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Keywords: Topshells, Trochidae, Trochus niloticus, Tectus coerulescens, Tectus pyramis, allozymes, population genetics, F-statistics, gene flow, Great Barrier Reef, Coral Sea, Australia

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P. Borsa · J. A. H. Benzie

Population genetics of *Trochus niloticus* and *Tectus coerulescens*, topshells with short-lived larvae

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Abstract *Trochus niloticus* L. and *Tectus coerulescens* Lmk., two coral reef trochid gastropods that have similar life-histories including a lecithotrophic larval stage, were sampled from reefs in the northern, central and southern sections of the Great Barrier Reef (GBR) in 1991. Significant sex-ratio biases were noted, and these varied among reefs, apparently with latitude. Demographic data suggested that highly discontinuous and localized recruitment occurs. Surveys of allozyme frequencies at 12 loci revealed no significant genetic differences among populations of *Trochus niloticus* at any geographical scale. High gene flow between zones of the GBR was inferred, with the number of migrants per generation (N_m) of the order of 100. Directional selection was thought to occur at one locus (*GDH**). Genetic variability in *T. niloticus* ($H = 0.069$ to 0.110, and only three loci polymorphic) was low compared with other trochids. This was thought to be due to smaller effective population size, resulting from an unbalanced sex-ratio, aggregative spatial distribution of adults, high variance in reproductive success, and/or the occurrence of population extinctions and recolonisations. In contrast, *Tectus coerulescens* exhibited significant genetic differences between zones, indicating a much lower rate of migration between populations ($N_m \sim 1$ to 10), and displayed high genetic diversity ($H = 0.225$ to 0.279). A trend for increasing genetic diversity from the northern to southern GBR was found in both species. It is not clear whether the occurrence of two contrasted population genetic structures in species with apparently similar life-histories is due to ecological or historical factors.

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P. Borsa (✉)[1] · J. A. H. Benzie
Australian Institute of Marine Science, PMB. No. 3,
Townsville M.C., Townsville, Queensland 4810,
Australia

Present address:
[1]ORSTOM UR 33, Zoologie, 911 avenue Agropolis, B.P. 5045,
34032 Montpellier-cedex 1, France

Introduction

The extent of gene flow between populations of benthic marine invertebrates depends on an array of factors: the presence or absence of a planktonic larval stage and its duration, the magnitude of the effective net transport of larvae by currents, the probability of encountering suitable habitats for settlement, success in subsequent recruitment, suitability of the new benthic habitat for development into adults and, finally, the contribution of the adults to subsequent generations (Strathmann 1980; Bertness and Gaines 1993). The mode of larval development can be either non-feeding (lecithotrophic) whereby larvae spend a few days in the plankton during which they rely exclusively on the energetic resources present in the egg, or feeding (planktotrophic) with durations in the plankton of, typically, one to several weeks (Strathmann 1985).

Species with planktotrophic larvae have broader geographic ranges (Scheltema 1989) and exhibit genetic homogeneity over greater distances (Berger 1983; Burton 1983; Ward 1990) than species with restricted dispersal such as those with brooded or encapsulated offspring. The sharp genetic structure reported in some species with long larval lives has been related to oceanographical discontinuities at the regional scale (lobster *Homarus americanus*: Tracey et al. 1975; blue mussel *Mytilus edulis*: Koehn et al. 1976) or ascribed to directional selection differently affecting successive swarms of pre-recruits (bivalve *Modiolus demissus*: Koehn et al. 1973; limpet *Siphonaria* sp.: Johnson and Black 1982; urchin *Echinometra matthaei*: Watts et al. 1990).

In contrast, species with lecithotrophic larvae are likely to have smaller neighbourhood sizes than species with planktotrophic larvae, a population structure that in turn may recognize the habitat as

large-grained and so respond more sharply to ecological discontinuities (e.g. Johnson and Black 1991).

Species with planktotrophic larvae from the Great Barrier Reef (GBR) such as the crown-of-thorns *Acanthaster planci* (Nash et al. 1988; Benzie and Stoddart 1992), the giant clam *Tridacna gigas* (Benzie and Williams 1992) and the starfish *Linckia laevigata* (Williams and Benzie 1993) have been shown to be genetically homogeneous throughout that region. Where deviations have been observed they have been ascribed to stochastic effects of selection prior to settlement (Benzie 1994; Burnett et al. 1994).

Currents in the GBR not only can transfer larvae between neighbouring reefs, but also can transport them considerable distances in a few days (Williams et al. 1984; Wolanski et al. 1989). However, the complex hydrology of the GBR does result in mesoscale eddies which can trap larvae and allow self-seeding of reefs (Wolanski et al. 1989). One might expect a short larval life to result in greater degrees of self-seeding, and hence significant genetic structuring on relatively small scales. Alternatively, there may be sufficient transfer between adjacent reefs to prevent genetic divergence of populations over large parts of the GBR. Data from the viviparous coral *Seriatopora hystrix* which has a short larval life (usually < 4 d) have revealed high genetic differentiation of populations consistent with self-seeding and inconsistent with a high degree of gene exchange (Ayre and Dufty 1994). It is important to extend the data set on species with short larval lives to determine whether the results on *S. hystrix* illustrate a general response of such species to the hydrodynamic patterns on the GBR.

