

A. O. Ball · G. R. Sedberry · M. S. Zatzoff
R. W. Chapman · J. L. Carlin

Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers

Received: 29 January 2000 / Accepted: 27 June 2000

Abstract We examined population structure in the wreckfish, *Polyprion americanus*, by assaying six microsatellite loci in 422 individuals collected throughout the geographic range. Eighteen hapuku, *P. oxygeneios*, were assayed at the same loci for use as an outgroup. Expected heterozygosities ranged from 0.49 to 0.88 and averaged 0.66. Allele-frequency distributions at those loci indicated that samples from the eastern North Atlantic, western North Atlantic and the Mediterranean were genetically similar, confirming the pattern seen in a previous analysis of mitochondrial DNA (mtDNA) restriction fragment length polymorphisms (RFLPs). Both mtDNA and microsatellite studies differentiated northern and southern wreckfish stocks. However, in contrast to the mtDNA studies, allelic variation at microsatellite loci clearly differentiated wreckfish from two Southern Hemisphere locations, Brazil and the South Pacific. Far more genetic variation was observed at microsatellite loci than with mtDNA RFLPs (haplotype diversity averaged 0.01), and we saw more evidence of population structure with the microsatellite loci. The differentiation between southern and northern wreckfish supports the distribution records, which indicate that wreckfish do not occur in the tropics. Temperature profiles and current patterns throughout the southern oceans apparently also prevent significant gene flow between the South Pacific and Brazilian samples.

Communicated by N. H. Marcus, Tallahassee

A. O. Ball (✉) · G. R. Sedberry · M. S. Zatzoff
R. W. Chapman · J. L. Carlin
South Carolina Department of Natural Resources,
217 Fort Johnson Road, P.O. Box 12559,
Charleston, South Carolina 29422-2559, USA

Fax: 001 843 762-5110
e-mail: balla@mrd.dnr.state.sc.us

Present address:
J. L. Carlin
University of Florida, Gainesville,
Florida 32653, USA

Introduction

An understanding of the relationship between dispersal capabilities and genetic structure in marine fishes is critical for formulating effective conservation measures and fisheries management policies as well as for our understanding of the evolution and population biology of marine organisms. The degree of population genetic structure is related to dispersal, which in turn is affected by oceanographic and climatic conditions, physical barriers (e.g. land masses), habitat availability, egg and larval dispersal, and variable spawning and recruitment success (Shulman and Bermingham 1995; Grant and Bowen 1998; Scoles et al. 1998). Varying degrees of genetic divergence have been reported for many continuously and discontinuously distributed pelagic marine fishes in which gene flow may be mediated by high adult vagility and/or dispersal of early life history stages (Grant and Bowen 1998; Graves 1998; Scoles et al. 1998). Similar results have been obtained for species with an antitropical distribution and, in some cases, more limited dispersal capabilities, such as orange roughy (Smith et al. 1997), bluefish (Goodbred and Graves 1996), and sardines (Bowen and Grant 1997), among others. The wreckfish *Polyprion americanus* (Bloch and Schneider, 1801) has an antitropical distribution and a long-lived pelagic phase (Roberts 1989), while adults have not been documented to be highly migratory. This study allows further examination of the relationships among life history, physical oceanography, and population genetics in a globally distributed marine species.

Demersal adult wreckfish occur in the western Atlantic from the Carolinas to the Florida Straits and from southern Brazil to the Valdes Peninsula, Argentina, including Bermuda but excluding the tropics. Pelagic juveniles have been observed in the western North Atlantic north of Cape Hatteras (Schroeder 1930; Gilhen 1986), but there are no records of pelagic juveniles from Bermuda. Demersal juveniles have been taken off southern Brazil (Haimovici et al. 1994). In the eastern Atlantic,

juvenile and adult wreckfish are found off the Norwegian coast, along shallow portions of the Mid-Atlantic ridge and associated islands (e.g. Azores), near Madeira and the Canary Islands, and along northern and southern Africa, including the Mediterranean but again excluding the tropics. In the southwestern Pacific, wreckfish occur near southern Australia and New Zealand (where they are sometimes referred to as *Polyprion maeone*), and there are occurrence records from the southern Indian Ocean (Heemstra 1986; Roberts 1989; Sedberry 2000).

The wreckfish is a component of directed and mixed-species fisheries throughout its range, and much of the available life-history data has been obtained from fisheries observations and fishery-independent studies, including submersible cruises (Sedberry et al. 1994, 1999; D. Wyanski unpublished observations). Spawning probably occurs throughout the North Atlantic, since wreckfish in spawning condition have been caught on the Blake Plateau grounds (D. Wyanski personal communication), and spawning has been documented in the Mediterranean (Hardy 1978) and probably occurs in the Azores and on other areas of the Mid-Atlantic Ridge (Fennessy 1998; Sedberry et al. 1999). The eggs, larvae and juveniles are pelagic, apparently for several months or years, and presumably drift with the surface currents (Hardy 1978; Goujon et al. 1993). Wreckfish apparently switch from a pelagic to demersal existence at about 50 cm total length (TL), and occur from depths of 42 to 1000 m in the Atlantic Ocean (Sedberry et al. 1996, 1998). North Atlantic wreckfish mature at 8 to 10 yr and about 80 to 90 cm TL, and grow to large size (up to 1.5 m TL and 47 kg) (Sedberry et al. 1999; D. Wyanski personal communication).

Landings from demersal longline fisheries in the Azores consist of juveniles averaging 60 to 70 cm TL (approx. 4 yr old, according to growth curves provided by Sedberry et al. 1999). However, Fennessy (1998) concluded that the absence of large wreckfish in the Azorean fishery is a result of the light tackle and shallow grounds usually fished there, and large wreckfish have been observed on the Mid-Atlantic Ridge near the Azores (Sedberry et al. 1999). In contrast, most fish harvested by the American fishery are mature fish, 8 to 12 yr old and about 100 cm TL (Sedberry et al. 1999). Submersible observations indicated that nearly all wreckfish on the Blake Plateau are large fish, and the rarity of juveniles in the fishery appears to reflect their absence from the area rather than a biased fishing method (Sedberry et al. 1994). Length-frequency data and the occurrence of foreign fish hooks in wreckfish landed in USA waters provide evidence that wreckfish are moving from the eastern North Atlantic, where pelagic juveniles are common, to the waters off the southeastern USA, where mainly large, mature fish are recorded from landings and submersible observations (Sedberry et al. 1996, 1999). The transport of long-lived pelagic stages via North Atlantic circulation and the possible movement of adults may provide a mechanism for gene flow in North Atlantic wreckfish.

Previous mtDNA studies indicated that North Atlantic wreckfish consisted of a single genetic stock extending from the major documented North Atlantic spawning grounds off South Carolina to the Madeiran archipelago and western Mediterranean Sea (Sedberry et al. 1996). These analyses could not distinguish among Southern Hemisphere wreckfish collected from Brazil and Australia and New Zealand, but revealed fixed haplotype differences between Northern and Southern Hemisphere wreckfish.

In other studies where both nuclear and mitochondrial genetic markers were used, microsatellite markers have frequently provided additional information about population structure, e.g. landlocked Atlantic salmon (Tessier et al. 1995) or Atlantic cod (Árnason et al. 1992; Bentzen et al. 1996). Microsatellite loci have high mutation rates, estimated at 10^{-3} to 10^{-4} events per locus per generation, and may be more powerful for elucidating finer population structure than mtDNA (for review see Avise 1994; Jarne and Lagoda 1996; Estoup and Angers 1998). Microsatellites consist of tandem repeats of nucleotides flanked by unique sequences (Tautz 1989), and variation results from different numbers of repeat units. Dinucleotide microsatellite loci like those used in this study are presumably noncoding regions and not under selective pressure (O'Reilly and Wright 1995). We developed assays for six microsatellite loci and applied them to wreckfish samples from throughout the range (with *Polyprion oxygeneios* as an outgroup) in order to test the hypothesis that North Atlantic wreckfish consist of one genetic stock, distinct from southern wreckfish, and to test the separate hypothesis that southern wreckfish from Brazil and the South Pacific are genetically similar.

Materials and methods

Specimens of *Polyprion americanus* were collected from 1993 to 1997 (Fig. 1, Table 1). Lengths of wreckfish specimens varied, and reflected the commercial fishery landings that we sampled (Sedberry et al. 1996). The small sample from Bermuda ($n = 17$) includes all fish caught since the fishery collapsed in 1983 (Luckhurst 1996), while the small samples from Majorca ($n = 16$) and West Madeira ($n = 19$) are the result of a single sampling effort. DNA was isolated as described in Sedberry et al. (1996). In addition to wreckfish, tissues were also obtained from hapuku, *Polyprion oxygeneios*, collected aboard a longline vessel operating out of St. Helens, Tasmania, or from the market in Sydney, New South Wales, Australia, and the DNA was isolated as for wreckfish.

The genomic library was constructed and screened as in Ball et al. (1998). We screened approximately 1000 clones, sequenced 48 positive clones, found 14 clones that contained one or more (GT)_n repeats, designed primers for 10 loci, and used 6 in this study (Table 2).

