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W. J. Burnett · J. A. H. Benzie · J. A. Beardmore
J. S. Ryland

High genetic variability and patchiness in a common Great Barrier Reef zoanthid (*Palythoa caesia*)

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Abstract Allozyme electrophoretic analysis of seven polymorphic enzyme loci suggested that 1261 samples of *Palythoa* collected along 1765 km of the Great Barrier Reef during 1992–1993 were members of a single taxon, identified as *Palythoa caesia* Dana, 1846, with high external morphological variability and possibly encompassing several previously described species. Populations were slightly genetically differentiated (standardized genetic variance, F_{ST}=0.010, $p< 0.05$), but there was no evidence of isolation by distance, or of the particular genetic distinction of geographic sets of reefs such as the Swains, as has been observed in other invertebrates. Differentiation was thought to be the result of random selection acting on patches of larvae, not the consequences of long-term reproductive isolation of populations.

Introduction

The order Zoanthidea (Anthozoa: Hexacorallia) is comprised of a relatively little studied group of clonal cnidarians, frequently abundant on coral reefs in the Great Barrier Reef (GBR) region and around the world. In spite of their ecological importance in some habitats such as reef flats, their taxonomy is in a state of confusion (Muirhead and Ryland 1985; Ryland and Muirhead 1993). This is due to high intraspecific morphological variation and a history of ambiguous descriptions in the literature, based upon badly preserved type-material. As a result it is almost impossible to identify most tropical Indo-Pacific zoanthid species with any degree of accuracy, leading to problems in understanding their ecology and levels of natural biodiversity.

The genera in Zoanthidea are generally well defined. Some groups of zoanthid morphs within genera stand out as being clearly different from one another. Within such fairly arbitrary groups there is a great range of minor variation in characters such as polyp colour, size and colony morphology which could represent differences within or between several species. Illustrations of many species in the literature, especially *Palythoa* spp., are very similar (for example see Carlgren 1937). Such species have been separated on the basis of characters that can only be examined by histological means, and the taxonomic significance of which is not clear. It was considered that allozyme electrophoresis would help resolve the taxonomic status of groups of *Palythoa* morphs by allowing an assessment of whether a group of morphs were freely interbreeding, and therefore members of the same species.

A number of papers have been published which have examined the population genetic structure of invertebrates on the GBR (Nash et al. 1988; Benzie 1991, 1992, 1993, 1994; Benzie and Pandolfi 1991; Benzie and Stoddart 1992a, b; Benzie and Williams 1992; Williams and Benzie 1993). These studies have generally shown high levels of gene flow within the GBR complex. In two species of giant clam, however, populations from the Swain Reefs region of the Southern GBR were genetically differentiated from the rest of the populations in the GBR complex (Benzie 1994). Apart from one, chiefly systematic, study (Stobart and Benzie 1994), no data have yet been published from GBR cnidarians, an extremely important group in the region. Such information is important in order to achieve an understanding of the interconnectedness of reefs in the GBR complex, and particularly in establishing to what extent faunas on individual reefs may be isolated genetically or are dependant upon one another for recruits, and the extent to which loss of genetic variability might result from damage to given reefs.

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W. J. Burnett (✉) · J. A. Beardmore · J. S. Ryland
School of Biological Sciences,
University of Wales, Swansea,
Singleton Park,
Swansea SA2 8PP, South Wales, UK

W. J. Burnett · J. A. H. Benzie
Australian Institute of Marine Science,
PMB 3, Townsville MC,
Queensland 4810, Australia

This study sought to establish patterns of genetic variation within a closely defined range of morphological variants, both as a starting point for a taxonomic revision of the family Zoanthidae and to provide information about broad-scale genetic structure of an ecologically important group of Cnidaria on the GBR.

Materials and methods

Sample collection

At least 30 individual colonies of *Palythoa* sp. were collected from two backreef sites at each of 19 reefs in six regions of the GBR, plus one site only at East Hope Island (Fig. 1), giving a total of 1261 samples over a distance of 1765 km, between Pandora Reef (Latitude 11°30′S) and Wistari Reef (Latitude 23°29′S). Sites within reefs were separated by at least 1 km. Colonies were collected from between 3 and 9 m depth by SCUBA divers, who prised them from the substratum (usually coral rock) using diving knives.