The topshells *Trochus niloticus* L. (3 d in the plankton; Heslinga and Hillmann 1981) and *Tectus coerulescens* Lmk. (a short larval life inferred from the large and yolky melon-green eggs characteristic of lecithotrophic archaeogastropods; Bell 1992) provide examples with which to test the generality of the finding from the coral *Seriatopora hystrix*. *Trochus niloticus* and *Tectus coerulescens* have similar life-histories in that both species graze on algae on the reef flat and have lecithotrophic larvae. *Trochus niloticus* inhabits the most exposed parts of the reef front and flat, while *Tectus coerulescens* inhabits more protected parts. The present paper reports surveys of demographic structure and allozyme variation at different geographic scales designed to determine recruitment patterns and population genetic structure, and to investigate the extent of dispersal between populations of *Trochus niloticus* and *Tectus coerulescens* on the GBR.

Materials and methods

The *Tectus* species sampled on the GBR (named *T. pyramis* on Fig. 2a of Borsa and Benzie 1993) fitted Lamarck's description of *T. coerulescens* (Lamarck 1822; Reeve 1862; Kiener and Fischer 1875). We therefore use the latter name in the present report.

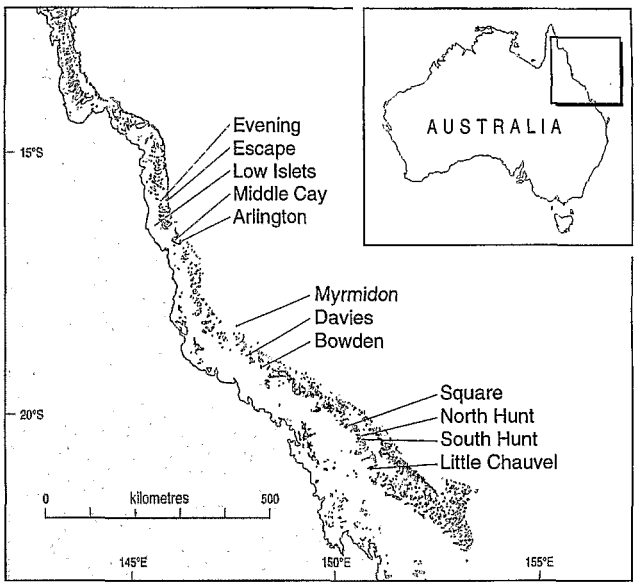

Fig. 1 Location of reefs sampled in Great Barrier Reef for *Trochus niloticus* (collected at all reefs except Myrmidon Reef where no live individual was found) and *Tectus coerulescens* (collected at Escape, Davies and Square Reefs)

Collection of samples

Sampling of *Trochus niloticus* followed a nested design. Within the three zones sampled (the northern, central and southern sections of the GBR), several reefs were sampled in each zone, and up to three sites were sampled at each reef. All individuals encountered during the dive at a site were collected. Collections were made by SCUBA divers in the turf zone at depths shallower than 5 m on the reef front up to the reef crest on the oceanic side of the reef. This practice followed Nash (1985) and our results from preliminary transects made at Davies Reef and Middle Cay which showed that these were the sites of main population density of *T. niloticus*. At Southern Hunt Reef, *T. niloticus* were collected from the reef flat behind the crest, because they were more abundant at this site.

A total of 840 *Trochus niloticus* were collected from 11 reefs in the GBR in 1991 (Fig. 1: all reefs except Myrmidon). The northern GBR Low Islets sample consisted of only five individuals. This sample was discarded for the study of within-zone population structure, and was pooled with the other samples of the northern GBR for between-zones comparisons. No live *T. niloticus* (only two large empty shells) were found on Myrmidon Reef in the outer margin of the central section of the GBR (Fig. 1), in spite of a searching effort (diver × time) about twice that spent on the other reefs.

The protected (north-western) hard-bottom habitat of three reefs was sampled for *Tectus coerulescens*. A total of 59 *T. coerulescens* were collected on Escape Reef (northern GBR), Davies Reef (central GBR) and Square Reef (southern GBR). The Escape Reef sample consisted of only two individuals. It was discarded for the study of inter-zone genetic variation in this species.

The topshells were kept alive on board the research vessel until they were dissected, their sex determined, and processed. The largest diameter of the base of the shell in each individual was measured to the nearest millimetre with a ruler. Portions of digestive gland and columellar muscle were snap-frozen and preserved in liquid nitrogen until transferred to $-80\,^{\circ}C$ in the laboratory.

Demographic analyses

Individuals were classed according to shell diameter and sex. Length-frequency distributions were plotted in size ranges of 10 mm in *Trochus niloticus*. This is an appropriate class interval according to both the range of sizes in a sample (60 to 90 mm) and sample size ($N = 13$ to 83) (see Scherrer 1984). The effect of such grouping was to smooth the size distributions while preserving the information on the presumed age-structure of a sample, to an extent compatible with the growth-rate variability reported in *T. niloticus* (Smith 1987; Bour 1992). Similarly, the class interval was chosen as 5 mm in *Tectus coerulescens*. The sex-ratio in a sample, defined as the number of females divided by the number of males, was compared to a binomial distribution, where the expected frequency of males equals that of females.

Allozyme electrophoresis

Fragments of digestive gland and columellar muscle were ground in a ceramic dish using a stainless steel pestle, and their soluble enzyme extracts were subjected to allozyme electrophoresis on starch or cellulose acetate gels. All protocols, from dissection to electrophoresis and staining, have been reported earlier (Borsa and Benzie 1992).