Primers were used to amplify total genomic DNA in reactions that included 10 ng template DNA, 0.3 μ M forward and reverse primer, 0.2 mM each dNTP, 3 mM MgSO₄, 17 mM (NH₄)₂SO₄, 10 mM β -mercaptoethanol, 67 mM Tris-HCl pH 8.8 and 0.25 units Taq polymerase (Promega) in 10 μ l. The forward primer was end-labeled with [γ -³²P]-ATP at 0.1 μ Ci pmol primer⁻¹. Cycling parameters were 3 min at 94 °C followed by 35 cycles of 40 s at 94 °C, 40 s at the annealing temperature, and 40 s at 72 °C. All amplifi-

Fig. 1 Collection locations of *Polyprion americanus* (BP Blake Plateau, Be Bermuda, Az Azores, NAz North Azores, WMd West Madeira, Md Madeira, Maj Majorca, Br Brazil, Aus Australia, NZ New Zealand)



Table 1 *Polyprion* spp. Collection data for specimens used in this study

Area, Site	Collection dates	Total length (mm) [mean \pm 1 SD (range)]	No. of individuals
<i>P. americanus</i>			
North Atlantic			
Blake Plateau	Jan 1994–Jun 1997	985 \pm 95 (686–1182)	95
Bermuda	Oct 1995–Jun 1997	1079 \pm 160 (744–1391)	17
North Azores	Oct 1996	1143 \pm 164 (340–1430)	40
Azores	Mar 1992–Jul 1997	675 \pm 168 (265–1320)	118
West Madeira	Oct 1996	1046 \pm 149 (710–1200)	19
Madeira	Mar 1992–Jun 1997	752 \pm 92 (600–900)	32
Majorca	Jul 1994	831 \pm 261 (570–1370)	16
South Atlantic			
Brazil	Feb 1995–Apr 1995	850 \pm 172 (600–1293)	28
South Pacific			
Australia	Oct 1994–Feb 1995	932 \pm 191 (630–1355)	30
New Zealand	Jun 1993–May 1995	788 \pm 71 (683–910)	30
<i>P. oxygeneios</i>			
Australia	Jun 1993, Aug 1995	717 \pm 106 (587–888)	16

Table 2 *Polyprion americanus*. Designations, DNA sequences, repeat and repeat type, and annealing temperature of wreckfish microsatellite primers

Locus	Sequence	Repeat	Type	Anneal ($^{\circ}$ C)
Pam006F	5' CTGATGGTTAAGCTGGTGC 3'	(GT) ₁₇	Imperfect	55
Pam006R	5' CAATGTGTCTAACATTCGCC 3'			
Pam010F	5' GTGGCCTTGGTGAAGCAG 3'	(GT) ₁₅	Perfect	55
Pam010R	5' CGCGCACTAGGTGCCAAATATC 3'			
Pam017F	5' CTGACTTTGTATGCATGTCCG 3'	(GT) ₁₅	Perfect	55
Pam017R	5' GTTTGAGACCTCAGGGCAAG 3'			
Pam021F	5' GATCTGACAATGACCACTTTACT 3'	(AC) ₁₅	Perfect	55
Pam021R	5' CCTCTATAGGAATGCTGCTTTTG 3'			
Pam025F	5' CAAATAACATATGCACACATCAGC 3'	(AC) ₁₇	Perfect	60
Pam025R	5' CTTCTCTGGCATGAATGTTTG 3'			
Pam035F	5' GGCTCGCTCTGGGCATTAC 3'	(GT) ₁₅	Perfect	55
Pam035R	5' ACAACGTGAGCTATACCCGCC 3'			

cations included a 5 min extension at 72 $^{\circ}$ C, except Pam021, which required a 60 min extension at 72 $^{\circ}$ C as the final step to ensure consistent addition of an extra adenosine (Smith et al. 1995). Amplifications were performed in an Ericomp Delta I thermalcycler, and the products were subjected to electrophoresis on 6% denaturing polyacrylamide gels alongside a standard M13 sequence ladder (Brooker et al. 1994). Analysis of 150 individuals with Pam006, Pam025, and Pam035 used fluorescently labeled primers obtained from Operon Technologies, Inc. and ABI instead of the radioactively-labeled primers. These reactions were analyzed on an ABI 377 automated sequencer at the Medical University of South Carolina Nucleic Acid Analysis Facility. Scoring was standardized

between the two methods by comparing the scores of amplifications containing [γ - 32 P]-ATP-labeled primers or fluorescently-labeled primers for these loci for 25 individuals.

To assess conformity of genotype distributions with Hardy–Weinberg expectations, probability tests were performed on all separate samples using the program GENEPOP v3.1 (Guo and Thompson 1992; Raymond and Rousset 1995). In addition, all North Atlantic and Mediterranean samples and the two South Pacific samples were combined, and a test of Hardy–Weinberg proportions within these groups was performed. Multilocus values of the probabilities of deviation from Hardy–Weinberg equilibrium were calculated using GENEPOP.

Allele-frequency distributions were tested for non-homogeneity across populations using an approximation of an exact test implemented in GENEPOP. A Bonferroni correction (Rice 1989) was used to calculate the level of significance for multiple comparisons. Fisher's method (Manly 1985) was used to combine independent probabilities. Linkage disequilibrium was also calculated using GENEPOP.

Several indices of population structure were calculated. F -statistics (Wright 1951, 1978) were estimated following Weir and Cockerham (1984), using Genetic Data Analysis, (Lewis and Zaykin 2000) for all samples and for North Atlantic samples only. (F_{IS} is a measure of the deviation from Hardy–Weinberg proportions within samples, F_{IT} a measure of the deviation in the total set of samples, and F_{ST} the standardized genetic variance among samples.) The genetic distance measure $(\delta\mu)^2$, a measure specifically designed for microsatellite data based on a single-step mutation process, was calculated following Goldstein et al. (1995). Nei's genetic distance (Nei 1972) and $(\delta\mu)^2$ were calculated and bootstrapped over loci using MICROSAT 1.5 (Minch 1996). These measures have been shown to be useful for estimating branch lengths (Takezaki and Nei 1996). For the comparison of allele-frequency distributions and genetic-distance analysis, *Polyprion oxygeneios* was included as an outgroup. PHYLIP (Felsenstein 1993) was used to generate the UPGMA phenogram for *P. americanus* (including *P. oxygeneios* for comparison) from Nei's genetic distance. We chose to use Nei's D for this analysis rather than $(\delta\mu)^2$ because interspecific pairwise distances were occasionally smaller than intraspecific distances with $(\delta\mu)^2$.

To examine the effect of the anomalous alleles at locus Pam021, which differed by a single base pair (bp), we performed all analyses considering Pam021 as a single bp mutation, with binned alleles to eliminate the single bp steps, or without Pam021 entirely, and we obtained the same qualitative results from the calculations of $(\delta\mu)^2$ and Nei's D . All results shown were calculated from the unbinned data file, with all alleles included. Haplotype diversity (h), nucleotide diversity (π), and nucleotide divergence (d) were calculated from the RFLP data of the ND1 region of mtDNA presented in Sedberry et al. (1996) using REAP, Version 4.0 (McElroy et al. 1992) in order to compare relative levels of variation in *Polyprion americanus* mtDNA with microsatellite data from this study. F_{ST} from mtDNA data was calculated using Arlequin (Schneider et al. 1997).

Results

Six of the ten microsatellite loci tested in *Polyprion americanus* were easily scored polymorphic loci at which the most common allele had a frequency < 0.95 (Fig. 2). In addition, all six microsatellite loci were successfully amplified in hapuku. We assayed 422 individual wreckfish at each locus (between 6 and 19 individuals did not amplify at any one locus due to technical problems) and observed 8 to 31 alleles at each locus (Fig. 2, Table 3). Observed heterozygosity for all loci and all samples of *P. americanus* ranged from 0.467 to 0.814, and expected heterozygosity ranged from 0.491 to 0.881. For each separate sample at each locus, within grouped North Atlantic and Mediterranean samples or grouped South Pacific samples, no significant deviations from Hardy–Weinberg equilibrium were noted. Multilocus tests of heterozygote deficiencies for separate samples, grouped North Atlantic and Mediterranean samples, or grouped South Pacific samples were also not significant. However, when all samples were combined, significant heterozygote deficiencies were evident at 5 of 6 loci. There was no

linkage disequilibrium within samples, consistent with independent loci (analysis not shown).

The probability of population differentiation based on allele-frequency distributions for each microsatellite locus indicated no significant differences among all North Atlantic and Mediterranean samples or between Australia and New Zealand (Table 4). There were significant differences in allele-frequency distributions among samples collected from all three ocean basins: the North Atlantic and Mediterranean, Brazil, and South Pacific. For these comparisons, allele-frequency distributions at 3 of the 6 loci were significantly different at $p = 0.00001$. A multilocus value for the probability of population differentiation, when corrected for multiple independent tests, showed that all comparisons between ocean basins were significant at $p < 0.001$, while no comparisons among North Atlantic and Mediterranean samples or between Australia and New Zealand revealed significant population differentiation. Loci Pam006 and Pam017 were significantly different at $p < 0.05$ for all pairwise comparisons involving different ocean basins, while locus Pam035 was only significantly different at $p < 0.05$ for about half of these comparisons. The ability to discriminate among populations was not related to expected heterozygosity of microsatellite loci, since Pam017 and Pam035 were the two least polymorphic loci, in contrast to Pam006 (Table 3).

F -statistics calculated over all samples confirmed the previous analyses (Table 5). Within the North Atlantic and Mediterranean, F_{ST} was not significantly different from zero, while for all populations over all loci, F_{ST} was significantly different from zero.

The magnitude of $(\delta\mu)^2$ and Nei's D differed, but overall patterns of pairwise genetic distances were the same: all North Atlantic and Mediterranean samples were similar, Australia and New Zealand were similar, but Brazil, Australia and New Zealand, and the North Atlantic samples differed from each other (Table 6). Nei's D within the North Atlantic and Mediterranean, and between Australia and New Zealand averaged 0.0, while between samples in different ocean basins it averaged 0.5. Similarly, $(\delta\mu)^2$ averaged 0.5 within North Atlantic and Mediterranean, and between Australia and New Zealand, but averaged 35.1 between samples from different ocean basins. Using $(\delta\mu)^2$, within-species comparisons were occasionally greater than between-species comparisons, while Nei's D was greatest for the between-species comparisons. A UPGMA phenogram based upon Nei's D grouped North Atlantic and Mediterranean samples, with little distance among these samples, while Brazil and the South Pacific formed separate branches (Fig. 3). The North Atlantic and South Pacific assemblage was not strongly supported by the bootstrap value.