Colonies were sampled that met the following criteria: colonies small, ovoid, generally 5 to 10 cm in diameter, with large polyps (8 to 10 mm across) completely immersed in a thick coenenchyme when retracted (Fig. 2a). When open at night (Fig. 2b), the polyps project 1 cm clear of the colony surface and extend long tentacles (6 to 10 mm). Colonies are very pale buff to dark brown, speckled more or less heavily with darker brown, and contain large amounts of incorporated sediment. They appear to fragment upon reaching a certain size, resulting in the formation of patches of genetically identical colonies. Such clones are often extensive, covering up to 2 m^2.

The *Palythoa* sampled could potentially include several species, including 2 from the Torres Strait (*P. howesii*, *P. kochii*; Haddon and Shackleton 1891), 4 from Low Isles (*P. australiae*, *P. shackletoni*, *P. stephensoni*, *P. haddoni*; Carlgren 1937), 1 one from the Red Sea [*P. tuberculosa* (Esper); redescribed by Walsh and Bowers (1971) from Hawaii] and 1 from Fiji (*P. caesia*; Dana 1846). They are easily distinguishable from the two other main groups of *Palythoa* morphs found on the GBR, one of which has small (3 to 4 mm) polyps and forms very large, continuous sheets, and the other of which forms intermediate sized colonies of irregularly sized polyps.

Six voucher specimens from each reef were photographed in situ and fixed in 10% sea water/formalin, for morphological examination. Samples for electrophoresis were chopped into small (5 mm × 5 mm × 1 mm) pieces, placed in numbered polypropylene screw-cap vials, and snap-frozen in liquid nitrogen within 2 h of collection. Following transport back to the laboratory, vials were placed in numbered boxes and stored at -80°C.

Sample preparation

Tissue extracts containing enzymes were prepared by softening single pieces of tissue on ceramic spot plates in two drops of 0.04% aqueous 3-mercaptoethanol (plus trace bromophenol blue) using a metal rod. Crushed samples were then transferred to 1.5 ml microcentrifuge tubes and ground to a smooth paste by hand using a Treff™ homogeniser. Samples were then centrifuged (Beckman Microfuge E) for 10 min at 15 900 ×*g* and refrozen until needed for electrophoresis.

Electrophoresis

Electrophoresis was carried out using 12% horizontal starch gels (Sigma S-4501) and cellulose acetate gels (Cellogel™, Chemotron, Milan) following the techniques of Harris and Hopkinson (1976) and Richardson et al. (1986). Extracts were removed from the freezer, thawed, and the clear, mucus-free supernatant was either absorbed onto chromatography paper wicks (Whatman's No. 3) for use in starch gels or loaded onto the surface of cellulose acetate gels using a comb or draughtsman's pen.