Nine presumed enzyme loci were scored for each individual of *Trochus niloticus* and of *Tectus coerulescens*: *DIA-1** and *DIA-2**, each encoding a diaphorase (EC No. 1.6.2.2); *EST-D**, encoding a 4-methylumbelliferyl specific esterase (EC 3.1.1.1); *GPI**, a glucose-phosphate isomerase (EC 5.3.1.9); *IDH-1**, an isocitrate dehydrogenase (EC 1.1.1.42); *MDH-2**, a malate dehydrogenase (EC 1.1.1.37); *ME-2**, a malic enzyme (EC 1.1.1.40); *PEP-2**, a peptidase (EC 3.4.11.–) catabolising the dipeptide Leu-Tyr, and *PGM**, a locus encoding a phosphoglucomutase (EC 2.7.5.1). A second malate dehydrogenase locus (*MDH-1**) was scored in *Trochus niloticus* and a second esterase locus (*EST-N**) was scored in *Tectus coerulescens*. An additional locus, *GDH**, encoding a glucose dehydrogenase (EC 1.1.1.47) was scored in only four samples of *Trochus niloticus* (Table 1). *IDH-2**, encoding a second isocitrate dehydrogenase, was scored in each sample of *Tectus coerulescens* and in only five samples of *Trochus niloticus* (Table 1).

We assumed that electrophoretic variation in these enzymes was determined in a simple Mendelian fashion, as (1) the electrophoretic banding patterns of enzymes polymorphic in either *Trochus niloticus*, *Tectus coerulescens* or other species in the same genera (Borsa and Benzie 1992) were consistent with the quaternary structures they usually have in other animal species (Richardson et al. 1986), and (2) all phenotypes expected according to a Mendelian model were present in the sample.

Analysis of electrophoretic data

Genetic correlations within and among populations were estimated using the *F*-statistic parameters f (for F_{IS}, the correlation of alleles at a locus in an individual relative to its subpopulation) and θ (for F_{ST}, the correlation of alleles at a locus in a subpopulation relative to the total population) of Weir and Cockerham (1984). Weighted averages of single-locus f and θ were calculated according to Eq. (10) of Weir and Cockerham. Their variances were estimated using the jackknife procedure over samples and over loci (Weir 1990). Estimates of gene flow were obtained from the estimates of θ as $N_m = (1 - \theta)/4\theta$ (Wright 1969), and also from the average frequency (p) of electromorphs specific to one sample as $N_m = (25/N) \exp[(\ln(p) + 2.44)/-0.505]$ (Slatkin 1985), where N is the average sample size.

Both equations were primarily derived under Wright's island model of population structure, whereby island population sizes are equal and constant over generations, and population differentiation depends on the balance between genetic drift and migration after the originally homogeneous ancestral population has been subdivided. We are aware that in real populations, patterns of colonisation and differentiation may be much more complex. We shall assume however that the approximate values for gene flow are correct in the case where both methods give similar results.

Correlations of non-allelic genes in populations were investigated by estimating Weir's parameter of genotypic disequilibrium, Δ_{AB} (Weir 1990). Single-locus genetic diversity in a population was estimated using the estimator $h = 2N(1 - \Sigma_i x_i^2)/(2N-1)$, where x_i = the frequency of allele i in the sample, and which is unbiased for sample size (N). The variance of the average h over loci (H) was estimated by jackknifing (Sokal and Rohlf 1981) the set of h in the population.

Other statistics

The sources for other statistical tests were Sokal and Rohlf (1981) and Weir (1990). The corresponding calculations, and the jackknifing were done using microcomputer programs written by P. Borsa. Statistics for Wilcoxon–Gros–Chessel rank test for the comparison of two distributions (Gros and Chessel 1982) and for normality test (Lilliefors 1967), were computed using the BIOMECO package (Lebreton et al. 1990).

Results

Demographic structure

Trochus niloticus

The distribution of *Trochus niloticus* was clumped, with aggregations of 2 to 11 individuals usually found in large holes or in the surge channels extending perpendicular to the reef front. Isolated individuals were rare.

The demographic structure of *Trochus niloticus* populations displayed contrasting patterns from reef to reef (Fig. 2). Body-size distributions revealed discrete cohorts that were different from one local population to the next, e.g. between neighbouring reefs Escape (ES) and Evening (EV), or Northern Hunt (NH) and Southern Hunt (SH). Some samples from local populations had monomodal size-frequency distributions: ES, Middle Cay (MC) and Davies (DA). Other samples such as EV, Square (SQ), NH, SH and Little Chauvel (LC) had bimodal distributions. The structure in two other samples, Arlington (AR) and Bowden (BO), was less clear, perhaps as a consequence of relatively small sample size or because of some differential structure between sexes. In each of the AR and BO samples, the mode in the female size-distribution did not correspond to any of the two modes observed in male size-distribution.

All individuals collected were sexually mature. The smallest individual *Trochus niloticus* collected was 48 mm wide. Sex-ratios departed significantly from the 1:1 binomial expectations in 6 of the 10 samples (ES, MC, AR, NH, SH and LC; see Fig. 2 legend). In two of these (MC and LC), the sex-ratio biases remained significant ($p < 0.01$ and $p < 0.001$, respectively) after the error rate was adjusted according to the Bonferroni

Table 1 *Trochus niloticus*. Electromorph frequencies in 11 populations of Great Barrier Reef (*ES* Escape Reef; *EV* Evening Reef; *LI* Low Islets; *MC* Middle Cay; *AR* Arlington Reef; *DA* Davies Reef; *BO* Bowden Reef; *SQ* Square Reef; *NH* North Hunt Reef; *SH* South Hunt Reef; *LC* Little Chauvel Reef; *N* sample size; – no data)