Average haplotype and nucleotide diversities calculated from mtDNA data presented in Sedberry et al. (1996) were very low (0.0125 and 0.000077, respectively). This may be due to the small number of informative enzymes used and nucleotides sampled. Nucleotide-

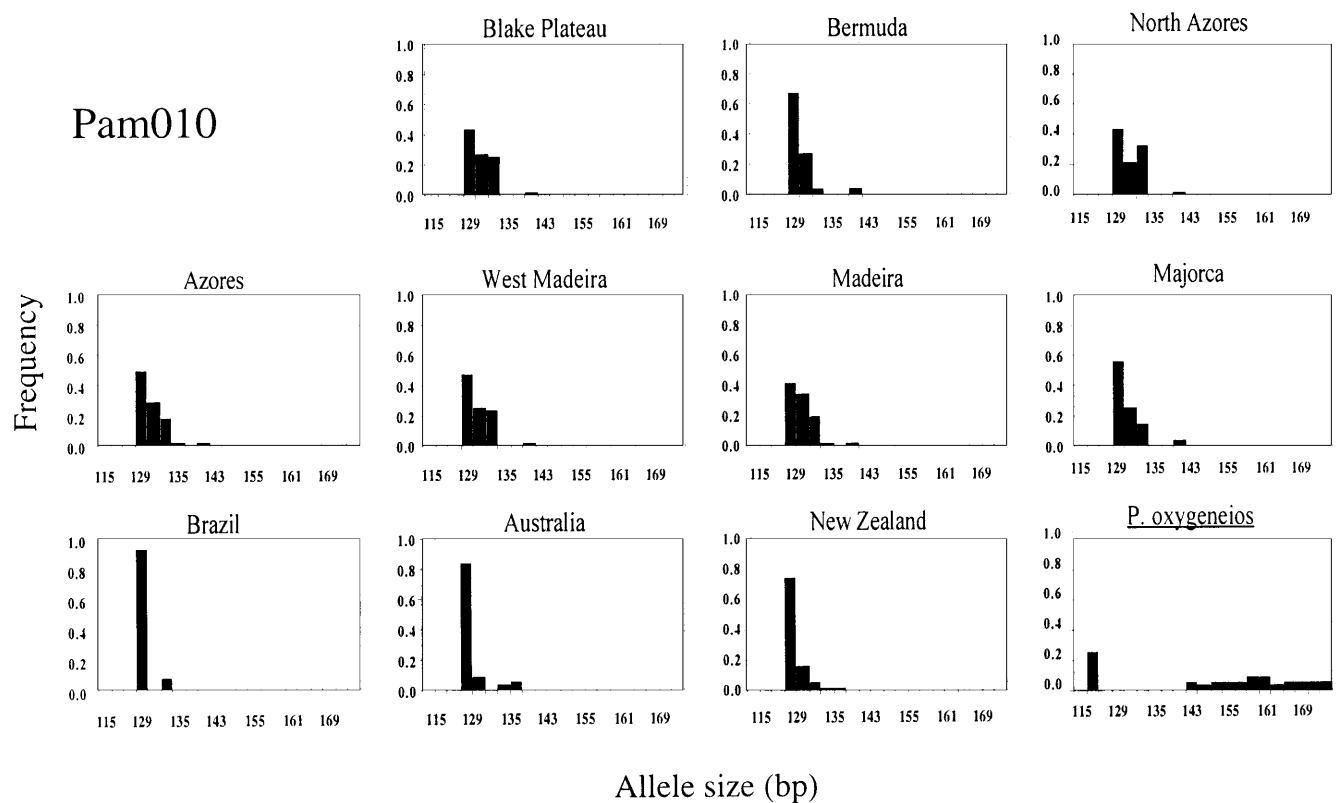
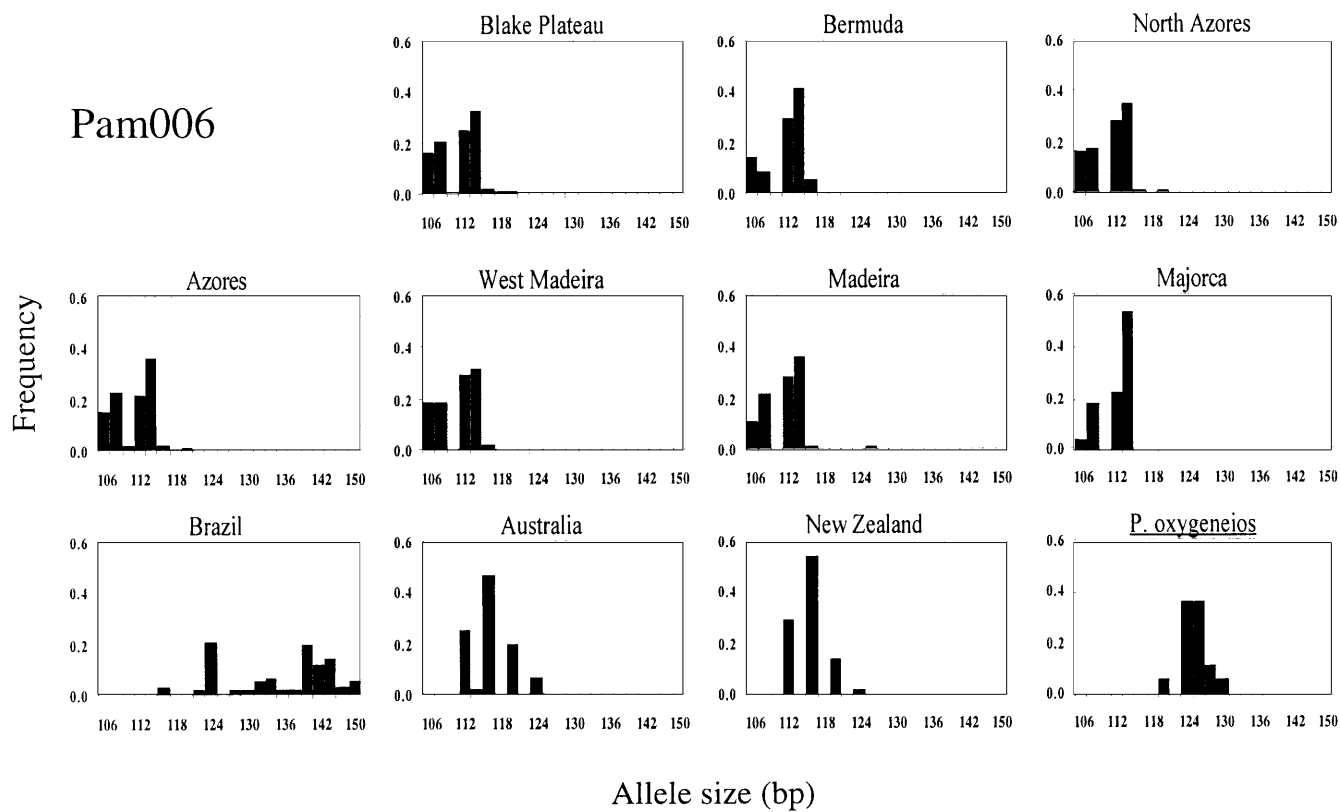


Fig. 2 *Polyprion* spp. Allele-frequency distribution histograms (*bp* base pairs)