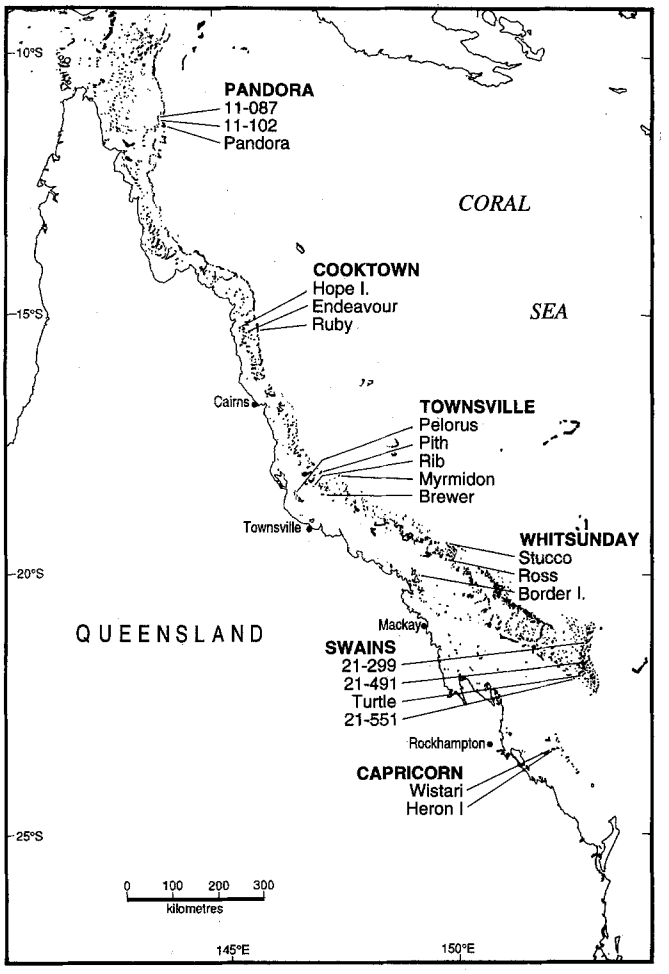

Fig. 1 Sampling localities within six regions of Great Barrier Reef

An initial survey of 42 enzymes detected 7 enzyme loci, coding for 7 different enzymes, which were polymorphic and consistently resolvable, and which were used in the analysis. The enzymes used were: glucose phosphate isomerase (GPI, E.C. 5.3.1.9), esterase-D (EST-D, E.C. 3.1.1.1), mannose-6-phosphate isomerase (MPI, 5.3.1.8), malate dehydrogenase (MDH, E.C. 1.1.1.37), malic enzyme (ME, E.C. 1.1.1.40), phosphoglucomutase (PGM, E.C. 5.4.2.2) and hexokinase (HK, E.C. 2.7.1.1). GPI and MPI were assayed on starch gels using a continuous Tris-citrate buffer, pH 8.0 (TC8.0, Borsa and Benzie 1992) run under constant current (50 mA) for 6 h. EST-D, MDH, PGM and HK were assayed on starch gels using a continuous Tris-EDTA-citrate buffer, pH 7.9 (TEC7.9, Goodall and Stoddart 1989) also run under constant current (35 mA) for 6 h. ME was assayed using cellulose acetate gels and a continuous phosphate buffer, pH 7.0 (Phos7.0, Richardson et al. 1986) run under constant potential (175 V) for 2.5 h. Zymograms were visualised using stain recipes modified from Harris and Hopkinson (1976).

Statistical analysis

The BIOSYS-1 program (Swofford and Selander 1981) was used to calculate gene frequencies and levels of genetic variability within populations, to carry out exact tests for deviations from Hardy–Weinberg predictions of genotype frequencies (Elston and Forthofer 1977), and perform hierarchical *F*-statistic analysis (Wright 1978).

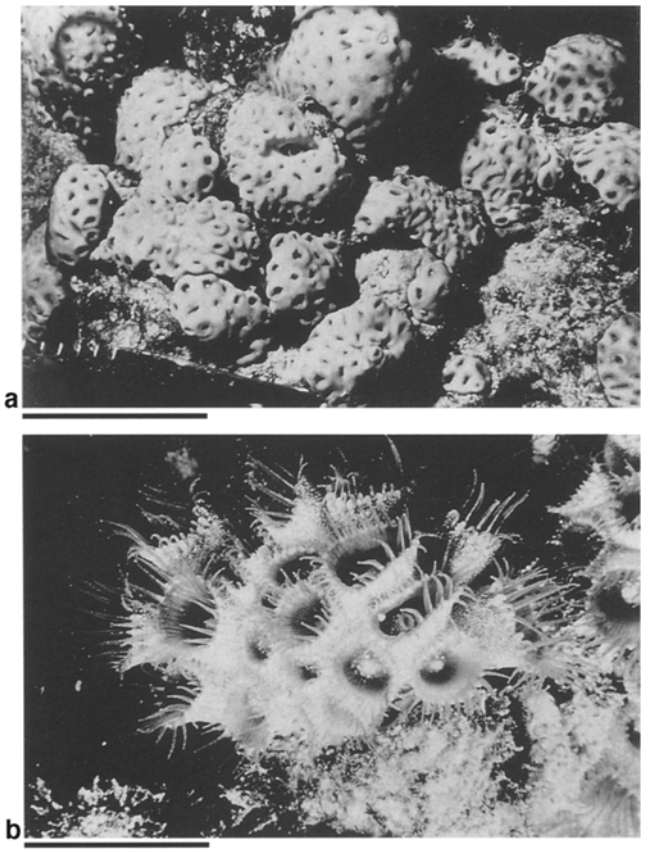

Fig. 2 *Palythoa caesia*. **a** Colonies on coral rock; all colonies are members of single clone (scale bar=10 cm). **b** Polyps open at night with tentacles extended (scale bar=5 cm)

Genetic homogeneity of subsites within reefs was tested using χ^2 and applying Yates' correction for small sample sizes. F_{ST} values of genetic differentiation between populations were calculated using the formulae of Weir and Cockerham (1984), which take into account differences in sample size, and χ^2 tests for significance of F_{ST} followed Waples (1987). Significance values of all χ^2 tests were appropriately corrected for multiple simultaneous tests using a simple Bonferroni technique (Miller 1980).

