recruitment. This was attributed to import of recruits from elsewhere. Our results support this conclusion and indicate that the large individuals within MPAs, which are present at an even sex ratio and which produce significantly more offspring than their smaller counterparts in exploited areas (Bohnsack 1990), represent a source of recruits for localities farther afield.

Dispersal direction

The direction in which dispersal takes place is of great importance, as mostly unidirectional dispersal may indicate that exploited areas upstream from an MPA will not benefit from larval spillover. Although Boyd et al. (1992) showed that near-shore surface currents along South Africa's south coast are mostly bidirectional, studies investigating dispersal direction of fish larvae out of the Tsitsikamma NP during the sparids' spawning season during spring and summer disagree about the dispersal direction of fish larvae in the surface layers. Tilney et al. (1996) suggested that most dispersal takes place during wind-driven upwelling events that primarily displace larvae in a south-westerly direction (up to 90 km offshore and up to 250 km longshore). Attwood et al. (2002) challenged the role of the wind on surface currents and suggested that dispersal was bidirectional, with westward-moving surface water moving mostly offshore and eastward-moving water moving onshore. Most recently, Brouwer et al. (2003) suggested that surface water from the Tsitsikamma NP in fact moves primarily in an eastward direction (range: 42–583 km in 30 days).

Genetic analyses present a potentially more suitable approach to address this issue, because they represent long-term averages and focus only on individuals that have dispersed successfully. Recent genetic studies on southern African marine animals have, however, produced similarly contradictory results. All have concluded that dispersal is bidirectional, but some have identified more eastwards dispersal east of Cape Agulhas (e.g., Teske et al. 2007a; von der Heyden et al. 2008) and others have suggested that dispersal is predominantly westwards (Neethling et al. 2008). Although this discrepancy could be attributed to various biotic and abiotic factors that are difficult to quantify, it must be conceded that estimates of gene flow may be unreliable when regional populations are not strongly differentiated (e.g., Kuhner 2006) such that recent migrants cannot be distinguished from longer-established individuals. This requirement was violated in most cases in the previous studies. The present microsatellite data set of *C. laticeps* did not contain sufficient structure to estimate gene flow using the program BAYESASS (Wilson and Rannala 2003). Unlike BAYESASS, most programs used to estimate gene flow using sequence data, such as MIGRATE (Beerli and Felsenstein 2001) or IM (Hey and Nielsen 2004), do not provide information about whether or not the data at hand are sufficiently informative to obtain meaningful results. Nonetheless, the lack of genetic structure found in this study indicates that dispersal in *C. laticeps* is of a magnitude sufficiently high to homogenize genetic structure along the South African south coast.

Relevance of marine biogeographic disjunctions and significance of outliers

Despite the higher than expected dispersal ability of both *Chrysoblephus laticeps* and the goby *Caffrogobius caffer* (Neethling et al. 2008), it is clear that the population structure of both species is nonetheless affected by the marine biogeographic disjunctions that separate genetic units in other coastal species. Cape Agulhas is sometimes considered to be the eastern limit of a transition zone between warm-temperate and cool-temperate biotas (Bolton and Anderson 1997) whose western limit is at Cape Point (Fig. 1), and several coastal species have phylogeographic breaks at either or both these localities (e.g., Norton 2005; Teske et al. 2007a, c; von der Heyden et al. 2008). The fact that Cape Point represents the western distribution limit of both *C. laticeps* and *C. caffer* suggests that neither species is firmly established in the cool-temperate province. Likewise, both species are affected by a biogeographic disjunction broadly stretching from approximately Bird Island to north of the Kei River (Fig. 1) that represents the approximate boundary between the warm-temperate and subtropical biogeographic provinces, as this region is the eastern distribution limit of the species' core distribution (Griffiths and Wilke 2002). As both species are essentially endemic to the warm-temperate south coast and phylogeographic breaks concordant with disjunctions between marine biogeographic provinces have been identified in coastal clinids with wider distribution ranges (von der Heyden et al. 2008), it would be premature to conclude that coastal teleosts are less likely to exhibit large-scale genetic structure than are invertebrates.

The identification of five individuals having mtDNA sequences that differed considerably from those of most of the other individuals sampled (the 'outlier' group) could be an indication that a second stock of *C. laticeps* exists in South Africa, or perhaps existed in the past. Outlier individuals were found at Plettenberg Bay, Tsitsikamma NP and Port Alfred and thus do not seem to be confined to a particular portion of the species' range. Comparisons of nucleotide diversity of the group of outliers relative to the main group (25 randomly sub-sampled sets of five sequences) revealed consistently higher diversity in the former ($\pi = 0.018$ for the outliers and $\pi = 0.008 \pm 0.002$ (SD) for the main group). This could be an indication that the outliers are migrants of an unsampled stock with a higher genetic diversity than the main group, although such a conclusion is highly speculative because of the low number of samples. Sample sizes from False Bay and from the offshore site (Alphard Banks) are low, but it is nonetheless clear that these habitats do not harbour genetically distinct populations. We therefore propose two alternative explanations for the existence of the outlier group: the existence of a genetic lineage adapted to warmer water on the south-east coast (*C. laticeps* has been reported near Port St Johns (Mann 2000, Fig. 1), a locality in the northern portion of a transition zone between the warm-temperate and subtropical provinces; e.g., Teske et al. 2008), or the existence of a lineage adapted to deeper water.

Directions for future research

A core distribution that is limited to a single marine biogeographic province indicates that the distributions of coastal teleosts such as *Chrysoblephus laticeps* may be strongly influenced by environmental conditions that differ between provinces, including water temperatures and nutrient concentrations. Adaptive differences have been identified between regional genetic lineages of southern African coastal invertebrates (Teske et al. 2008, 2009a; Zardi et al. 2010) and similar adaptive differentiation has been reported in marine fish species elsewhere (e.g., Rocha et al. 2005). In southern African teleosts whose distributions span more than one biogeographic province, regional genetic units have so far only been identified in clinids, i.e., species with very low dispersal potential (von der Heyden et al. 2008), whereas species with actively dispersing adults were either panmictic (e.g., Klopper 2005; Oosthuizen 2007) or genetic patterns did not correspond with biogeographic patterns (Norton 2005). Studies of Californian teleosts (reviewed in Dawson 2001) indicate that the absence of phylogeographic breaks across biogeographic disjunctions is indeed linked to high dispersal potential, but in most species whose adults do not disperse actively, genetic breaks were identified irrespective of the duration of planktonic larval development. This suggests that future research into the stock structure of southern African fishery species should focus on species whose adults are not only philopatric, but which are well established in more than one marine biogeographic province. These are most likely to be comprised of regionally adapted stocks that need to be managed individually.

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