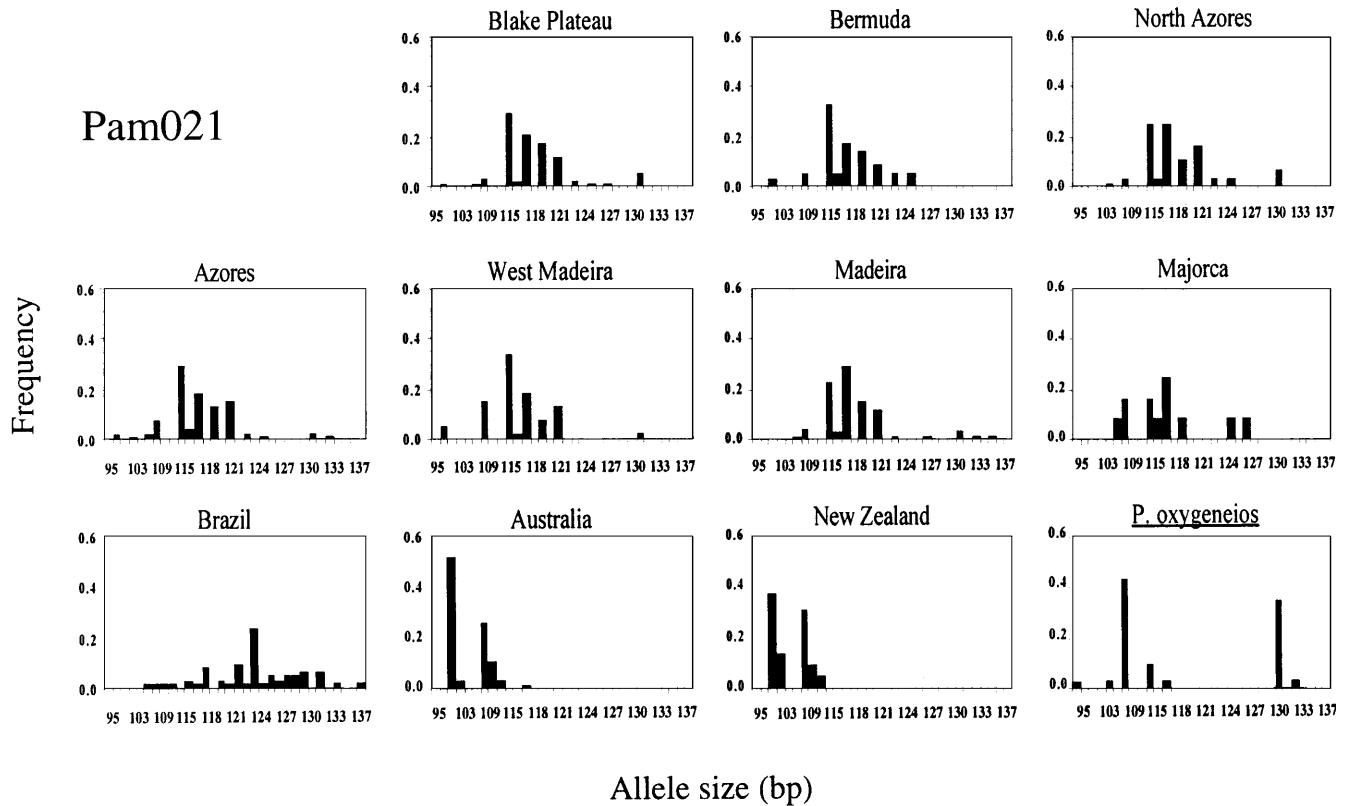
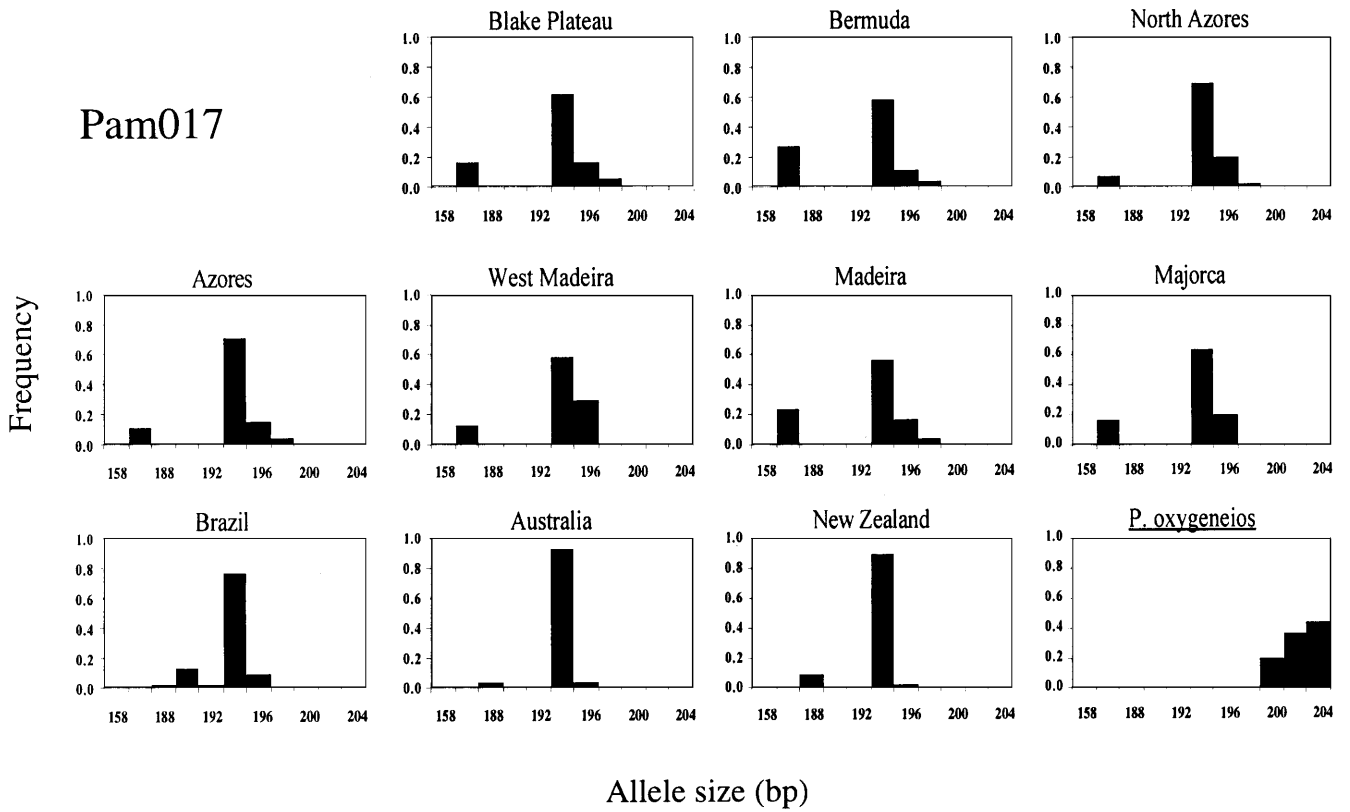


Fig. 2 (Continued)

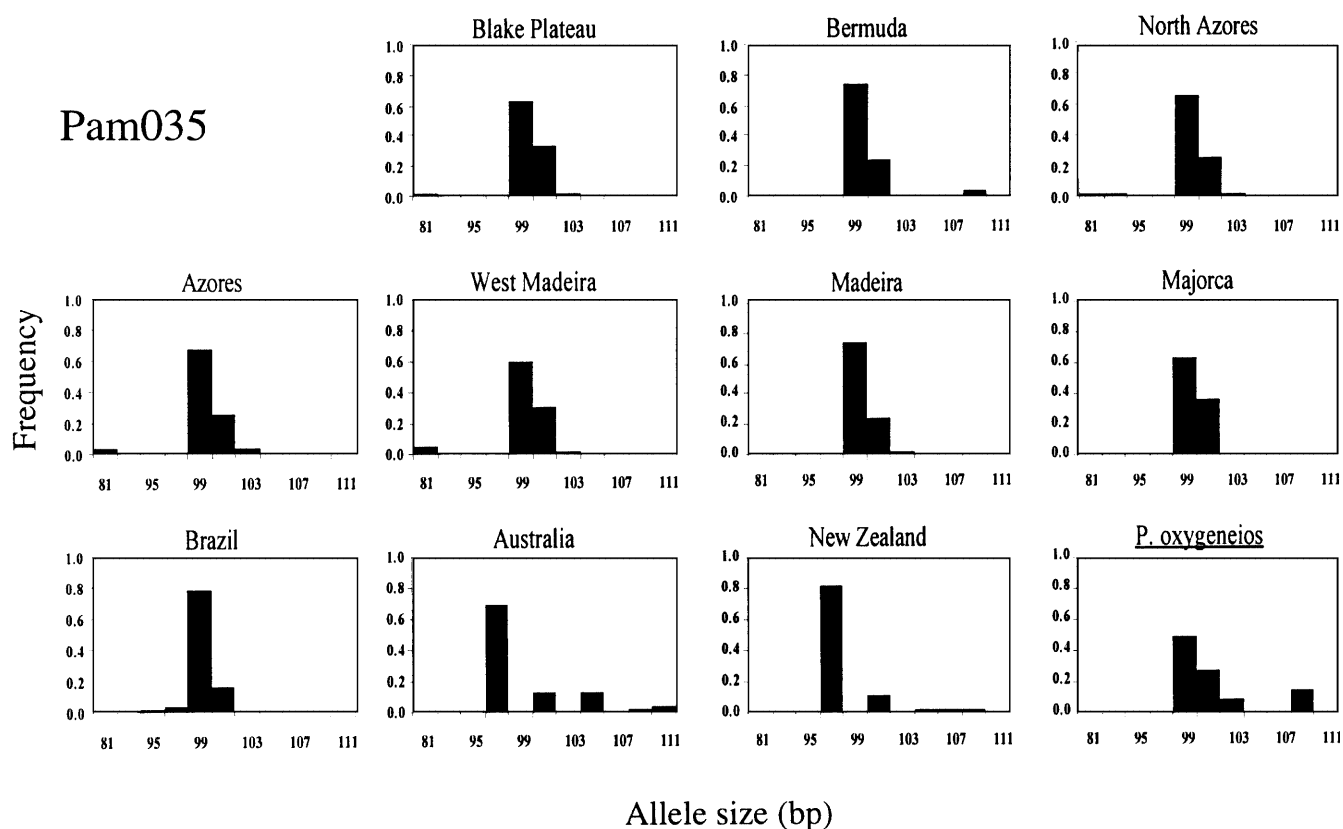
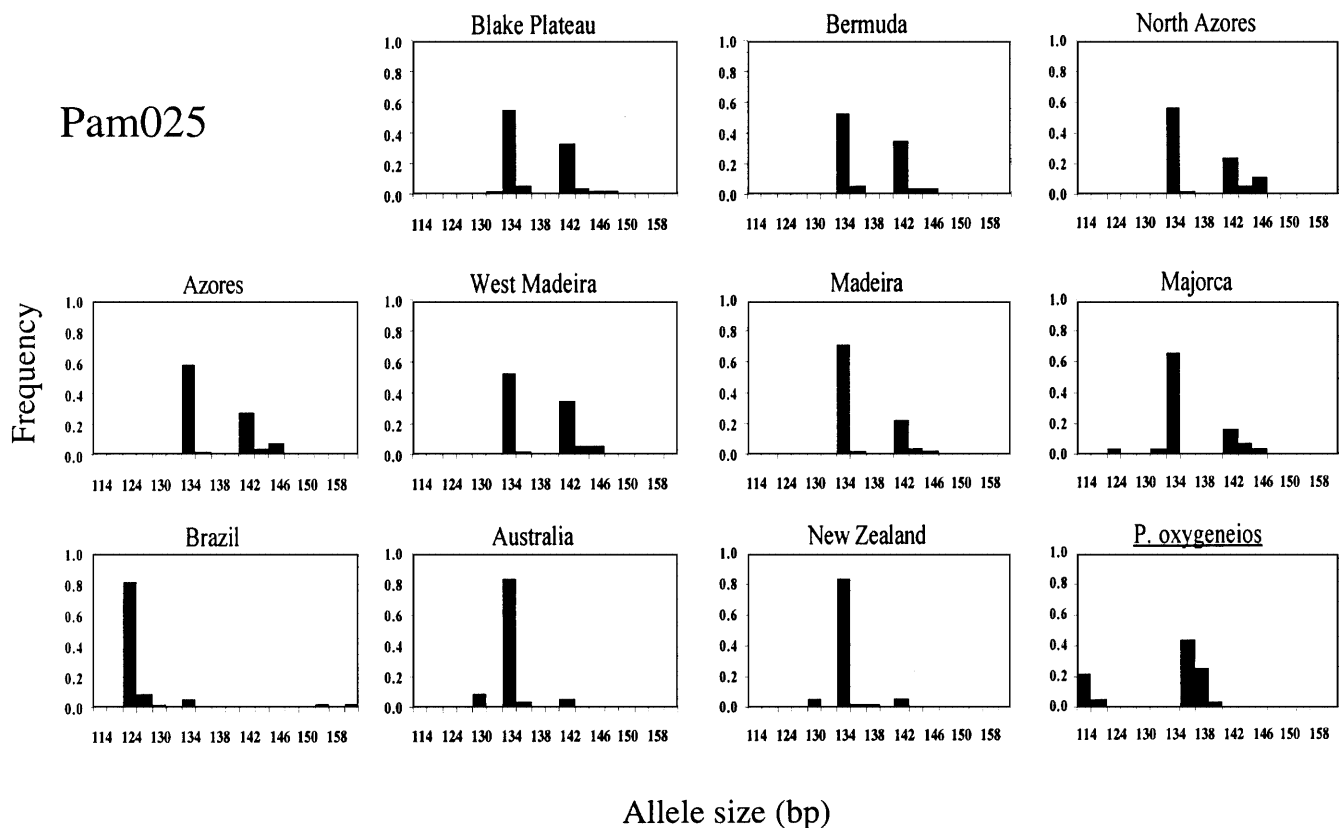


