POPULATION GENETICS OF *DRUPELLA CORNUS*

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BACKGROUND

The nature of recruitment and the connections among populations are fundamental to the spatial scale of local populations. The scope for recruitment over large distances is especially great for marine species with planktotrophic larvae, which means that local populations are not necessarily independent. On the other hand, the potential for dispersal is not always realized, resulting in substantial local autonomy of populations.

The outbreak of *Drupella cornus* at Ningaloo Reef highlighted our ignorance of basic aspects of the population structure of this species. The history of the outbreak seems to have been one of spreading outwards from the initial area of infestation. This pattern suggests local recruitment, rather than extensive mixing of planktonic larvae. In addition, the outbreak has been largely confined to the backreef areas, whereas adjacent forereef and lagoonal habitats appear to have been much less affected, again raising questions about the extent of mixing of populations even over short distances.

Genetical analyses provide useful approaches to the study of connectedness and the structure of populations, and are especially important in situations in which more direct approaches are difficult. Planktonic dispersal presents such a situation, as marking of larvae is generally impossible. In addition, the different stages of the outbreak of *D. cornus* at Ningaloo Reef, along with the differences between habitats, could favour genetic divergence among local populations.

With this background, we have examined aspects of the population genetics of *D. cornus* in Western Australia. Based on an electrophoretic study of enzyme variation at 10 polymorphic loci, we have attempted to answer three major questions. First, are recruits produced locally or are they from distant sources? Mixing over large distances will cause relative genetic homogeneity among areas, whereas isolation will allow genetic differences to accumulate among local populations. Second, are there detectable genetic differences between expanding and declining populations, or between populations from different habitats? Third, is it possible that some of the variation in the effects of *Drupella* is due to the presence of more than one species?

ADULT POPULATIONS

Within Ningaloo Reef, samples were collected from 9 sites between Bundegi in the north and Coral Bay in the south, a distance of approximately 180 km. Each sample included 70 to 82 adults. Three of these sites were taken from the forereef, backreef, and lagoon habitats within 2.5 km of each other near Yardie Creek. Of the other 6 sites, 5 were lagoonal (Bundegi, Tantabiddi, Mesa, Osprey Bay, Coral Bay) and 1 was backreef (Fraser Island). These samples represented stages of

infestation ranging from none (Bundegi), through early (Tantabiddi, Osprey Bay, Yardie forereef, Coral Bay), and established (Yardie lagoon and backreef, Fraser Island), to old (Mesa). To place the genetic variation at Ningaloo Reef into its broader geographic context, samples were also obtained from Dampier in the north and the Abrolhos Islands (Beacon Island and Rat Island) in the south, spanning an overall distance of 1170 km.

None of the genetic comparisons suggested that there might be more than one species of *Drupella* in our samples. The overall picture of allelic frequencies at the 10 polymorphic loci is one of small differences among sites (Figure 1). The degree of subdivision can be quantified as the standardized variance in allelic frequencies, F_{ST} (Weir and Cockerham 1984), which is the proportion of allelic variation due to differences among populations. The summary in Table 1 makes three important points. First, there are statistically significant differences in the genetic composition of the samples. Second, this variation is not a function of distance between samples except at a scale of a few km. Inclusion of the samples from outside Ningaloo Reef does not increase the range of genetic divergence, and sets of allelic frequencies do not characterize particular geographic sets of populations (Figure 1). Within Ningaloo Reef, the variation was not associated with habitat or stage of infestation. Third, regardless of their statistical significance, the variations in allelic frequencies are small.

The overall F_{ST} of 0.008 is typical of species with extensive genetic mixing. On the Western Australian coast, for example, F_{ST} is 0.003 for the limpet *Siphonaria jeanae* over distances up to 500km and 0.013 for the urchin *Echinometra mathaei* over distances of 1300 km (Johnson and Black 1984; Watts et al. 1990). For both of those species, significant variation occurs on a scale of a few km, with little additional variation over distances of hundreds of km. Furthermore, genetic differences among cohorts of recruits in *S. jeanae* and *E. mathaei* within sites are as great as the differences among populations hundreds of km apart. From these comparisons, it is clear that the small genetic differences observed among populations of *D. cornus* do not imply isolation of local populations. Nevertheless, the observed differences could reflect recent changes due to localized recruitment. Interpretation of these small differences requires analysis of the genetic composition of recruits in the local populations.

RECRUITS

If the genetic differences observed in the adults reflect real subdivision of the populations, recruits at different sites should show the same differences as the adults (or possibly greater differences if divergence is recent). Our attempts to make such comparisons proved unsuccessful, however, because of the complexity of patterns of recruitment.

Recruits of *D. cornus* are generally found in aggregations on small digitate corals, and not on the tabular corals preferred by the adults. There are marked differences in size-frequency distributions of recruits on different coral heads, suggesting that settlement of aggregates of recruits occurs on different heads at different times.

We examined the genotypes of 484 recruits from a total of 22 groups on individual coral heads from 5 sites: Tantabiddi (2 groups); Yardie forereef (4); Yardie backreef (7); Yardie lagoon (5); and Fraser Island (4). Only groups with at least

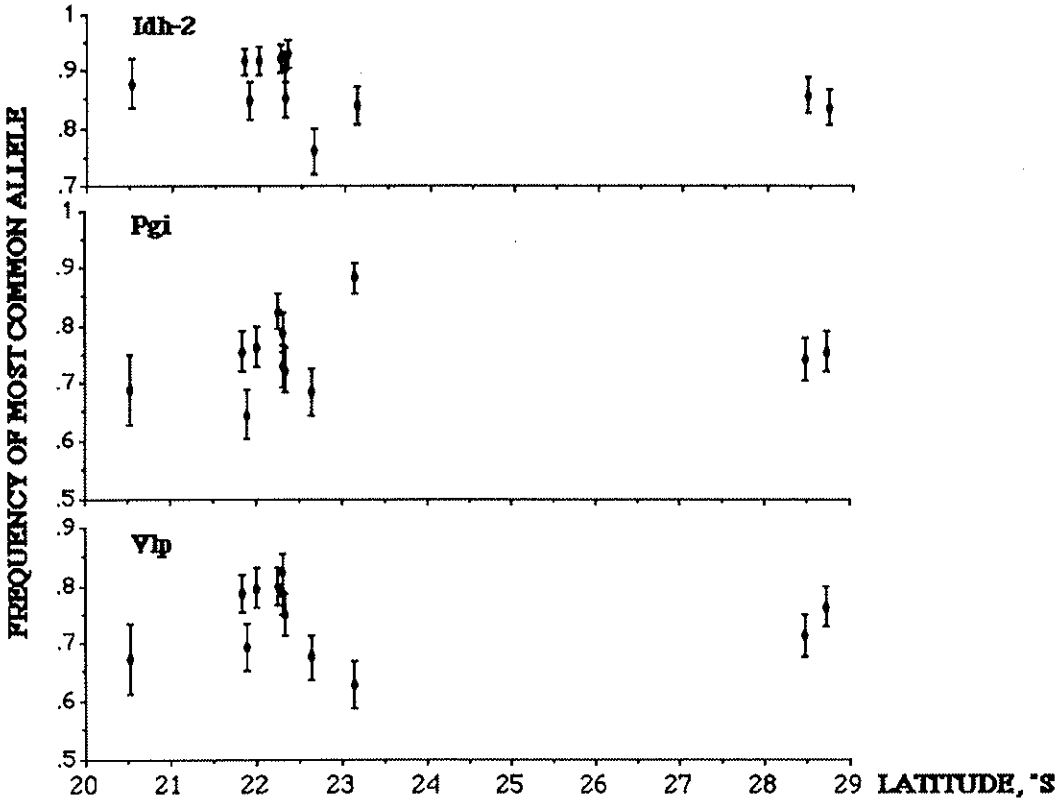

FIGURE 1. Frequencies of the most common allele at each of the 3 loci which show significant variation among 11 samples of adult Drupella cornus. Vertical lines = S.E.

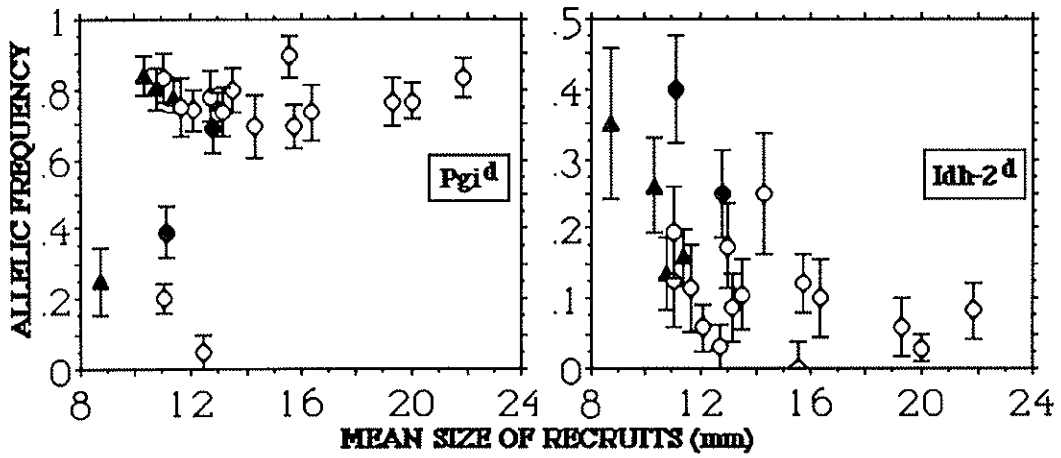

FIGURE 2. Allelic frequencies for Pgi and Idh-2 in recruits from individual coral heads. Circles = Yardie. Dots = Tantabiddi. Triangles = Fraser. Vertical lines = S.E.

10 individuals were included.

Genetic differences among these groups of recruits were much larger than those found among the adult populations. Among all 22 groups, the average F_{ST} was 0.0499, nearly 7 times as large as that for the adults (Table 1). The differences in allelic frequencies among the recruits do not parallel the geographic patterns found for the adults. Instead, heterogeneity among the recruits occurs on a very local scale. The average F_{ST} among groups of recruits from the same site was 0.0441. Thus, more than 90% of the genetic differences among groups of recruits is within sites. This heterogeneity makes it difficult to compare recruits with adults, because the group on an individual coral head, and not the individual recruit, is the appropriate unit of replication.

Of the 10 loci examined, *Idh-2* and *Pgi* contribute most to the heterogeneity among the recruits. In each case, the genetic differences are associated with the mean size of recruits (Figure 2). The Pgi^d allele occurs at a frequency of at least 0.69 in all but 4 groups, in which the frequency is 0.05 to 0.39. All 4 of the peculiar groups had relatively small recruits. Similarly, at the *Idh-2* locus, the frequency of $Idh\text{-}2^d$ is negatively correlated with mean size of recruits. These patterns are local, rather than geographical, indicating that they result from patterns of recruitment at a local scale. This finding suggests that groups of larvae produced by few adults may retain a high degree of cohesion.

CONCLUSIONS

The genetic similarities among populations of *D. cornus* are consistent with extensive gene flow. There is no evidence of different genetic groups related to habitat, stage of infestation, or geography over more than 1100 km. It appears that extensive dispersal is the norm for *D. cornus*, but this does not necessarily mean that there is no local recruitment associated with the outbreak. If, for example, infestations were associated with a switch to predominantly local recruitment, it would take several generations for genetic differences to accumulate.

Tests of such subtle genetic changes would require comparisons of different cohorts. The fine-scale genetic heterogeneity of the recruits, however, greatly complicates such comparisons. That heterogeneity is not evidence for subdivision of the populations. Instead, it indicates that the process of recruitment is patchy, and very likely involves settlement of aggregated groups of larvae.

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TABLE 1. Levels of genetic subdivision, measured as F_{ST}, among populations of adult *Drupella cornus* and among groups of recruits at different spatial scales.

	Spatial Scale of Comparisons of Adults			Recruits
Locus	1170 km All Sites	180 km Ningaloo Reef	2.5 km Local Habitats	90 km
Idh-1	0.013	0.003	0.000	0.149[n]
Idh-2	0.015***	0.019***	0.009	0.053*
Mdh-1	0.002	0.001	0.004	0.024[n]
Mdh-2	0.002	0.002	0.006	0.026
Mdh-3	0.005	0.005	0.006	0.007
Mpi	0.006	0.007	0.007	0.035
Pgi	0.012**	0.016***	0.003	0.190***
Pgm-1	0.001	0.002	0.001	0.019
Pgm-2	0.007	0.007	0.011*	0.025
Vlp	0.011*	0.014***	0.002	0.014
Mean	0.0075	0.0074	0.0048	0.0499
±S.E.	0.0016	0.0021	0.0011	0.0008

*P<0.05; **P<0.01; ***P<0.001; [n]Statistical test not possible.