Results

All the enzymes assayed were polymorphic at a single locus. Of these, six (*GPI**, *EST**, *MPI**, *MDH**, *ME**, *PGM**) showed a single most common allele which was the same in every *Palythoa* sp. population examined (Table 1). *HK** had the same two common alleles in every population. Proportions of the less frequently occurring alleles varied widely between populations, but there were no alleles unique to particular populations. χ^2 tests of genetic homogeneity showed no significant differences between sites within reefs. Data from sites within reefs were pooled for further analysis.

Palythoa sp. populations were highly variable, with mean heterozygosity of 0.319, and mean number of alleles per locus between 3.4 and 4.3 (Table 2). Observed heterozygosities within reefs were consistently, but not significantly, lower than those expected under conditions of Hardy–Weinberg equilibrium. Exact tests of conformance to expected genotype frequencies, corrected for multiple simultaneous tests, showed no significant deviations with one exception – *PGM** in the Turtle Reef population showed significant deficits of the *122*/100** heterozygote (observed frequency=2, expected frequency=5), the *111*/100** heterozygote (obs.=9, exp.=15) and the *100*/80** heterozygote (obs.=1, exp.=4). There were no significant linkage disequilibria within the data set.

The average value of F_{ST} (genetic differentiation) over all loci for the total set of twenty populations was 0.016, indicating significant differentiation ($p< 0.001$) between populations (Table 3). This was primarily due to variation in two populations, Border Island and Reef 21-491. Removal of these two outliers from the analysis reduced F_{ST} to 0.010 ($p< 0.05$), suggesting some population structuring even in the absence of these two populations. All loci except *GPI** and *ME** showed significant values of F_{ST}. Values of F_{ST} calculated pairwise between reefs were not correlated with geographical separation (Fig. 3). When reefs within regions were pooled, F_{ST} was reduced to 0.008, but was highly significant ($p< 0.001$) due to the reduced number of degrees of freedom in the χ^2 test caused by pooling populations.

Hierarchical analysis showed most variation to occur between individual reefs within the GBR rather than between the regions sampled (Table 4).

Discussion and conclusions

Populations of *Palythoa* sp. on the GBR are highly genetically variable. Levels of heterozygosity are similar to those found in non-outbreak populations of *Acanthaster planci* (Benzie and Stoddart 1992a) and in giant clams (*Tridacna* spp., Benzie 1993), and are above average for marine invertebrates (Ferguson 1980).

The general lack of deviations from Hardy–Weinberg equilibrium suggested random mating within populations. These data provide strong evidence that all samples were members of a single taxon. This was further supported by the absence of any linkage disequilibria in the data. It is expected that morphological variation within this species will encompass several previously described species from the region, and that such species will be synonymised. Of the seven described species to which our *Palythoa* sp. might belong, uncertainty shrouds the identity of *P. tuberculosa*, leaving *P. caesia* as the senior valid name, and specimens apparently identical to ours from Fiji and from the GBR have earlier been identified as *P. caesia* (Dana, 1846) by one of us (Ryland and Muirhead 1993). We therefore name our samples as that species.

Table 1 *Palythoa caesia*. Gene frequencies at seven polymorphic enzyme loci in each of 20 populations, together with sample sizes (*N*)