Fig. 2 (Continued)

Table 3 *Polyprion* spp. Basic allele statistics for each sample at each locus, for North Atlantic and Mediterranean, and South Pacific samples combined, and for all *P. americanus* and all *P. oxygeneios* [N number of individuals scored; a number of alleles observed in that sample; H_{exp} expected heterozygosity (unbiased

estimate, Nei 1978); H_{obs} observed heterozygosity; *single locus* p probability of deviation from Hardy–Weinberg equilibrium when $H1$ = heterozygote deficiency or heterozygote excess; *multi-locus* p probability of deviation from Hardy–Weinberg equilibrium when $H1$ = heterozygote deficiency]

Site, Locus	Pam006	Pam010	Pam017	Pam021	Pam025	Pam035	Multi-locus
Blake Plateau							
N	94	94	95	94	91	94	
a	8	6	5	15	7	7	
H_{obs}	0.755	0.606	0.537	0.809	0.505	0.479	
H_{exp}	0.763	0.669	0.572	0.826	0.592	0.493	
p	0.298	0.115	0.132	0.763	0.038	0.595	0.035
Bermuda							
N	17	17	17	17	17	17	
a	5	4	4	9	5	3	
H_{obs}	0.647	0.529	0.706	0.765	0.529	0.412	
H_{exp}	0.733	0.485	0.586	0.845	0.608	0.415	
p	0.622	1	0.710	0.265	0.086	1	0.083
North Azores							
N	40	40	40	40	40	40	
a	6	4	4	10	5	5	
H_{obs}	0.850	0.675	0.475	0.800	0.625	0.550	
H_{exp}	0.747	0.660	0.470	0.837	0.618	0.497	
p	0.016	0.010	0.349	0.533	0.908	0.862	0.853
Azores							
N	114	116	115	115	110	113	
a	7	5	6	16	7	5	
H_{obs}	0.772	0.578	0.478	0.826	0.573	0.487	
H_{exp}	0.754	0.644	0.478	0.833	0.575	0.488	
p	0.920	0.117	0.668	0.787	0.835	0.514	0.225
West Madeira							
N	19	19	19	19	19	19	
a	5	4	3	8	5	4	
H_{obs}	0.737	0.526	0.316	0.737	0.684	0.474	
H_{exp}	0.768	0.667	0.579	0.818	0.616	0.545	
p	0.688	0.190	0.031	0.558	0.226	0.454	0.038
Madeira							
N	32	32	32	32	31	31	
a	6	5	4	12	5	3	
H_{obs}	0.656	0.656	0.750	0.938	0.387	0.419	
H_{exp}	0.743	0.673	0.608	0.824	0.451	0.397	
p	0.366	0.976	0.310	0.588	0.336	0.354	0.876
Majorca							
N	10	14	15	6	14	15	
a	4	4	3	8	6	2	
H_{obs}	0.300	0.571	0.467	1.000	0.429	0.733	
H_{exp}	0.679	0.611	0.549	0.924	0.566	0.480	
p	0.020	0.578	0.437	1	0.302	0.085	0.014
Brazil							
N	27	28	28	28	28	28	
a	13	2	5	19	4	3	
H_{obs}	0.926	0.036	0.393	0.893	0.250	0.357	
H_{exp}	0.877	0.036	0.421	0.909	0.230	0.305	
p	0.743	–	0.675	0.643	1	1	0.510
Australia							
N	30	30	30	30	30	30	
a	5	4	3	6	4	5	
H_{obs}	0.633	0.333	0.133	0.667	0.333	0.467	
H_{exp}	0.686	0.300	0.129	0.639	0.300	0.505	
p	0.973	1	1	0.856	1	0.557	0.632

Table 3 (Continued)

Site, Locus	Pam006	Pam010	Pam017	Pam021	Pam025	Pam035	Multi-locus
New Zealand							
<i>N</i>	24	27	27	25	24	23	
<i>a</i>	4	5	3	5	5	5	
<i>H_{obs}</i>	0.625	0.519	0.222	0.760	0.292	0.348	
<i>H_{exp}</i>	0.613	0.428	0.205	0.735	0.303	0.311	
<i>p</i>	0.485	0.854	1	0.228	0.541	1	0.814
North Atlantic							
<i>N</i>	326	332	333	323	322	329	
<i>a</i>	9	6	6	19	9	7	
<i>H_{obs}</i>	0.742	0.599	0.523	0.824	0.540	0.492	
<i>H_{exp}</i>	0.749	0.651	0.533	0.831	0.578	0.480	
<i>p</i>	0.128	0.025	0.694	0.743	0.042	0.820	0.061
South Pacific							
<i>N</i>	54	57	57	55	54	53	
<i>a</i>	5	5	3	6	5	6	
<i>H_{obs}</i>	0.630	0.421	0.175	0.709	0.315	0.415	
<i>H_{exp}</i>	0.651	0.362	0.165	0.686	0.299	0.426	
<i>p</i>	0.769	0.929	1	0.803	0.802	0.552	0.728
<i>P. americanus</i>							
<i>N</i>	407	417	418	406	404	410	
<i>a</i>	22	7	8	31	13	11	
<i>H_{obs}</i>	0.740	0.537	0.467	0.813	0.490	0.473	
<i>H_{exp}</i>	0.814	0.608	0.491	0.881	0.609	0.580	
<i>p</i>	0.000	0.002	0.319	0.000	0.000	0.000	0.000
<i>P. oxygeneios</i>							
<i>N</i>	8	16	15	16	16	18	
<i>a</i>	5	13	3	7	5	4	
<i>H_{obs}</i>	0.875	1	0.733	0.750	0.938	0.778	
<i>H_{exp}</i>	0.742	0.915	0.660	0.700	0.716	0.665	
<i>p</i>	0.865	0.452	0.913	0.711	0.012	0.509	0.997

Table 4 *Polyprion* spp. Probability of population differentiation based on allele frequencies. All tests for significance are corrected for multiple comparisons using sequential Bonferonni procedure [Loci that are not underscored did not show significant differences in allele frequencies among the sites (also indicated by "all ns" if all loci showed no significant differences between the two sites being

compared). *Loci with triple underscore* = $p < 0.00001$, significant at alpha = 0.001; *double underscore* = significant at alpha = 0.01; *single underscore* = significant at alpha = 0.05; Loci are coded as 1 Pam006; 2 Pam010; 3 Pam017; 4 Pam021; 5 Pam025; 6 Pam035]

Site	Blake Plateau	Bermuda	Azores	North Azores	Madeira	West Madeira	Majorca	Brazil	Australia	New Zealand
Bermuda	all ns									
North Azores	all ns	all ns								
Azores	all ns	all ns	all ns							
West Madeira	all ns	all ns	all ns	all ns						
Madeira	all ns	all ns	all ns	all ns	all ns					
Majorca	all ns	all ns	all ns	all ns	all ns	all ns				
Brazil	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>			
Australia	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>		
New Zealand	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	all ns	
<i>P. oxygeneios</i>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>	<u>123456</u>

sequence divergence was also low (average = 0.5168%) and failed to reveal differentiation within the North Atlantic or South Atlantic/South Pacific, but did indicate separation between the Northern and Southern Hemispheres. F_{ST} overall, calculated from mtDNA data, was 0.98 and averaged 0.00 within the North Atlantic or within the South Pacific.