Locus, electromorph	Sample:										
	ES	EV	LI	MC	AR	DA	BO	SQ	NH	SH	LC
*DIA-1**											
100	1	1	1	1	1	1	1	1	1	1	1
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*DIA-2**											
100	1	1	1	1	1	1	1	1	1	1	1
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*EST-D**											
100	0.987	1	–	1	1	1	1	1	1	1	1
070	0.013	0	–	0	0	0	0	0	0	0	0
(*N*)	(38)	(68)	(0)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*GDH**											
123	0.154	0.182	–	–	–	0.146	–	–	0.422	–	–
100	0.846	0.818	–	–	–	0.854	–	–	0.578	–	–
(*N*)	(13)	(22)	(0)	(0)	(0)	(41)	(0)	(0)	(32)	(0)	(0)
*GPI**											
160	0.158	0.096	0.100	0.110	0.085	0.086	0.088	0.121	0.149	0.122	0.107
133	0	0	0	0	0	0	0.007	0	0.006	0	0.004
100	0.842	0.904	0.900	0.890	0.915	0.911	0.905	0.874	0.845	0.877	0.888
063	0	0	0	0	0	0.004	0	0.005	0	0	0
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*IDH-1**											
160	0.013	0	0	0.006	0	0.007	0	0	0	0	0
100	0.987	1	1	0.994	1	0.993	1	1	0.995	1	1
021	0	0	0	0	0	0	0	0	0.005	0	0
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*IDH-2**											
100	1	1	–	–	–	1	–	–	1	–	1
(*N*)	(38)	(20)	(0)	(0)	(0)	(22)	(0)	(0)	(4)	(0)	(75)
*MDH-1**											
100	1	1	1	0.994	1	1	0.993	1	1	1	1
014	0	0	0	0.006	0	0	0.007	0	0	0	0
(*N*)	(38)	(68)	(4)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*MDH-2**											
125	0	0	0	0	0	0	0.007	0	0.005	0	0
100	1	1	1	0.994	1	1	0.993	1	0.995	1	1
068	0	0	0	0.006	0	0	0	0	0	0	0
(*N*)	(38)	(68)	(4)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*ME-2**											
125	0	0	–	0.006	0	0	0	0	0	0	0
110	0	0	–	0.006	0	0	0	0	0	0	0
100	1	1	–	0.988	1	0.996	1	1	1	1	1
087	0	0	–	0	0	0.004	0	0	0	0	0
(*N*)	(38)	(68)	(0)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*PEP-2**											
106	0	0.007	0	0	0	0	0.014	0.005	0.015	0	0.045
100	0.539	0.522	0.600	0.593	0.532	0.504	0.595	0.575	0.557	0.535	0.483
094	0.368	0.375	0.400	0.314	0.372	0.389	0.311	0.318	0.356	0.342	0.360
089	0.092	0.096	0	0.093	0.096	0.107	0.081	0.103	0.072	0.123	0.112
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)
*PGM**											
100	1	1	1	1	1	1	1	1	0.995	1	0.996
089	0	0	0	0	0	0	0	0	0.005	0	0.004
(*N*)	(38)	(68)	(5)	(86)	(47)	(140)	(74)	(107)	(97)	(57)	(121)

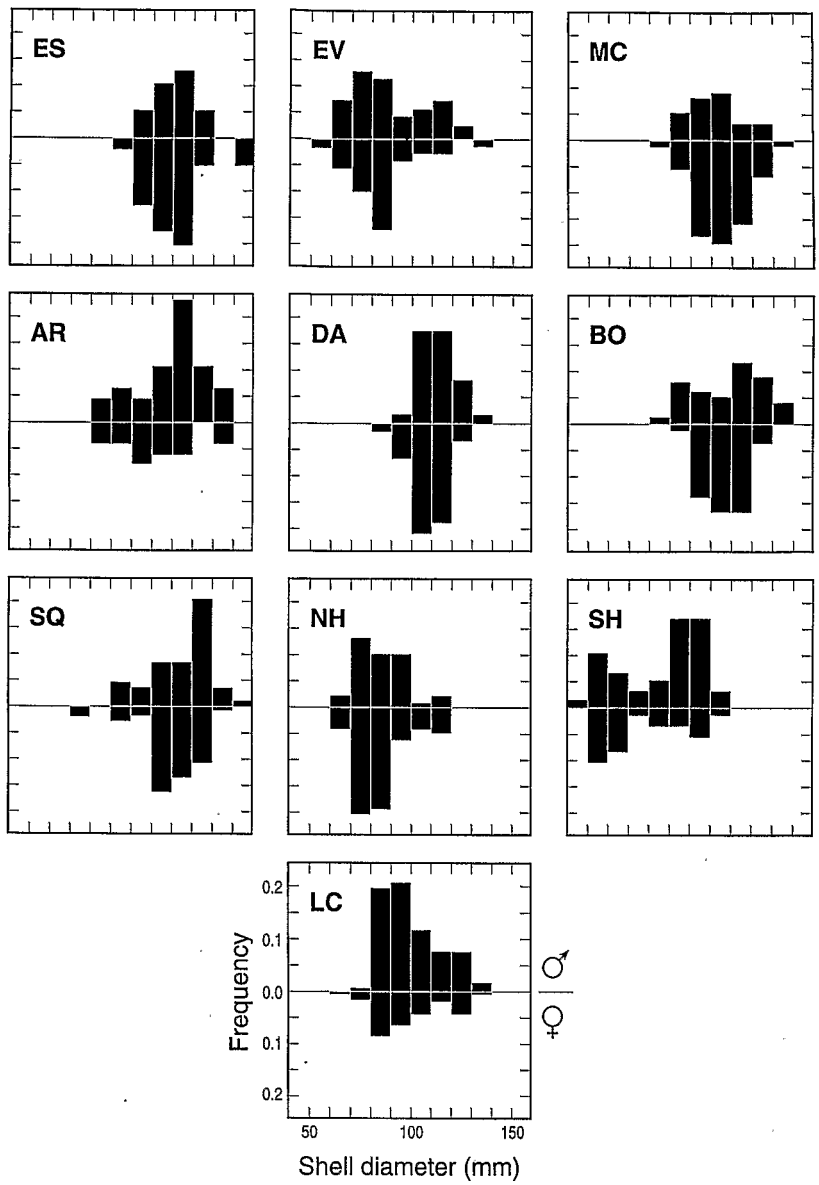

Fig. 2 *Trochus niloticus*. Shell-diameter frequency (plotted as proportion) as a function of sex and reef. Female to male ratios (along with associated probabilities under null hypothesis of 1:1 binomial distribution) were: ES, 1.92 ($p = 0.035$); EV, 0.89 ($p = 0.542$); MC, 2.31 ($p < 0.001$); AR, 0.59 ($p = 0.020$); DA, 1.12 ($p = 0.447$); BO, 1.17 ($p = 0.424$); SQ, 0.98 ($p = 0.849$); NH, 1.53 ($p = 0.032$); SH, 0.53 ($p = 0.026$); LC, 0.45 ($p < 0.0001$) (*Reef abbreviations* as in legend to Table 1)

procedure (Weir 1990). Females were more prevalent in the north (e.g. sample MC), males in the south (e.g. sample LC) and the sex-ratio at intermediate latitudes was balanced (samples DA and BO: sex-ratio = 1.12 and 1.17, with $p > 0.44$ and $p > 0.42$, respectively), although the correlation between sex-ratio and latitude was not significant (Spearman's rank correlation coefficient = 0.539; 8 *df*; $p > 0.05$). No relationship between size-class and sex-ratio was apparent, either within samples (Fig. 2) or among all samples.

Tectus coerulescens

Shell diameters ranged from 44 to 78 mm, and all individuals collected were sexually mature. The sex-ratio was biased towards females (sex-ratio = 2.38, $p = 0.05$ at DA and sex-ratio = 1.73, $p = 0.2$ at SQ; combined $p < 0.06$). Size-frequency distributions at DA and SQ were monomodal (Fig. 3). They were not significantly different between sexes (Wilcoxon–Gros–Chessel test on pooled data, $p > 0.15$) nor did they significantly depart from normality ($p > 0.05$ at both DA and SQ).

Genetic structure

Trochus niloticus

Only 3 (*GDH**, *GPI** and *PEP-2**) of the 12 loci screened in up to 11 populations of *Trochus niloticus*

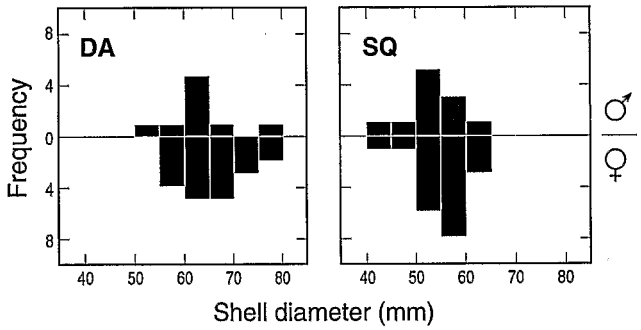

Fig. 3 *Tectus coerulescens.* Shell-diameter frequency (plotted as number of individuals) as a function of sex and reef (*DA* Davies Reef; *SQ* Square Reef)

Table 2 *Trochus niloticus.* Estimates of Weir and Cockerham's θ at three geographic scales: between sites at a reef, between reefs within each zone, and between zones of the Great Barrier Reef (*GBR*) (*N* average sample size per, site, reef and zone, respectively; *SD* jackknife estimate of standard deviation over populations)

Geographic scale locus	(*N*)	$\theta \pm$ SD
Between sites within reef		
*GPI**	(40.5)	0.0067 ± 0.0110
*PEP-2**	(40.5)	− 0.0049 ± 0.0038
Between reefs within zone		
Northern GBR		
*GDH**	(17.5)	− 0.0491
*GPI**	(59.8)	− 0.0003 ± 0.0065
*PEP-2**	(59.8)	− 0.0035 ± 0.0050
Central GBR		
*GPI**	(107.0)	− 0.0047
*PEP-2**	(107.0)	0.0084
Southern GBR		
*GPI**	(95.5)	− 0.0017 ± 0.0032
*PEP-2**	(95.5)	0.0002 ± 0.0035
Between zones		
*GDH**	(36.0)	0.0997 ± 0.1080
*GPI**	(280.0)	0.0019 ± 0.0034
*PEP-2**	(280.0)	− 0.0012 ± 0.0004

could be considered as polymorphic, in that the frequency of the most common electromorph in a sample was < 0.95 (Table 2). The other loci exhibited either little polymorphism or sample monomorphism.

F-statistics analyses showed the following: (1) A consistent trend for heterozygote excess was observed at *GPI** and *PEP-2**, where the weighted averages of $f \pm$ their jackknife estimates of standard deviations over ten samples (all samples except Low Islets) were $f = -0.0639 \pm 0.0234$ and $f = -0.0459 \pm 0.0226$, respectively. The distributions over populations of single-locus f estimates did not depart from normality (normality test; Lilliefors 1967; $p > 0.05$ for *GPI** and $p > 0.20$ for *PEP-2**), so their average values were compared to 0 by a Student's *t*-test (Sokal and Rohlf 1981). The heterozygote excess at *GPI** was significant ($p = 0.024$) and that at *PEP-2** was close to significance ($p = 0.077$). (2) A significant heterozygote deficiency was present at *GDH**, where the weighted average of $f \pm$ its jackknife estimate of standard deviation over all four samples surveyed at this locus was $f = 0.4287 \pm 0.0878$ (Student's *t*-test; $p = 0.018$). (3) No genetic differences were evident between sites at a reef, nor between reefs within a zone (Table 2). (4) Little if any difference was observed between zones at the scale of the entire GBR with one possible exception: the South GBR was differentiated from the two other regions at *GDH**. This was the source of heterogeneity leading to the large θ value recorded for that locus (Table 2).

There was no evidence for correlations between genotypes at *GPI** and *PEP-2**. Weir's (1990) estimator of genotypic disequilibrium, Δ_{AB}, calculated for each population, ranged from −0.0189 to 0.0247. The corresponding χ^2 probabilities under the null hypothesis of no disequilibrium ranged from 0.61 to 0.06 (not significant). Therefore, these two loci could be used as independent markers of population genetic structure. Independence of other pairs of loci could not be tested because of either lower polymorphism or small sample sizes (see Brown 1975).

Tectus coerulescens

Nine allozyme loci out of 11 scored in 3 populations of *Tectus coerulescens* showed electrophoretic polymorphism (Table 3). Some of these loci were discarded for the analysis of population structure, *IDH-1** and *IDH-2** because of their limited polymorphism, and *PGM** because of the small number of individuals scored in each population at that locus. As in *Trochus niloticus*, the distribution of single-locus f-values was heterogeneous (Table 4). We assumed that the set of single-locus θ values was normally distributed (normality test; Lilliefors; $p > 0.20$). Hence the null hypothesis of $\theta = 0$ was tested and we rejected it (one-tailed Student's *t*-test; 5 *df*; $p < 0.05$).

Gene flow between zones

In *Trochus niloticus*, values of single-locus (*GDH**, *GPI** and *PEP-2**) θ-based pairwise estimates of gene flow between zones ranged from $N_m = 1.3$ to $N_m = \infty$ genes per generation (mean ± SD: $N_m = 7.5 \pm 6.2$). The estimate based on private allele frequencies was calculated on a different set of loci (*EST-D**, *IDH-1**, *MDH-2**, *ME-2** and *PGM**). Its value was $N_m = 158.3$. A closer look at the data showed that the private allele estimate of gene flow was consistent with the θ-based estimates at loci *GPI** and

Table 3 *Tectus coerulescens.* Electromorph frequencies in reef populations of GBR (*Reef abbreviations* as in legend to Table 1)

Locus, electromorph	Sample		
	ES	DA	SQ
*DIA-1**			
126	1	1	1
(*N*)	(2)	(27)	(30)
*DIA-2**			
142	1	1	1
(*N*)	(2)	(27)	(30)
*EST-D**			
223	0	0	0.083
189	0	0.019	0.017
174	1	0.981	0.900
(*N*)	(2)	(26)	(30)
*EST-N**			
094	0	0.423	0.207
090	1	0.269	0.310
088	0	0.115	0.224
086	0	0.192	0.259
(*N*)	(1)	(26)	(29)
*GPI**			
300	0	0.019	0.021
290	0.250	0.444	0.396
263	0	0.111	0.042
248	0.500	0.185	0.375
230	0.250	0.019	0.063
223	0	0.204	0.083
204	0	0.019	0.021
(*N*)	(2)	(27)	(24)
*IDH-1**			
200	0	0	0.017
166	1	1	0.983
(*N*)	(2)	(27)	(30)
*IDH-2**			
144	0	0	0.017
125	1	1	0.983
(*N*)	(2)	(27)	(30)
*MDH-2**			
200	0.500	0.222	0.250
139	0.500	0.778	0.750
(*N*)	(2)	(27)	(30)
*ME-2**			
054	0.250	0	0
027	0.750	1	0.917
009	0	0	0.083
(*N*)	(2)	(27)	(30)
*PEP-2**			
106	0	0	0.017
100	0	0	0.017
094	1	1	0.967
(*N*)	(2)	(27)	(30)
*PGM**			
135	0	0	0.150
124	0	0.042	0
120	0	0.208	0.250
117	0.500	0.208	0.200
110	0.500	0.542	0.400
(*N*)	(2)	(11)	(10)

Table 4 *Tectus coerulescens.* Estimates of Weir and Cockerham's (1984) parameters of population structure (*N* average population sample size; *SD* jackknife estimate of standard deviation over loci)

Locus	(*N*)	f	θ
*EST-D**	(28.0)	0.2437	0.0336
*EST-N**	(27.5)	0.3368	0.0189
*GPI**	(25.5)	− 0.0135	0.0218
*MDH-2**	(28.5)	− 0.0024	− 0.0157
*ME-2**	(28.5)	0.3611	0.0569
*PEP-2**	(28.5)	− 0.0078	0.0064
Mean		0.1441	0.0162
(SD)		(0.1287)	(0.0071)

*PEP-2** ($N_m = 833.1 \pm 249.8$), but not at *GDH** ($N_m = 2.3 \pm 2.1$).

In *Tectus coerulescens*, these estimates of gene flow were derived from θ and from private allele data, respectively: $N_m = 15.2 \pm 35.0$ and $N_m = 1.9$.

Genetic diversity

The values for single-locus genetic diversities and their averages in samples of *Trochus niloticus* and *Tectus coerulescens* grouped by zone showed that the genetic diversity in the southern GBR population of *T. coerulescens* was significantly higher than in the central GBR (Wilcoxon's sign test for paired observations, $p < 0.01$), and a similar trend was observed in *Trochus niloticus* (Table 5).

Discussion

Recruitment in marine invertebrates with pelagically dispersed larvae may vary by several orders of magnitude from year to year and site to site (Loosanoff 1966; Gaines et al. 1985; recent reviews in Underwood and Fairweather 1989 and Fogarty et al. 1991). The demographic structures observed in *Trochus niloticus* populations provided evidence that recruitment is sporadic in this species. In some samples, size classes were separated by gaps which presumably corresponded to several years without recruitment, as inferred from the von Bertalanffy relationships of shell diameter to age provided by several authors (Rao 1936; Bour et al. 1982; Smith 1987). The absence of live *T. niloticus* on Myrmidon Reef, in spite of the presence of apparently favourable habitat, and the inference of past presence in the form of two large dead shells, supported the hypothesis that local *T. niloticus* populations may become extinct or nearly so. This is particularly likely on a relatively isolated reef on the ocean margin of the GBR such as Myrmidon, where larvae are probably exported to the ocean and generally lost.

Table 5 *Trochus niloticus* and *Tectus coerulescens*. Estimates of single-locus genetic diversity and its average (H) in zones of GBR (SD jackknife estimate of standard deviation over loci; – no data)

Locus	*Trochus niloticus*			*Tectus coerulescens*		
	North	Central	South	North	Central	South
*DIA-1**	0	0	0	0	0	0
*DIA-2**	0	0	0	0	0	0
*EST-D**	0.004	0	0	0	0.038	0.186
*EST-N**	–	–	–	0	0.712	0.757
*GDH**	0.288	0.252	0.496	–	–	–
*GPI**	0.195	0.167	0.225	0.833	0.727	0.704
*IDH-1**	0.008	0.009	0.003	0	0	0.034
*IDH-2**	0	0	0	0	0	0.034
*MDH-1**	0.004	0.005	0	–	–	–
*MDH-2**	0.004	0.005	0.003	0.667	0.352	0.381
*ME-2**	0.008	0.005	0	0.500	0	0.155
*PEP-2**	0.322	0.574	0.585	0	0	0.065
*PGM**	0	0	0.005	0.667	0.647	0.752
H	0.069	0.085	0.110	0.242	0.225	0.279
(SD)	(0.036)	(0.050)	(0.061)	(0.104)	(0.096)	(0.095)

Species with migrating juveniles and sedentary adults which undergo local population extinctions and recolonisations can be modelled as a metapopulation (Hastings and Harrison 1994). The expected genetic consequences of the metapopulation structure in such species are a relatively low level of differentiation between local populations, little correlation between genetic and geographic distances (Barrett and Husband 1989) and, in the long term, loss of heterozygosity both within and among populations (McCauley 1992). Data from *Trochus niloticus* populations appeared to fit these general expectations.

Genetic differences among *Trochus niloticus* populations on the GBR were not significant at any geographical scale: between sites at a reef; between reefs within, respectively, the northern, central and southern sections of the GBR; and at the scale of the whole GBR. The interpretation of population differentiation, based on average Weir and Cockerham's θ estimates over three polymorphic loci was complicated by some discrepancy among loci. The θ estimates for *GPI** and *PEP-2** were close to zero, while the estimate for *GDH** was high. These results imply differential selection among loci. The consistent heterozygote excesses at *GPI** and *PEP-2** suggested the occurrence of overdominant selection at these loci, as has been documented at allozyme loci in other marine molluscs (Koehn et al. 1988; Karl and Avise 1992). Strong heterozygote deficiencies present at *GDH** suggested directional or underdominant selection at this or at a closely linked locus. Private allele frequency-based estimates of gene flow between zones based on the data at six other slightly polymorphic enzyme loci (*EST-D**, *IDH-1**, *MDH-1**, *MDH-2**, *ME-2** and *PGM**) were high. These results were compatible with the independent θ-based estimates at *GPI** and *PEP-2**, suggesting that *GDH** was an outlier possibly subjected to directional or underdominant selection. But this does not exclude the possibility that overdominant selection acts to maintain the higher levels of homogeneity between populations, and the higher level of within-population polymorphism at *GPI** and *PEP-2**. To test that hypothesis would require additional data which were not available here, such as genotype frequencies at other types of nuclear markers (e.g. microsatellites or anonymous single-copy DNAs; see Rassmann et al. 1991 and Karl and Avise 1992, respectively).

Under the neutral theory of population genetics, populations or species with high effective population size (N_e) are expected to have higher neutral genetic diversity than those with lower N_e (Crow and Kimura 1970). Overall allozyme polymorphism in *Trochus niloticus* was low compared to that of other species in the same family sharing the same gross habitat (Borsa and Benzie 1993). A few loci (*GDH**, *GPI** and *PEP-2**) had a high degree of genetic diversity but all other loci, including highly polymorphic loci in other trochids (Borsa and Benzie 1993), exhibited little or no variation in *T. niloticus*. In addition to the effect of local extinctions and recolonisations (McCauley 1992), several demographic factors may contribute to reducing the effective population size in *T. niloticus*. These are clumped distribution, biased sex-ratio, and high female fecundity. Aggregates of a few *T. niloticus* of up to no more than a dozen individuals were found in the surge channels perpendicular to the reef crest, the distance between two aggregates typically being several tens of metres. It is likely that most fertilisation takes place within these dense groups of individuals, as external fertilisers have to be close enough to each other to generate sufficient gamete concentrations for successful fertilisation (Oliver and Babcock 1992). Random fluctuations in the distributions of sexes in these aggregates would be enhanced by the skewed sex-ratios observed

in several of the *T. niloticus* populations. Furthermore, high female fecundity (10^4 to 10^5 eggs per clutch; Heslinga and Hillmann 1981) together with high larval mortality would enhance variance in numbers of viable offspring per female.

Past genetic work on the GBR has concentrated on species with relatively long larval lives. Little genetic structure was found in crown-of-thorns starfish (Nash et al. 1988; Benzie and Stoddart 1992), giant clams (Benzie and Williams 1992), the starfish *Linckia laevigata* (Williams and Benzie 1993) or the zoanthid *Palythoa caesia* (Burnett et al. 1994). The GBR consists of a linear succession of reefs, a geography that should favour the connection of populations through the occasional movement of larvae from one reef to the next in a stepping-stone fashion across generations. Such a structure might allow species with a short larval life to disperse effectively. However, data from the only species with a short dispersal stage investigated genetically in the GBR, the coral *Seriatopora hystrix* which has a planktonic phase of 1 to 4 d (90% of larvae settle after 4 d, most after 1 d), demonstrated considerable genetic differentiation not only between reefs, but between sites within reefs (Ayre and Dufty 1994). This was attributed to the larval life of *S. hystrix* being much shorter than the retention time of water in reef lagoons, or larvae being trapped by eddies, and to the effects of disturbance of reef systems by predation leading to patchy recruitment. Yet the pattern of population structure in *S. hystrix* is different from that in *Trochus niloticus*, where no significant genetic differentiation was evident throughout the GBR, and similar to that in *Tectus coerulescens*, where genetic differentiation between zones was significant ($\theta = 0.016 \pm 0.007$), as expected in a species with a short larval life, but slightly lower than in *S. hystrix* [$F_{GT}(\equiv \theta) = 0.03$]. Substantial gene flow among populations throughout the GBR was inferred in *Trochus niloticus*, whereas limited gene flow between zones of the GBR and a significantly higher level of genetic diversity were observed in *Tectus coerulescens*.

It is not possible on present evidence to distinguish whether ecological or historical factors explain these discrepancies among species. *Trochus niloticus* and *Tectus coerulescens* share the same gross habitat and they have similar life-histories including inferred short larval duration as a consequence of lecithotrophy, but *T. coerulescens* could have higher mortality of larvae, a shorter larval stage, or local adaptations resulting in a lower fitness of immigrants compared with locally produced individuals. *T. coerulescens* may not have been subjected to cycles of local extinctions and recolonisations leading to the increased gene flow and loss of genetic diversity presumed to have occurred in *Trochus niloticus*. Demographic data for *Tectus coerulescens* was limited to two populations, but provided no evidence to suggest the same degree of temporal variability in recruitment success or of local extinction. Alternatively, *T. coerulescens* may have been present on the GBR long enough to allow differentiation between populations, while the colonisation by *Trochus niloticus* may have been recent.

As gene flow is limited between populations of *Tectus coerulescens*, it should be possible to define stock structures and identify sets of reefs that could be considered to be interconnected in order to assist management of this potentially commercial species, which is fished for its shell (Long et al. 1993) and its meat (Borsa personal observations) in some islands of the western Pacific. The lack of population structure in *Trochus niloticus* suggests that only one stock of this commercially important species exists on the GBR. However, given the sporadic recruitment of *T. niloticus* and the possibility that individual reef populations may undergo extinctions or near-extinctions for generations [e.g. the failure to sample live *T. niloticus* on Gable Reef (Nash 1985) and Myrmidon Reef (present survey)], individual reefs should be considered as vulnerable to overfishing (Fogarty et al. 1991).

Interestingly, genetic diversity increased from North to South in both *Trochus niloticus* and *Tectus coerulescens*. From the neutralist point of view, this would mean that N_e also increases. This hypothesis would be compatible with some oceanographical features such as lower temperatures in the southern GBR (Pickard et al. 1977), a factor which increases larval development time and hence dispersal ability and the probability of encountering suitable habitat for settlement, and stronger tidal flush and currents (Anonymous 1984), another factor facilitating increased dispersal potential.

The much higher proportion of females at some locations in the northern GBR (e.g. ES and MC), the much higher proportion of males at the southernmost location sampled (LC), and the balanced sex-ratios in the Central GBR all suggest a trend between sex-ratio and latitude in *Trochus niloticus*. Significant excesses of males have also been observed in the southern New-Caledonian lagoon (Bour 1992), which is located at approximately the same latitude as LC. Latitude is itself correlated with temperature, photoperiod, and seasonality. Temperature-dependent sex determination is not known in marine gastropods, but well known in reptiles (Bull 1983). Some marine gastropods (e.g. the slipper limpet *Crepidula fornicata* and the limpet *Patella vulgata*) exhibit sequential hermaphroditism (Charnov 1982), with younger individuals reproducing as males and older individuals as females. Bour (1992) suggested that gender may be affected by age in *T. niloticus*, but the apparent lack of relationship between sex-ratio and size-class in our data does not support Bour's implicit hypothesis of sequential hermaphroditism in this species. The biased sex-ratio in samples of *T. niloticus* and *Tectus coerulescens* and the latitudinal trend in sex-ratio in *Trochus niloticus* may be due to some degree of environmental determination of sex, in

which case *T. niloticus* would provide an interesting model system for studying sex determination in marine gastropods.

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