Locus/ allele	11-087	11-102	Pand-dora	Ruby	Endea-vour	Hope	Pelorus	Pith	Rib	Myrm-idon
*GPI**										
(*N*)	(60)	(57)	(64)	(71)	(70)	(35)	(60)	(67)	(74)	(76)
*124**	–	–	–	0.007	–	0.014	–	–	–	–
*111**	0.083	0.070	0.070	0.077	0.086	0.057	0.150	0.090	0.128	0.112
*100**	0.883	0.912	0.875	0.915	0.871	0.929	0.825	0.881	0.851	0.862
*93**	0.033	0.018	0.055	–	0.036	–	0.025	0.030	0.020	0.026
*86**	–	–	–	–	0.007	–	–	–	–	–
*EST**										
(*N*)	(60)	(55)	(64)	(69)	(68)	(35)	(58)	(65)	(73)	(76)
*150**	–	–	–	–	–	–	–	–	–	–
*142**	–	0.009	0.008	–	–	0.029	0.009	–	–	0.020
*137**	–	–	–	0.007	–	–	–	–	–	–
*125**	0.217	0.218	0.328	0.246	0.199	0.143	0.207	0.254	0.158	0.250
*100**	0.767	0.773	0.648	0.696	0.699	0.829	0.784	0.738	0.842	0.730
*87**	–	–	–	–	0.007	–	–	–	–	–
*72**	0.017	–	0.016	0.051	0.088	–	–	0.008	–	–
*65**	–	–	–	–	0.007	–	–	–	–	–
*51**	–	–	–	–	–	–	–	–	–	–
*MPI**										
(*N*)	(60)	(57)	(52)	(61)	(67)	(35)	(53)	(62)	(74)	(76)
*105**	0.042	0.088	0.010	0.025	0.075	0.043	0.009	0.032	0.014	0.033
*100**	0.767	0.833	0.846	0.828	0.858	0.829	0.877	0.887	0.939	0.868
*93**	0.192	0.079	0.144	0.131	0.067	0.086	0.104	0.081	0.047	0.099
*90**	–	–	–	0.008	–	0.014	0.009	–	–	–
*86**	–	–	–	0.008	–	0.029	–	–	–	–
*MDH**										
(*N*)	(60)	(57)	(63)	(69)	(71)	(35)	(60)	(67)	(74)	(76)
*120**	–	–	–	0.007	–	–	–	–	–	0.013
*116**	0.050	0.088	0.024	0.087	0.085	0.057	0.042	0.075	0.068	0.046
*100**	0.933	0.912	0.976	0.906	0.915	0.929	0.958	0.910	0.919	0.928
*96**	–	–	–	–	–	–	–	0.007	0.007	–
*89**	0.017	–	–	–	–	–	–	0.007	0.007	0.013
*82**	–	–	–	–	–	0.014	–	–	–	–
*ME**										
(*N*)	(60)	(57)	(62)	(69)	(68)	(35)	(60)	(65)	(74)	(75)
*122**	0.058	0.044	0.048	0.051	0.015	0.014	–	0.015	0.020	0.040
*100**	0.800	0.851	0.806	0.862	0.890	0.914	0.892	0.800	0.872	0.847
*92**	0.142	0.105	0.145	0.087	0.096	0071	0.108	0.185	0.108	0.113
*PGM**										
(*N*)	(60)	(56)	(63)	(67)	(69)	(35)	(58)	(66)	(74)	(76)
*135**	–	0.009	–	0.015	0.014	–	–	–	–	–
*128**	–	–	–	–	–	–	–	–	–	0.007
*122**	0.067	0.071	0.087	0.030	0.109	0.014	0.017	0.061	0.020	0.053
*111**	0.108	0.116	0.040	0.112	0.043	0.071	0.086	0.197	0.081	0.112
*104**	0.058	–	–	0.007	–	0.014	0.095	0.045	0.034	–
*100**	0.692	0.741	0.857	0.776	0.797	0.857	0.776	0.644	0.838	0.796
*80**	0.067	0.036	0.016	0.022	0.007	0.043	–	0.045	0.020	0.020
*63**	0.008	0.027	–	0.037	0.029	–	0.026	0.008	0.007	0.013
*HK**										
(*N*)	(60)	(57)	(57)	(68)	(70)	(31)	(57)	(66)	(74)	(75)
*132**	0.008	0.053	0.044	–	–	0.016	–	–	–	–
*126**	0.158	0.132	0.132	0.015	0.043	0.032	0.044	0.030	0.054	0.027
*122**	0.025	0.009	0.035	0.206	0.157	0.097	0.140	0.189	0.135	0.193
*115**	0.333	0.281	0.219	0.287	0.321	0.435	0.368	0.288	0.365	0.280
*106**	–	0.009	–	–	–	0.016	–	0.061	0.007	–
*100**	0.300	0.316	0.421	0.331	0.307	0.339	0.289	0.295	0.324	0.360
*87**	0.175	0.167	0.096	0.140	0.157	0.065	0.158	0.106	0.108	0.140
*78**	–	0.035	0.053	0.022	0.014	–	–	0.030	0.007	–

John Brewer	Stucco	Ross	Border	Turtle	21-491	21-299	21-551	Wistari	Heron
(51)	(62)	(60)	(59)	(61)	(63)	(64)	(64)	(64)	(60)
–	–	–	–	–	0.008	–	–	–	–
0.127	0.056	0.117	0.093	0.156	0.177	0.070	0.141	0.156	0.067
0.824	0.919	0.817	0.881	0.828	0.815	0.922	0.852	0.828	0.883
0.039	0.024	0.067	0.025	0.016	–	0.008	0.008	0.016	0.050
0.010	–	–	–	–	–	–	–	–	–
(51)	(62)	(59)	(60)	(62)	(63)	(64)	(64)	(64)	(60)
–	0.008	–	–	–	–	–	–	–	–
–	0.008	0.017	–	–	0.016	0.008	–	0.031	0.017
–	–	–	0.008	–	0.008	–	0.008	–	–
0.206	0.210	0.144	0.408	0.202	0.349	0.078	0.227	0.211	0.125
0.775	0.766	0.822	0.583	0.774	0.587	0.883	0.734	0.719	0.842
–	0.008	–	–	–	–	–	0.008	–	–
0.010	–	0.017	–	0.024	0.040	0.031	0.023	0.039	0.017
–	–	–	–	–	–	–	–	–	–
0.010	–	–	–	–	–	–	–	–	–
(47)	(59)	(60)	(59)	(62)	(62)	(63)	(64)	(64)	(60)
0.053	0.017	0.042	0.017	0.016	0.032	0.040	0.031	0.070	0.042
0.777	0.881	0.875	0.864	0.839	0.694	0.849	0.859	0.781	0.775
0.149	0.102	0.083	0.102	0.145	0.274	0.111	0.109	0.148	0.183
0.011	–	–	0.017	–	–	–	–	–	–
0.011	–	–	–	–	–	–	–	–	–
(51)	(62)	(60)	(59)	(61)	(63)	(62)	(64)	(64)	(59)
–	0.008	–	–	–	–	0.008	0.008	–	–
0.137	0.121	0.183	0.076	0.221	0.278	0.089	0.109	0.086	0.085
0.853	0.863	0.817	0.924	0.770	0.722	0.887	0.859	0.906	0.907
–	–	–	–	–	–	0.008	–	–	–
0.010	–	–	–	0.008	–	0.008	0.023	0.008	0.008
–	0.008	–	–	–	–	–	–	–	–
(49)	(58)	(57)	(58)	(61)	(63)	(64)	(64)	(64)	(60)
0.031	0.009	0.018	0.009	0.033	0.008	–	0.039	0.016	0.008
0.878	0.914	0.877	0.966	0.885	0.849	0.874	0.867	0.867	0.825
0.092	0.078	0.105	0.026	0.082	0.143	0.125	0.094	0.117	0.167
(51)	(61)	(58)	(57)	(59)	(62)	(62)	(64)	(64)	(60)
–	–	–	–	–	–	–	–	–	0.008
–	–	–	–	0.008	0.008	–	–	0.023	0.008
0.108	–	–	0.035	0.059	0.105	0.056	0.078	0.063	0.067
0.098	0.033	0.095	0.237	0.178	0.202	0.105	0.039	0.156	0.192
0.039	0.090	0.172	0.140	–	0.008	–	–	–	–
0.725	0.820	0.690	0.553	0.703	0.621	0.806	0.867	0.742	0.675
0.010	0.033	0.034	0.035	0.051	0.040	0.024	0.016	0.008	0.042
0.020	0.025	0.009	–	–	0.016	0.008	–	0.008	0.008
(51)	(57)	(56)	(58)	(59)	(63)	(63)	(64)	(63)	(59)
–	0.026	0.009	–	0.008	0.056	0.008	0.008	0.016	0.034
0.039	0.035	0.089	0.034	0.237	0.127	0.151	0.055	0.048	0.093
0.176	0.132	0.134	0.198	0.008	0.024	0.040	0.180	0.190	0.153
0.284	0.333	0.375	0.405	0.373	0.357	0.254	0.336	0.238	0.246
0.059	–	0.027	–	–	–	0.048	–	0.032	–
0.373	0.351	0.232	0.310	0.322	0.302	0.357	0.320	0.302	0.364
0.069	0.096	0.116	0.043	0.042	0.127	0.135	0.094	0.151	0.110
–	0026	0.018	0.009	0.008	0.008	0.008	0.008	0.024	–

Table 2 *Palythoa caesia*. Genetic variability in the 20 populations sampled. Standard errors in parentheses. A locus is considered polymorphic if more than one allele was detected, and expected heterozygosity is Nei's unbiased estimate (Nei 1978)

Population	Mean sample size/locus	Mean no. alleles/locus	% loci polymorphic	Mean heterozygosity (direct count)	Mean heterozygosity (Hardy–Weinberg expected)
11-087	60.0 (0.0)	3.9 (0.6)	100.0	0.295 (0.065)	0.382 (0.076)
11-102	56.6 (0.3)	4.0 (0.8)	100.0	0.328 (0.082)	0.351 (0.080)
Pandora	60.7 (1.7)	3.7 (0.6)	100.0	0.299 (0.081)	0.336 (0.084)
Ruby	67.7 (1.2)	4.4 (0.6)	100.0	0.311 (0.070)	0.353 (0.078)
Endeavour	69.0 (0.5)	4.1 (0.6)	100.0	0.316 (0.070)	0.346 (0.079)
Hope	34.4 (0.6)	4.1 (0.6)	100.0	0.231 (0.072)	0.284 (0.073)
Pelorus	58.0 (1.0)	3.4 (0.5)	100.0	0.314 (0.096)	0.324 (0.079)
Pith	65.4 (0.6)	4.1 (0.6)	100.0	0.338 (0.075)	0.377 (0.084)
Rib	73.9 (0.1)	4.0 (0.7)	100.0	0.251 (0.066)	0.293 (0.077)
Myrmidon	75.7 (0.2)	3.9 (0.5)	100.0	0.329 (0.061)	0.341 (0.074)
John Brewer	50.1 (0.6)	4.4 (0.5)	100.0	0.343 (0.067)	0.389 (0.066)
Stucco	60.1 (0.8)	4.3 (0.6)	100.0	0.283 (0.070)	0.315 (0.078)
Ross	58.6 (0.6)	4.0 (0.8)	100.0	0.325 (0.082)	0.376 (0.074)
Border	58.6 (0.4)	3.7 (0.5)	100.0	0.303 (0.089)	0.356 (0.094)
Turtle	60.7 (0.5)	3.9 (0.6)	100.0	0.346 (0.072)	0.383 (0.062)
21-491	62.6 (0.2)	4.3 (0.8)	100.0	0.452 (0.077)	0.467 (0.063)
21-299	63.1 (0.3)	4.3 (0.7)	100.0	0.263 (0.071)	0.309 (0.080)
21-551	64.0 (0.0)	4.1 (0.6)	100.0	0.306 (0.063)	0.343 (0.071)
Wistari	63.9 (0.1)	4.3 (0.7)	100.0	0.366 (0.075)	0.389 (0.077)
Heron	59.7 (0.2)	4.1 (0.6)	100.0	0.326 (0.077)	0.371 (0.078)

Table 3 *Palythoa caesia*. F_{ST} (standardised genetic variance) for seven individual loci for total data set of 20 populations, and with two outlying populations (Border Island and Reef 21-491) removed. (* $p < 0.05$; ** $p < 0.02$; *** $p < 0.001$

Locus	All populations	2 outliers removed
*GPI**	0.004	0.004
*EST-D**	0.024***	0.012***
*MPI**	0.014***	0.008
*MDH**	0.029***	0.019***
*ME**	0.005	0.001
*PGM**	0.029***	0.018***
*HK**	0.011**	0.010**
Mean	0.016***	0.010*

Table 4 *Palythoa caesia*. Hierarchical F_{ST} analysis (Wright 1978) of variation among populations

Comparison	Variance component	F_{ST}
Reefs within regions	0.03545	0.014
Reefs within total	0.04103	0.016
Regions within total	0.00558	0.002

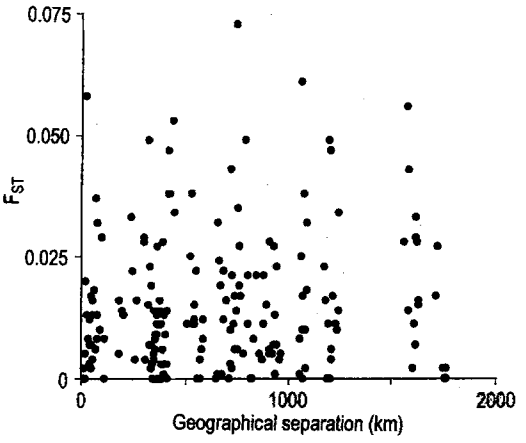

Fig. 3 *Palythoa caesia*. Pairwise F_{ST} (genetic differentiation) between sample sites as a function of geographical separation

Taxonomic problems in other zoanthid genera have arisen for much the same reasons as in the genus *Palythoa*. It might, therefore, be expected that there has been a general exaggeration of the numbers of extant zoanthids, and that further work will allow a complete revision of the order and a substantial reduction in the number of species, as in the revision of *Isaurus* spp. (Muirhead and Ryland 1985) in which several nominate species were synonymised within the pantropical *I. tuberculatus* Gray.

Significant genetic differentiation between populations was observed, but was not correlated with geographical separation. The fact that 5 of the 7 loci screened contributed to the significant average value of F_{ST} provided sound evidence that the patterns found reflect general trends of genetic exchange among populations and not the effects of selection at particular loci. The lack of relationship between genetic differentiation and geographical separation implies that there was no isolation by distance effect among *Palythoa caesia* populations over the geographical scale surveyed.

Zoanthids have long been known to have long-lived, dispersive, pelagic larvae (Menon 1902, 1926), with larvae of *Palythoa* spp. potentially able to cross the Atlantic Ocean in equatorial currents (Scheltema 1968). Babcock and Ryland (1990) described the development of a *Protopalythoa* sp., a closely related genus, from Orpheus Island, Queensland, which takes 17 to 19 d to become capable of

settlement. They suggested this larval duration is near the minimum for zoanthids. No data exist for a *Palythoa* sp. from the GBR, but a long larval life provides a mechanism for the extensive dispersal suggested by high gene flow in an otherwise sessile organism. This strong potential for long-distance genetic exchange is, however, in marked contrast to differentiation observed among some reefs separated by relatively short distances.

The distribution of dispersive larvae of mass-spawning scleractinians is known to be spatially patchy (Willis and Oliver 1990; Oliver et al. 1992). Colonies of *Palythoa* spp. have been observed mass-spawning 3 to 5 d after the November full moon in 1992 and 1993 (W. J. B. personal observation), and larval distributions are likely to be similar to those found in corals. Johnson and Black (1984) suggested that differential selection between patches of planktonic larvae might result in patches of genetically differentiated recruits in populations of south-western Australian limpets. This might also provide a mechanism to explain genetic patchiness in zoanthid populations on the GBR in the face of long-distance dispersal by pelagic larvae. The arrival of large numbers of larvae which have been subject to some unusual selection pressure might cause perturbations in gene frequencies in a few populations. While most populations would be genetically similar, a few would stand out as being strongly differentiated until subsequent recruitment events brought gene frequencies back within the normal range of variance.

GBR *Palythoa caesia* populations show marginally significant genetic differentiation between most reefs. Two reefs stand out as being strongly differentiated. We consider that this differentiation is unlikely to represent long periods of reproductive isolation of these reefs, due to the absence of any private alleles in these populations and due to the close proximity of the most differentiated population, Reef 21-491, to other, non-differentiated, populations. We believe this differentiation represents ephemeral genetic patchiness rather than long-term genetic isolation of these reefs.

F_{ST} was found to be lower, although still significant, between regions than between individual reefs. This was consistent with the results of the hierarchical analysis, which suggested that most variation occurred between individual reefs. Although significant differentiation of the Swains region from the rest of the GBR has been shown in two species of giant clam (*Tridacna maxima* and *T. derasa*; Benzie 1994), there was no indication from *Palythoa caesia* that populations within the Swains were more highly differentiated than were those from other regions.

No isolation by distance effect was apparent over the geographic scale surveyed between reefs or between regions. This suggests that gene flow in *Palythoa caesia* is best described by an island model (Wright 1978), in which recruits to any one population are equally likely to arrive from any other population. Our results suggest that gene flow, while uneven over short time scales, is sufficient to prevent genetic isolation of particular regions of the GBR.

Palythoa caesia is a common and widespread zoanthid encompassing a range of morphological variants, with high levels of genetic variability and high average gene flow among populations. The high gene flow between reefs is likely to result in rapid recolonisation of damaged areas by *P. caesia*, at least on an evolutionary time scale. The abundance and high gene flow of this species suggests that there is no requirement to protect specific reefs in the GBR region in order to preserve genetic variability within this taxon.

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