Discussion

The results reported here revealed three genetically distinct *Polyprion americanus* stocks: the North Atlantic and Mediterranean, Brazil, and the South Pacific (Australia and New Zealand). All samples from each of these

Table 5 *Polyprion americanus*. F -statistics for all samples and for North Atlantic samples (F_{IS} deviation from Hardy–Weinberg proportions within samples; F_{IT} deviation in total set of samples; F_{ST} standardized genetic variance among samples)

Locus	All samples			North Atlantic		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
Pam006	0.0101 ^{NS}	0.1071	0.0980***	0.0086 ^{NS}	0.0050	-0.0036
Pam010	0.0615 ^{NS}	0.1281	0.0709***	0.0754 ^{NS}	0.0801	0.0051 ^{NS}
Pam017	0.0122 ^{NS}	0.0527	0.0411***	0.0114 ^{NS}	0.0171	0.0058 ^{NS}
Pam021	0.0048 ^{NS}	0.0898	0.0854***	0.0093 ^{NS}	0.0071	-0.0022
Pam025	0.0563 ^{NS}	0.2104	0.1632***	0.0574 ^{NS}	0.0588	0.0015 ^{NS}
Pam035	-0.0186 ^{NS}	0.2162	0.2305***	-0.0240 ^{NS}	-0.0265	-0.0024
All loci	0.0203 ^{NS}	0.1319	0.1139***	0.0237 ^{NS}	0.0241	0.0004 ^{NS}

Table 6 *Polyprion* spp. Pairwise comparisons for genetic distance, $(\delta\mu)^2$ (Goldstein et al. 1995) (upper triangle) and Nei's genetic distance, D (Nei 1972) (lower triangle). Averages of bootstrapped values are shown

	BP	Berm	NAz	Az	WMad	Mad	Maj	Braz	Aust	NZ	<i>P. ox</i>
Blake Plateau (BP)		0.26	0.09	0.34	1.31	0.05	0.64	39.45	29.08	26.59	31.90
Bermuda (Berm)	0.008		0.55	0.14	0.65	0.33	0.23	40.80	24.62	22.35	33.33
North Azores (NAz)	-0.002	0.022		0.57	1.67	0.20	1.05	39.23	31.03	28.42	31.45
Azores (Az)	0.001	0.005	-0.001		0.32	0.47	0.18	43.13	23.50	21.19	32.28
West Madeira (WMad)	-0.016	-0.006	-0.014	-0.011		1.55	0.41	47.82	18.87	16.77	33.25
Madeira (Mad)	0.000	0.006	0.002	0.002	-0.002		0.65	37.69	29.31	26.82	31.34
Majorca (Maj)	0.006	-0.011	0.000	-0.003	-0.010	-0.014		40.73	21.30	19.22	30.99
Brazil (Braz)	0.820	0.710	0.778	0.783	0.841	0.859	0.622		81.93	80.05	38.03
Australia (Aust)	0.651	0.579	0.642	0.605	0.408	0.673	0.548	1.337		0.13	52.80
New Zealand (NZ)	0.668	0.616	0.662	0.628	0.610	0.688	0.577	1.509	0.001		51.73
<i>P. oxygeneios</i>	2.098	2.258	2.223	2.210	2.195	2.153	2.970	2.259	2.710	2.830	

areas differed from all samples from the other areas, and there were no differences within the North Atlantic and Mediterranean or between Australia and New Zealand. Statistical measures for the individual sample comparisons, including analysis of gene frequencies, distance measures and F -statistics, were consistent. While single samples, grouped North Atlantic and Mediterranean samples, and grouped Australia and New Zealand samples did not deviate from Hardy–Weinberg equilibrium, we did observe a significant heterozygote deficiency for all samples combined, consistent with the Wahlund effect when genetically distinct populations are combined for Hardy–Weinberg analysis. The small sizes of some samples (Bermuda, Majorca, or West Madeira) limit the power of these tests (Sokal and Rohlf 1995), and thus the biological significance of a deviation from Hardy–Weinberg equilibrium for some of these samples is suspect. Fennessy (1998) indicated some degree of isolation within North Atlantic wreckfish stocks, based on parasite faunas, while mtDNA and microsatellite analyses indicated widespread gene flow within the North Atlantic.

In this study, microsatellites did not reveal fine population structure within the North Atlantic or South Pacific, but rather large differences among ocean basins coupled with genetically homogeneous populations within the North Atlantic and South Pacific samples. The large values of $(\delta\mu)^2$ obtained for some pairwise comparisons of *Polyprion americanus* samples were similar to or greater than those observed for pairwise comparisons between *P. americanus* and *P. oxygeneios*. These distance measures appeared to approach a plateau with these

data, consistent with the observed and inferred effects of homoplasy (Paetkau et al. 1997; Viard et al. 1998).

Previous mtDNA studies of wreckfish (Sedberry et al. 1996) could differentiate the Northern from the Southern Hemisphere, but could not distinguish between South Atlantic and South Pacific samples. It seems likely that increased population structure was revealed by analysis of microsatellites because of the different mutation rate of these two markers (see Avise 1994). Clearly, for the loci analyzed for wreckfish, diversity and divergence measures are both higher for the microsatellite loci than for the mtDNA RFLP analysis of the ND1 region. Other studies of teleosts have found higher genetic diversity with microsatellite loci than with mtDNA, and more evidence of population structure, using distances derived from microsatellite data (e.g. Tessier et al. 1995; Bentzen et al. 1996).

Gene flow among North Atlantic wreckfish is probably mediated by pelagic juveniles drifting in surface currents, and perhaps by migratory adults (Sedberry et al. 1996, 1999). Wreckfish in spawning condition have been caught on the Blake Plateau (D. Wyanski personal communication); and the Gulf Stream flow, North Atlantic Drift, the Azores Current, and the Canary Current could carry juveniles to eastern Atlantic wreckfish habitats (Defense Mapping Agency 1973). Pelagic juvenile wreckfish are abundant in the surface waters of the eastern Atlantic, and appear there during the months following the spawning period on the Blake Plateau (Goujon et al. 1993). Since juveniles are only rarely observed in the western North Atlantic (Schroeder 1930; Gilhen 1986), we hypothesize that juveniles observed in

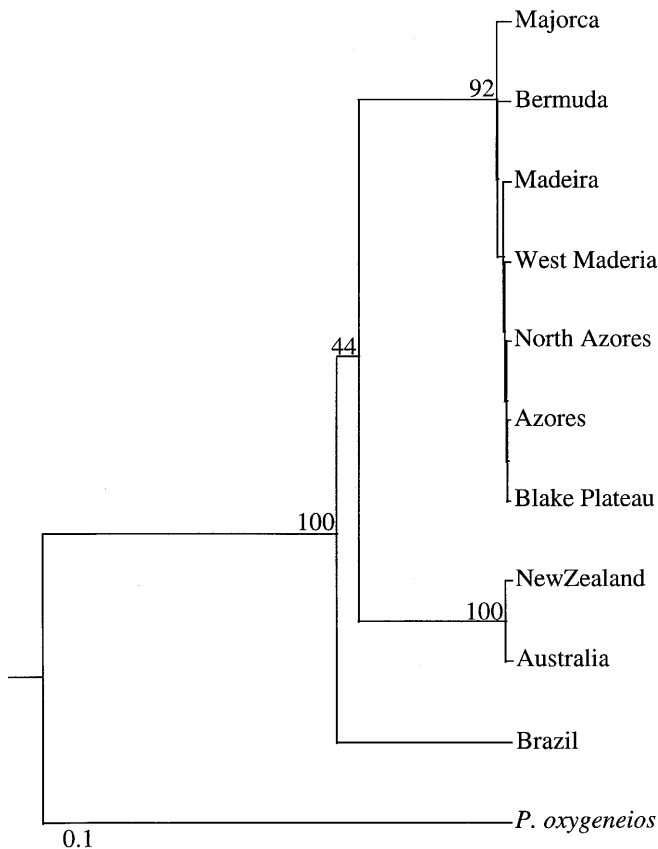


Fig. 3 *Polyprion* spp. Nei's *D* phenogram of relationships among *P. americanus*, with *P. oxygeneios* as an outgroup. Percentages of replications of observed topology based on 1000 bootstraps are given for major branches. Bootstrap values are not given for branches within North Atlantic or within South Pacific (Nei's *D* < 0.01 for pairwise comparisons)

the eastern north Atlantic originate at least in part from spawning on the Blake Plateau. Spawning probably occurs in the Azores and the Mid-Atlantic Ridge outside the Azorean Exclusive Economic Zone as well (Fennessy 1998; Sedberry et al. 1999), and the Azores Current, Canary Current and North Atlantic Subtropical Gyre could carry progeny spawned in the Azores to Madeira, the Canaries and perhaps Bermuda and America (Sverdrup et al. 1942; Pingree et al. 1996). Surface flows could carry pelagic juveniles into the Mediterranean (Sverdrup et al. 1942), where spawning has also been documented (Hardy 1978). Taken together, these observations suggest that currents mediate substantial gene flow around the North Atlantic.

Tagging studies of *Polyprion oxygeneios* throughout New Zealand waters have shown that this species is capable of long-distance migrations (Beentjes and Francis 1999). Solid information about the migratory patterns of adult wreckfish is absent from the literature, and tagging studies on *P. americanus* carried out by the South Carolina Department of Natural Resources are ongoing. The single tag return reported was a juvenile wreckfish, which moved 217 km eastward in the central

region of the Azores over a period of 3 mo (Sedberry et al. 1998).

Bermuda lies outside the main Atlantic circulation and inside the North Atlantic Subtropical Gyre (Tomczak and Godfrey 1994). Wreckfish are overfished in Bermuda and the Mediterranean, and in Bermuda the stock became commercially extinct in 1983 and has not recovered (Sedberry et al. 1999). In spite of the documented population bottleneck in Bermuda, this sample was not statistically genetically distinct from the rest of the North Atlantic. As the age of first maturity for wreckfish is 8 to 10 yr, the population remnants probably retain the genetic makeup of the original sample, since extensive inbreeding or genetic drift would not yet have occurred after fewer than two generations (Nei et al. 1975). There may also be some exchange between Bermuda and the rest of the North Atlantic, although not enough recruitment to provide for a rapid regeneration of the stock.

While mechanisms exist to promote gene flow within the North Atlantic, very little Atlantic surface water from higher latitudes where wreckfish occur (> 25°N or S) crosses the equator (Sverdrup et al. 1942). The Brazil Current, the South Atlantic Subtropical Gyre and South Equatorial Current would preclude pelagic wreckfish from known localities in the eastern or western South Atlantic from crossing the equator (Sverdrup et al. 1942). Furthermore, it is highly unlikely that food resources needed to support a large robust fish such as *Polyprion americanus* exist at appropriate depths in the tropics (Anderson et al. 1986), and for this reason large demersal wreckfish are probably excluded from occupying slope depths in latitudes lower than 25°. Therefore, cross-equatorial movement of wreckfish in the Atlantic is unlikely, consistent with both mtDNA and microsatellite data which clearly differentiated North Atlantic wreckfish from South Atlantic wreckfish.

The waters of the Southern Ocean permit free inter-basin circulation among the Atlantic, Pacific and Indian Oceans (Gordon 1971). However, summer sea temperatures at the surface are below 10 °C in the Antarctic Circumpolar Current or West Wind Drift (Sverdrup et al. 1942; Deacon 1984; Lutjeharms 1990), well below sea-surface temperatures where juvenile wreckfish or adults have been observed (Sedberry et al. 1999). Genetic data indicate that wreckfish are not able to utilize the dominant circumpolar flow in the Southern Hemisphere for dispersal of genotypes among Southern Ocean basins.

The pattern of genetic divergence found in wreckfish is similar to that found in other species with disjunct antitropical distributions, e.g. bluefish and chub mackerel (Goodbred and Graves 1996; Graves 1998; Scoles et al. 1998). Mitochondrial DNA RFLPs of bluefish (*Pomatomus saltatrix*) revealed a similar pattern to that found in this study: eastern and western North Atlantic samples, and eastern and western Australian samples were closely related, while Brazilian fish were genetically distinct from all other groups. Analysis of chub mackerel

(*Scomber japonicus*) mtDNA RFLPs revealed some genetic differences among North Atlantic samples, but very large differences between North Atlantic and South Pacific samples suggest that the South Pacific population may be a distinct species (Scoles et al. 1998). In all these species, the dispersal characteristics arising from a pelagic or migratory existence are apparently limited by physical oceanographic conditions and an intolerance of tropical waters (Goodbred and Graves 1996; Scoles et al. 1998). In other cases, Stepien and Rosenblatt (1966) found varying patterns of genetic structure between North and South American samples of three antitropical fishes, and Grant and Bowen (1998) saw considerable variability in genetic divergence among regional populations of ecologically similar sardines and anchovies. In these cases, changing paleoclimatic and oceanographic conditions, differences in reproductive and dispersal abilities, and differences in temperature tolerance between species are among the factors that probably contribute to such variations in population structures in taxonomically or ecologically similar species.

The origin of antitropical distributions has been the subject of debate for over a century (see Briggs 1987), and a number of theories and interpretations have been put forward to account for the limited gene flow and phylogeographical patterns exhibited by antitropical species. Recent analyses of bluefish (Goodbred and Graves 1996) and mussels (Hilbish et al. 2000) suggest that dispersal rather than vicariance is responsible for present-day genetic patterns of these species, while genetic divergence between many paired Atlantic and Pacific species is compatible with vicariance due to the formation of the Isthmus of Panamá (see Grant 1987). The data presented here indicate that whatever mechanisms allowed transequatorial movement in the past, gene flow in wreckfish is certainly limited in the present. Wreckfish with its global, antitropical distribution lends itself to further study of this particular issue; however, sequence analysis providing estimates of times of divergence would be more appropriate than microsatellite data to answer this question.

Polyprion spp. are also present in the eastern South Atlantic and the Indian Ocean (Sedberry in press), but preliminary analysis of DNA from fish collected near South Africa found highly distinctive mtDNA profiles and microsatellite genotypes (data not shown). These were sampled for us by local fishery biologists, but as we did not observe the specimens from which tissues were taken, we could not verify the identity of these fish and left them out of the analysis. Early records of *Polyprion* from southern Africa, Tristan da Cunha, Gough Island and nearby seamounts were assigned to *P. americanus* (Rowan and Rowan 1955; Penrith 1967, 1976), but recent publications and records indicate that they may be records of *P. oxygeneios* (Andrew et al. 1995; Heemstra personal communication). In addition, there may be a third species of *Polyprion* in the Indian Ocean waters of southern Africa (Heemstra personal communication). Given the taxonomic uncertainties, we could not eluci-

date the distribution of wreckfish genotypes on both sides of the South Atlantic.

The genetic data presented here indicated a deep separation among *Polyprion americanus* samples, similar to that between any *P. americanus* and *P. oxygeneios*. Roberts (1986) revised the systematics of *Polyprion* and synonymized about 20 nominal species to two names, *P. americanus* and *P. oxygeneios*. His revision synonymized *P. moeone*, originally described from New Zealand, with *P. americanus* described from America. However, Paxton et al. (1989) listed *P. moeone* and *P. oxygeneios* as the only valid species occurring in Australia and New Zealand (see also Last et al. 1983). The data presented here are consistent with the suggestion that *P. moeone* is a valid species, and imply that further clarification of *Polyprion* systematics is necessary.

Acknowledgements We thank J. Ahlquist, A. Strand, and three anonymous reviewers for valuable advice on the manuscript. R. Wingrove assisted in the mtDNA data analysis. The following colleagues assisted in field collections and observations: G. Ulrich (Charleston, South Carolina); F. Alvarez (Majorca); P. Conolly and J. Kotas (Brazil); N. Elliott, K. Rowling and R. Ward (Australia); M. Francis (New Zealand) and H. Martins (Azores). Wreckfish fishermen S. Ray and P. Reiss (USA); E. Bier (Australia); A. Peat (New Zealand); J. Bassa (Majorca); and B. Doe and A. Card (Bermuda) also provided specimens. This work was supported with grants from the National Geographic Society (Grant No 4950-93 to GRS) and the National Marine Fisheries Service (MARFIN Project NA57FF0290 to GRS; MARMAP Contract 50WCNF006002 to GRS). Sequences for the microsatellite loci used in this work are available through GenBank Accession Nos. AF222037 to AF222042. This is Contribution No 446 from the South Carolina Marine Resources Center and FISHTEC Contribution 00-01.

References

- Anderson ME, Crabtree RE, Carter HJ, Sulak KJ, Richardson MD (1986) Distribution of demersal fishes of the Caribbean Sea found below 2000 meters. *Bull mar Sci* 37: 794-807
- Andrew TG, Hecht T, Heemstra PC, Lutjeharms JRE (1995) Fishes of the Tristan da Cunha group and Gough Island, South Atlantic Ocean. *Ichthyol Bull JLB Smith Inst Ichthyol Grahamstown* 63: 1-43
- Árnason E, Pálsson S, Arason A (1992) Gene flow and lack of population differentiation in Atlantic cod, *Gadus morhua* L., from Iceland, and comparison of cod from Norway and Newfoundland. *J Fish Biol* 40: 751-770
- Avise JC (1994) *Molecular markers, natural history and evolution*. Chapman & Hall, New York
- Ball AO, Leonard S, Chapman RW (1998) Characterization of (GT)_n microsatellites from native white shrimp (*Penaeus setiferus*). *Molec Ecol* 7: 1251-1253
- Beentjes MP, Francis MP (1999) Movement of hapuku (*Polyprion oxygeneios*) determined from tagging studies. *N Z J mar Freshwat Res* 33: 1-12
- Bentzen P, Taggart CT, Ruzzante DE, Cook D (1996) Microsatellite polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. *Can J Fish aquat Sciences* 53: 2706-2721
- Bowen BW, Grant WS (1997) Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperate upwelling zones. *Evolution* 51: 1601-1610
- Briggs JC (1987) Antitropical distribution and evolution in the Indo-West Pacific Ocean. *Syst Zool* 36: 237-247

- Brooker AL, Cook D, Bentzen P, Wright JM, Doyle RW (1994) Organization of microsatellites differs between mammals and cold-water teleost fishes. *Can J Fish Aquat Sciences* 51: 1959–1966
- Deacon G (1984) The Antarctic circumpolar ocean. Cambridge University Press, Cambridge, UK
- Defense Mapping Agency (1973) Pilot chart of the North Atlantic Ocean. No 16. Defense Mapping Agency Hydrographic Center, Washington, DC
- Estoup A, Angers B (1998) Microsatellites and minisatellites for molecular ecology: theoretical and empirical considerations. In: Carvalho GR (ed) Advances in molecular ecology, IOS Press, Amsterdam, pp 55–86 (NATO Adv Sci Inst Ser A: Life Sciences)
- Felsenstein J (1993) PHYLIP (Phylogeny Inference Package). Version 3.5c. (Distributed by the author). Department of Genetics, University of Washington, Seattle
- Fennessy CJ (1998) The parasite fauna of the wreckfish, *Polyprion americanus*, in the North Atlantic Ocean: application to host biology and stock identification. MA thesis. College of William and Mary, Williamsburg, Virginia
- Gilhen J (1986) First three records of the wreckfish, *Polyprion americanus*, for Nova Scotia. *Can Fld Nat* 100: 381–382
- Goldstein DB, Ruiz Linares A, Cavalli-Sforza LL, Feldman MW (1995) Genetic absolute dating based on microsatellites and the origin of modern humans. *Proc natn Acad Sci USA* 92: 6723–6727
- Goodbred CO, Graves JE (1996) Genetic relationships among geographically isolated populations of bluefish (*Pomatomus saltatrix*). *Mar Freshwat Res* 47: 347–355
- Gordon AL (1971) Oceanography of Antarctic waters. In: Reid JL (ed) Antarctic oceanology. I. American Geophysical Union, Washington DC, pp 169–203
- Goujon M, Antoine L, Collet A, Fifas A, Fifas S (1993) Approche de l'impact ecologique de la pecharie thoniere au filet maillant derivant en Atlantique nord-est. Rapport Interne de la Direction des Ressources Vivantes de l'IFREMER I 93.034. IFR-EMER, Brest, France
- Grant WS (1987) Genetic divergence between congeneric Atlantic and Pacific Ocean fishes. In: Ryman N, Utter F (eds) Population genetics and fishery management. University of Washington Press, Seattle, pp 225–246
- Grant WS, Bowen BW (1998) Shallow population histories in deep evolutionary lineages of marine fishes: insights from sardines and anchovies and lessons for conservation. *J Hered* 89: 415–426
- Graves JE (1998) Molecular insights into the population structures of cosmopolitan marine fishes. *J Hered* 89: 427–437
- Guo SW, Thompson EA (1992) Performing the exact test of Hardy–Weinberg proportion for multiple alleles. *Biometrics* 48: 361–372
- Haimovici M, Martins AS, de Figueiredo JL, Vieira PC (1994) Demersal bony fish of the outer shelf and upper slope of the southern Brazil subtropical convergence ecosystem. *Mar Ecol Prog Ser* 108: 59–77
- Hardy JD (1978) Development of fishes of the Mid-Atlantic Bight. Vol. III. Aphredoderidae through Rachycentridae. US Fish Wildl Serv Biol Services Program, FWS/OBS-78/12
- Heemstra PC (1986) Family No 165: Polyprionidae. In: Smith MM, Heemstra PC (eds) Smiths' sea fishes. 6th edn. Springer-Verlag, Berlin, p 509
- Hilbish TJ, Mullinax A, Dolven SI, Meyer A, Koehn RK, Rawson PD (2000) Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. *Mar Biol* 136: 69–77
- Jarne P, Lagoda PJJ (1996) Microsatellites, from molecules to populations and back. *Trends Ecol Evolut* 11: 424–429
- Last PR, Scott EOG, Talbot FH (1983) Fishes of Tasmania. Tasmanian Fisheries Development Authority, Hobart
- Lewis PO, Zaykin D (2000) Genetic data analysis: computer program for the analysis of allelic data. Version 1.0 (d15). Free program distributed by the authors over the internet from the GDA Home Page at <http://alleyn.eeb.uconn.edu/gda/>
- Luckhurst BE (1996) Trends in commercial fishery landings of groupers and snappers in Bermuda from 1975 to 1992 and associated fishery management issues. Proc 48th int Center living aquat Resour Mgmt (ICLARM) Conf 48: 286–297 [In: Arreguin-Sanchez F, Munro JL, Balgos MC, Pauly D (eds) International Center for Living Aquatic Resources Management, Manila]
- Lutjeharms JRE (1990) The oceanography and fish distribution of the Southern Ocean. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, Republic of S. Africa, pp 6–27
- Manly BFJ (1985) The statistics of natural selection on animal populations. Chapman & Hall, London
- McElroy D, Moran P, Bermingham E, Kornfield I (1992) REAP: an integrated environment for the manipulation and phylogenetic analysis of restriction data. *J Hered* 83: 157–158
- Minch E (1996) MICROSAT 1.5. Stanford University, Stanford, California
- Nei M (1972) Genetic distance between populations. *Am Nat* 106: 283–292
- Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10
- O'Reilly P, Wright JM (1995) The evolving technology of DNA fingerprinting and its application to fisheries and aquaculture. *J Fish Biol* 47(A): 29–55
- Paetkau D, Waits LP, Clarkson PL, Craighead L, Strobeck C (1997) An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. *Genetics*, Austin, Tex 147: 1943–1957
- Paxton JR, Hoese DF, Allen GR, Hanley JE (1989) Pisces. Petromyzontidae to Carangidae. In: Walton DW, Longmore R (eds) Zoological catalogue of Australia. Vol 7. Brown Prior Anderson Pty Ltd, Burwood, Victoria
- Penrith MJ (1967) The fishes of Tristan da Cunha, Gough Island and the Vema Seamount. *Ann S Afr Mus* 48: 524–548
- Penrith MJ (1976) Distribution of shallow water marine fishes around southern Africa. *Cimbebasia (Ser A)* 4: 137–154
- Pingree RD, Sinha B, New AL, Waddington I, Head RN, Nechvolodov LV (1996) Will deep subtropical ring 'Storm Physalia' cross the Mid-Atlantic Ridge and reach America? *J mar biol Ass UK* 76: 553–567
- Raymond M, Rousset F (1995) GENEPOP (Ver. 1.2): population genetics software for exact tests and ecumenicism. *J Hered* 86: 248–249
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43: 223–225
- Roberts CD (1986) Systematics of the percomorph fish genus *Polyprion* Oken, 1817. PhD dissertation. Victoria University of Wellington, Wellington, NZ
- Roberts CD (1989) Reproductive mode in the percomorph fish genus *Polyprion*. *J Fish Biol* 34: 1–9
- Rowan MK, Rowan AN (1955) Fishes of Tristan da Cunha. *S Afr J Sci* 52: 129
- Schneider S, Kueffer J-M, Roessli D, Excoffier L (1997) Arlequin Ver. 1.1: a software for population genetic data analysis. Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland
- Schroeder WC (1930) A record of *Polyprion americanus* (Bloch and Schneider) from the northwestern Atlantic. *Copeia* 1930: 46–48
- Scoles DR, Collette BB, Graves JE (1998) Global phylogeography of mackerels of the genus *Scomber*. *Fish Bull US* 96: 823–842
- Sedberry GR (in press) Polyprionidae. In: Carpenter KE (ed) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Atlantic. FAO, Rome
- Sedberry GR, Andrade CAP, Carlin JL, Chapman RW, Luckhurst BE, Manooch CS, III, Menezes G, Thomsen B, Ulrich GF (1999) Wreckfish *Polyprion americanus* in the North Atlantic: fisheries, biology, and management of a widely distributed and long-lived fish. *Am Fish Soc Symp* 23: 27–50
- Sedberry GR, Carlin JL, Chapman RW, Eleby B (1996) Population structure in the pan-oceanic wreckfish, *Polyprion americanus*

- (Teleostei: Polyprionidae), as indicated by mtDNA variation. *J Fish Biol* 49(Suppl A): 318–329
- Sedberry GR, Carlin JL, Menezes GM (1998) Movement of a pelagic-phase wreckfish, *Polyprion americanus* (Schneider, 1801), as indicated by tag and recapture. *Arquipélago (Life mar Sci)* 16A: 69–72
- Sedberry GR, Ulrich GF, Applegate AJ (1994) Development and status of the fishery for wreckfish (*Polyprion americanus*) in the Southeastern United States. *Proc Gulf Caribb Fish Inst* 43: 168–192
- Shulman MJ, Bermingham E (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49: 897–910
- Smith JR, Carpten JD, Brownstein MJ, Ghosh S, Magnuson VL, Gilbert DA, Trent JM, Collins FS (1995) Approach to genotyping errors caused by nontemplated nucleotide addition by *Taq* DNA polymerase. *Genome Res* 5: 312–317
- Smith PJ, Benson PG, McVeagh SM (1997) A comparison of three genetic methods used for stock discrimination of orange roughy, *Hoplostethus atlanticus*: allozymes, mitochondrial DNA, and random amplified polymorphic DNA. *Fish Bull US* 95: 800–811
- Sokal RR, Rohlf FJ (1995) *Biometry. The principles and practice of statistics in biological research*. 3rd edn. WH Freeman & Company, New York
- Stepien CA, Rosenblatt RH (1966) Genetic divergence in antitropical pelagic marine fishes (*Trachurus*, *Merluccius*, and *Scomber*) between North and South America. *Copeia* 3: 586–598
- Sverdrup HU, Johnson MW, Fleming RH (1942) *The oceans: their physics, chemistry and general biology*. Prentice-Hall Inc, Englewood Cliffs, New Jersey
- Takezaki N, Nei M (1996) Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics*, Austin, Tex 144: 389–399
- Tautz D (1989) Hypervariability of simple sequences as a general source for polymorphic DNA markers. *Nucleic Acids Res* 17: 6463–6471
- Tessier N, Bernatchez L, Presa P, Angers B (1995) Gene diversity analysis of mitochondrial DNA, microsatellites and allozymes in landlocked Atlantic salmon. *J Fish Biol* 47(Suppl A): 156–163
- Tomczak M, Godfrey JS (1994) *Regional oceanography: an introduction*. Pergamon, New York
- Viard F, Franck P, Dubois M-P, Estoup A, Jarne P (1998) Variation of microsatellite size homoplasy across electromorphs, loci, and populations in three invertebrate species. *J molec Evolut* 47: 42–51
- Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution* 38: 1358–1370
- Wright S (1951) The genetical structure of populations. *Ann Eugen* 15: 323–354
- Wright S (1978) *Evolution and the genetics of populations*, vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago