

# Genetic structure of marine organisms and SE Asian biogeography

J. A. H. Benzie

*Australian Institute of Marine Science, PMB No 3, Townsville, QLD 4810, Australia*

*Email: j.benzie@aims.gov.au*

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## Abstract

SE Asia has been considered a hot spot for marine speciation, and the likely source for much of the marine biota in the Pacific. Evidence from recent genetic studies has important implications for SE Asian biogeography. Although not conclusive, these data question ideas about the origin of marine biodiversity in the region. For example, the genetic differentiation of widespread starfish species appears to be related to the separation of Indian and Pacific Oceans at times of lowered sea level. This supports data from other taxonomic work that marine biodiversity in SE Asia has resulted more from the mixing of taxa evolved in the two ocean basins than has been thought to date. Similarly, patterns of gene flow in giant clams do not parallel present-day ocean currents. Clams may disperse by other present-day mechanisms such as surface drift, or have been dispersed by palaeocurrents at times of low sea level. However, both past and present mechanisms indicate movement of material from the Pacific to SE Asia. The high marine biodiversity in the region may result more from the accumulation of species evolved in the Pacific, relative to speciation within the SE Asian region, than has been believed traditionally. The mechanisms giving rise to marine biodiversity in the SE Asian region are not well-understood, therefore, and more work is urgently required to enable effective management of these resources.

## Introduction

The SE Asian region is one of the most biologically diverse in the world. The diversity of the terrestrial biota results from the meeting and mixing of the floras and faunas from two major zoogeographic regions, and the opportunities for speciation on the islands of the Indo-Malay region (Wallace, 1860, 1881; Burrett *et al.*, 1991; Michaux, 1991). Much work has focused on de-

fining the nature of exchange between these biotas through identifying major breaks in species composition such as Wallace's line.

Knowledge of the marine biota of the region is less than that of the terrestrial sphere, and the concept of the region as a zone of overlap of two zoogeographic provinces (the Indian and the Pacific Oceans) has been considered of lesser significance. This is partly because the Indo-Pacific has generally been thought to be one major biogeographic region (Ekman, 1953; Briggs, 1974, 1987). Many taxa are found in both the Indian and Pacific Oceans, and the occurrence of widespread species in both oceans has led to the view that the floras and faunas of the two oceans are closely related.

Explanations for the high diversity of marine species in SE Asia have concentrated on the idea that most species have evolved within the region (Potts, 1983, 1985; McManus, 1985). Sea-level changes over the last few million years are thought to have created isolated seas in which marine species have had a chance to diverge and speciate. This approach has tended to dominate thinking about the origin of marine biodiversity in SE Asia and the Indo-Pacific, although a number of alternative views have been expressed with respect to the origin of species in the Pacific and Indian Oceans (Ladd, 1960; McCoy and Heck, 1976, 1983; Kay, 1980, 1984; Kay and Palumbi, 1987; Springer, 1982; Springer and Williams, 1990).

Molecular data provide the means to determine genetic structure within taxa (the spatial and temporal patterns of occurrence of gene

variants, and patterns of association of different gene variants) and to assess the evolutionary relationships between species. Molecular phylogenies can be used to test whether SE Asian species were likely to have evolved in-situ, or were derivatives from the Indian or Pacific Oceans. The nature of the genetic structure of species can provide information on the principal factors influencing genetic change in populations in the region (*i.e.*, random shifts called genetic drift, strong patterns at only one gene locus suggesting natural selection at that gene, or similar patterns at several loci that are not linked and which would reflect levels of dispersal among populations).

By comparing the structure of gene products, genes or sections of DNA that evolve at different rates, at least the relative timing of speciation or dispersal events can be determined. Molecular data on marine organisms in the region are rare and it is not yet possible to examine evolutionary processes within the region in any detail. Nevertheless, new findings emerging from work throughout the Indo-Pacific is changing the way in which the dispersal and evolution of marine species is considered (Palumbi, 1992, 1994, 1997; Benzie and Williams, 1997), and this has implications for theories concerning the origin and evolution of species in the SE Asian region.

Widespread marine species have traditionally been viewed as having a high dispersal capacity that allows them to undertake long-distance movements throughout their range, presumably on major ocean currents (Briggs, 1974; Scheltema, 1977; Scheltema and Williams, 1983; Jackson, 1986). However, the notion that widespread species may not always reach their dispersal potential is increasingly recognised. A growing number of cryptic taxa within widespread species are being discovered and some widespread species have been shown to consist of a series of regionally distributed cryptic taxa (Knowlton, 1993; Knowlton and Jackson, 1994; Palumbi, 1994; Kelly-Borges and Valentine, 1995; Foltz *et al.*, 1996).

The few genetic data that have been available for widespread marine species over the last 25 years were consistent with traditional views in that little or no genetic differentiation of populations over thousands of kilometres are observed. Where structure was detected, the populations have been relatively isolated, being situated on remote islands or cut off by currents from other populations. However, new data emerging from detailed genetic studies of Indo-Pacific species over broad geographical scales

demonstrates unexpected structure that is not consistent with dispersal by present-day ocean currents.

This paper reviews the new findings, and considers their implications for the extent and timing of dispersal of marine species, for the origin and maintenance of genetic variation in the Indo-Pacific, and the implications of these discoveries for SE Asian biogeography.

### The nature and utility of genetic data

The aim of this section is not to give an exhaustive discussion of population genetics, but to provide a general background on key aspects of this approach for those not familiar with the topic. Details of the field of population genetics are available in a number of excellent texts such as Avise (1994) who covers different molecular techniques, their application to different problems and summarises the results of work on wild populations, Nei (1987) who provides a more theoretical approach, and Kimura (1983) who specifically addresses the issue of whether frequencies of molecular variants in wild populations reflect the processes of natural selection or are, to all intents, neutral markers. Each of these texts cites a number of reviews and key papers on the topic.

The assortment of genotypes within and among populations, and the relationships among these genotypes, provide an integrated history of the events which affect the genetic structure of populations (Avise, 1994). DNA molecules are changed by mutations which accumulate over time. Comparison of gene sequences (either directly or by examining genetically based variation in the proteins produced from the DNA) can identify the degree of relatedness of these individuals, and determine family trees (*i.e.*, gene genealogies) of the genotypes described (Zuckerandl and Pauling, 1962; MacIntyre, 1985).

A simple case, where there is a strong association of closely related genotypes with geographical location throughout the range of a sexually reproducing species, implies that little gene exchange occurs between locations, and that each of the populations has developed from a discrete genetic base. The occurrence of asexual reproduction can lead to greater genetic divergence in the frequencies of genetic variants among populations, not because of any fundamental difference in the factors acting upon the populations, but because the ability to produce

many copies of a genotype means that the effects of processes such as genetic drift (random sampling errors) or natural selection (targeted change at a locus) are magnified (Avise, 1994). A considerable reduction in population size, often referred to as a bottleneck, can result in considerable loss of variation and a marked and rapid shift in the frequency of variants (Nei, 1978). This is the result of sampling error, and can be thought of as an extreme form of genetic drift. However, bottlenecks can be recognised because the populations they affect have much reduced genetic diversity.

The time for which groups have been separated can be estimated from the degree of genetic difference between the genotypes and, all else being equal, would depend on the rate(s) of evolution of the gene(s) assayed, and factors affecting the frequencies of different variants within the groups (genetic drift, selection, dispersal among groups). While the specific rate of evolution of any gene is difficult to determine (Li and Graur, 1991), it has been established that some genes generally evolve at relatively slow rates (*e.g.*, the 18S ribosomal gene), others at a fast rate (*e.g.*, D-loop region of the mtDNA genome) and others at rates in between (*e.g.*, cytochrome oxidase I gene: the CO I gene). In general terms, genes in the mtDNA genome evolve at a faster rate than those in the nuclear genome, although the actual rate can vary considerably (Martin *et al.*, 1992). Subject to accounting for these influences, it is possible to determine the relative order of evolutionary events within and between species, and to indicate the general time scale of events, using estimates of the genetic divergence of populations derived from a variety of genetic markers (for marine examples see Cunningham and Collins, 1994).

In addition to the accumulation of mutations, genes are exchanged between populations as a result of migration and, in sexual species, between individuals through reproduction. These processes lead to the mixing of variants among populations. All else being equal, the extent to which the frequencies of variants are similar between populations provides a measure of the gene exchange between them. A survey of the spatial patterns of occurrence of gene variants can therefore provide valuable information on the degree of gene exchange between populations. Where variants are produced in relatively short time-scales (*e.g.*, mtDNA) the spatial patterns of the frequency of variants are more likely to reflect recent dispersal events than those patterns from genes that evolve at

slower rates (*e.g.*, allozymes). Slower evolving markers, though, can provide information on the nature of past gene exchange, or of gene flow integrated over longer time periods.

A number of other factors can influence gene frequencies in natural populations, hence the qualification "all else being equal" being made above with reference to estimating gene exchange or dispersal among populations. These factors include molecular processes (such as meiotic drive) which might influence the frequency of particular variants, some aspects of population size (such as founder effect and other sampling effects of genetic drift) which can speed change, but probably the most important is natural selection. The extent to which selection is responsible for population genetic structure has been the subject of intense debate — the selectionist-neutralist debate (Kimura, 1983). The frequency of a gene which is favoured in particular circumstances will be likely to be maintained in the face of the influx of other variants, and would not provide an appropriate estimate of gene flow.

Although one needs to be aware of the potential influence of selection, in practice, sampling several loci provides a reasonable set of markers that can be assumed to be neutral elements (see Hillis and Moritz, 1990: pp. 5-6). This is the great advantage of many molecular markers over morphological characteristics. Selection and environmental factors are likely to have played important roles in determining the phenotypes and frequency of morphological characters. The examination of spatial patterns of gene frequencies, therefore, provides a powerful means of examining dispersal among populations over a variety of time scales. Gene genealogies are a powerful means of determining the relative order and estimating the timing of events in the evolution of natural populations. An introduction to the interpretation of such data is provided by Avise (1994) and specific examples relating to marine biogeography are illustrated by Cunningham and Collins (1994).

One of the recent interesting discoveries concerning the Indo-Pacific fauna is the number of cryptic species being revealed, and it is useful to identify criteria that can be used to determine whether the observed genetic variation reflects intra- or inter-specific differences. There is no prescribed level of genetic difference that defines species but where genetic differentiation is very great (*i.e.*, Nei's D values of 0.8 or more) it is likely that one is dealing with two taxa. More powerful evidence comes from the number of

fixed gene differences between the populations (*i.e.*, no variant at a given locus found in one taxon is shared with the other taxon). The occurrence of several fixed gene differences between populations that are sympatric is strong evidence for the occurrence of two species that are reproductively isolated.

Where there are several fixed gene differences between populations that are geographically isolated from each other, the pattern may result from species differences or simply genetic differentiation as a result of isolation. The geographic pattern of genetic variation can give some clues as how to interpret such a result: if most local populations show considerable differentiation from each other, or if the differentiation of the allopatric population fits the expectations of an isolation by distance model of genetic structure, then it is less likely that the allopatric population deserves specific status.

Where genetic differentiation is within the range observed within well-defined species, abrupt shifts in gene frequency might suggest the possibility of geographically distinct taxa. In this case the default assumption would be that the populations both belonged to a more widespread taxon unless there was other biological data to indicate otherwise (*e.g.*, lack of fertility between experimental matings between members of the two populations).

### Genetic data on SE Asian marine species

Genetic surveys of marine organisms from SE Asia are rare. Most focus on local areas or coastlines, or address specific questions relating to fisheries management. However, some of these are providing evidence of cryptic species in groups where it might have been expected that the taxonomy was well-based. For example, genetic studies of the northern Australian fisheries thought to be based on *Photololigo edulis* and *Photololigo chinensis* were shown to consist of four cryptic species, none of which corresponded to *P. edulis* or *P. chinensis* from type localities in the China Sea, and all of which were new to science (Yeatman and Benzie, 1994). Cryptic species in taxa of coral which occur in the region (*Montipora* spp.) have been described in Australia (Stobart and Benzie, 1994).

These data suggest that many more cryptic and regionally defined taxa may occur in the region. Studies which examine genetic variation on a variety of geographical scales and/or using a variety of genetic markers that might provide

information pertinent to the evolution and biogeography of the SE Asian region are restricted to those on the butterfly fish *Cbaetodon* spp. (McMillan and Palumbi, 1995), the starfish *Acanthaster planci* (Benzie, unpublished data) and *Linckia laevigata*, (Williams and Benzie, 1997) the milkfish *Chanos chanos* (Winans, 1980), and the giant clams *Tridacna gigas*, *Tridacna derasa* and *Tridacna maxima* (Macaranas *et al.*, 1992; Benzie and Williams, 1995, 1997). Within the context of the patterns of variation revealed by these taxa, information from Pacific populations of the pearl oyster *Pinctada margaritifera* (Benzie and Ballment, 1994), the sea urchin *Echinometra mathei* and related taxa (Palumbi and Metz, 1991; Palumbi, 1997), are interesting.

### Patterns of gene flow in the Pacific

Early work on the genetic structure of marine species supported the view that long-distance dispersal occurred and was consistent with present day ocean circulation (Campbell *et al.*, 1975). This is well illustrated by the work on milkfish by Winans (1980). The patterns of population subdivision which emerged from his allozyme study showed populations in Hawaii were consistently and significantly differentiated from those in the Philippines, the Marshall Islands, Christmas Island and Fanning Island at all loci. The Philippines populations were differentiated from the Marshall Islands, Christmas Island and Fanning Island at some loci but not at others. He showed that there was no significant differentiation of milkfish populations over several thousand kilometres between the Marshall Islands, Christmas Island and Fanning Island. Even where gene frequencies were significantly different, genetic distances between these populations were low.

Emphasis was placed, therefore, on the extensive gene flow among all populations with the exception of the Hawaiian Islands which were considered isolated not only in respect of their geographic position but by the fact that currents flow perpendicular to the route between Hawaii, and the Christmas and Fanning Islands. The small genetic distance between the Hawaiian populations and the others (of the order of the average value among populations within species), and the lack of fixed gene differences between the Hawaiian populations and the others is evidence that the Hawaiian populations are not a cryptic species.

One of the earliest studies of genetic variation in marine organisms was on the giant clam, *Tridacna maxima*, by Ayala *et al.* (1973) and Campbell *et al.* (1975). The very small genetic distance between populations from the Great Barrier Reef and the Marshall Islands (Nei's  $D = 0.035$ ) was also thought to imply that dispersal occurred throughout the species range, and over distances of several thousand kilometres. However, a more detailed survey of populations of *T. maxima* from the Coral Sea (Benzie and Williams, 1992) demonstrated as great a genetic distance between populations separated by only 400 km, as that observed by Campbell *et al.* (1975) over 5,000 km. Differences in the genes sampled in the two studies did not allow any more than a general comparison. However, the differences suggested that gene exchange was unrestricted between *T. maxima* populations up to a neighbourhood size of about 400 km, and that *T. maxima* might show a pattern of geographic variation consistent with isolation by distance.

These data provided little reason to question the traditional view that widespread marine invertebrates with a long larval phase were distributed widely over the Pacific, presumably on ocean currents, and that dispersal was contemporary. Other studies, such as those testing the origin of populations of several fish species separated by the Pacific Barrier from the American coastline (Rosenblatt and Waples, 1986), or those examining the genetic structure of tuna populations over the Pacific (Richardson, 1983; Ward *et al.*, 1994), pearl oysters in French Polynesia (Durand and Blanc, 1988), crown-of-thorns starfish over the Pacific (Nishida and Lucas, 1988), or butterfly fish over the Pacific (McMillan and Palumbi, 1995), have also provided evidence consistent with long-range dispersal.

However, Benzie and Williams (1995, 1997) noted that work has been restricted to highly vagile fish species such as tuna or coastal regions of high connectedness and that most other studies have sampled only a few widespread populations. This has restricted the capacity to evaluate any patterns of gene flow. In the case of the milkfish, the populations showing no genetic variation were all situated in the track of the strong equatorial currents that would have facilitated dispersal. Analyses of geographic variation with a reasonable density of sampling over a wide region of the Pacific has recently been achieved for giant clams, and has shown a very different picture.

#### *The giant clams Tridacna gigas, T. derasa and T. maxima*

Analysis of geographic variation in three giant clam species demonstrated much more complex genetic structures in the western Pacific (Fig.1). The best geographical coverage was achieved in *T. maxima* where nineteen populations were sampled throughout the western Pacific (Benzie and Williams, 1997). These data form a template for the interpretation of a smaller amount of data from *T. gigas* (Benzie and Williams, 1995), *T. derasa* (Macaranas *et al.*, 1992) and the pearl oyster *Pinctada margaritifera* (Benzie and Ballment, 1994). The principal patterns of gene flow in all three clam species was found to be parallel to the major island chains (following a NW-SE axis) and perpendicular to the major ocean currents flowing through the region (following a NE-SW axis) (Fig.1).

It was argued that longshore coastal currents might influence dispersal locally, but that some of the island groups are separated by several hundreds of kilometres of water and larvae entering these should be entrained in large numbers and transported in the direction of the major circulation. Relatively large gene flows were observed between the Philippines and the Marshall Islands between which there are few reefs that might act as staging posts for dispersal. In contrast, little direct gene flow was observed between the Solomon Islands and the Great Barrier Reef. This was despite the existence of many reefs in the Coral Sea that might act as staging posts, the shorter distance separating the two locations, and the fact that the South Equatorial Current flows directly from the Solomon Islands to the Great Barrier Reef.

Detailed oceanographic information is lacking for many areas of the Pacific, and the effects of local currents cannot be entirely ruled out. Similarly, wind drift, which moves thin sheets of surface water (only a few centimetres thick) and surface spray predominantly from the SE to the NW, might entrain clam larvae. This mechanism has been inferred to explain the temporal sequence of occurrence of a bacterial disease of coralline algae (Hale and Mitchell, 1995), but direct information on the nature of surface drift in the south eastern Pacific is limited. Benzie and Williams (1995, 1997) noted that currents at depths of 100 m or more were parallel to the island chains, and inferred that, at times of lowered sea level, surface currents may well have flowed from the SE to the NW. They concluded that the patterns of spatial differentiation in gi-

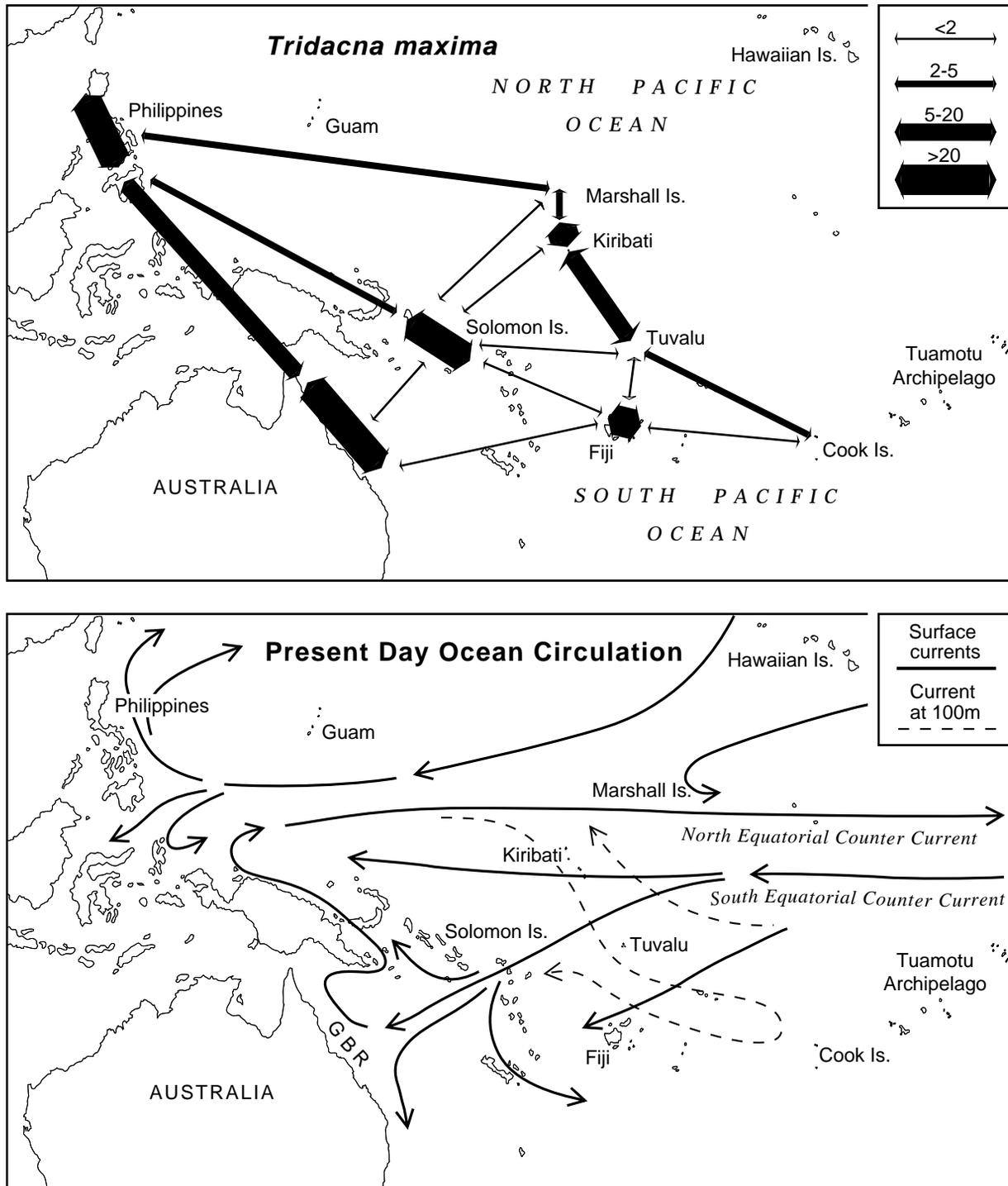


Fig.1. Patterns of gene flow among giant clam (*Tridacna maxima*) populations in the western Pacific, given as the average number of migrants per generation (a). The figure demonstrates that the major axes of gene flow are perpendicular to the major surface currents (b) in the region, but are parallel to deeper current flows (after Benzie and Williams, 1997).

ant clams were the ghosts of dispersal past, and that these had not been altered by changed oceanographic conditions since at least the early Holocene (6 Ka).

The principal finding of this work is that the general notion that widespread marine organisms with a larval phase are distributed widely throughout their range on major ocean currents is

not consistent with the genetic evidence. Irrespective of whether dispersal is contemporary and occurring on surface drift, or whether major patterns of marine diversity are related to past events, it is clear we do not understand the processes driving the origin and maintenance of marine biodiversity. Given that sea-level changes are related to climatic fluctuations that may be related to periodic astronomical events (Bennet, 1990), dispersal is likely to be pulsed at periods of low sea-level when circulation might have been more intense within ocean basins, as well as different in direction. The important role these processes are likely to have played in determining connectedness of coral populations has been discussed by Rosen (1988) and Veron (1995).

These findings are of particular interest with respect to the SE Asian region. Traditional views have SE Asia as a regional centre of speciation, with species radiating from SE Asia eastwards across the Pacific. Benzie and Williams (1997) noted that the NW-SE axis of gene flow was not necessarily inconsistent with this view, since the genetic data could not determine the direction of movement along this axis. However, the mechanisms of dispersal identified (present-day surface drift or palaeocurrents) both provide for potential dispersal from the Pacific into the SE Asian region. These data therefore provide some support for a model developed by Jokiel and Martinelli (1992) which demonstrated that, when speciation was limited to islands in the Pacific, species diversity increased at the western edge of the Pacific Ocean, in the SE Asian region. The fact that there is a reduction in species diversity eastwards into the Pacific does not mean there has to be dispersal of species eastwards from a centre of origin. It is possible, for example, that the smaller size of populations on isolated islands and relatively less heterogeneous environment on a given scale may result in a greater extinction of species in the Pacific.

#### *The sea urchins Echinometra spp.*

Palumbi (1977) has summarised patterns of genetic structure based on mtDNA data for four species of closely related sea urchins. The limited mtDNA divergence between species in the central and west Pacific indicates that they have diverged in the last 1-3 myr (Palumbi, 1996) and that speciation is on-going within the Pacific basin. Strong geographic patterns of differentiation were observed within each species, but were not concordant, suggesting that different proc-

esses played a role in each case or that chance played a strong role in population differentiation. However, the wide spread of a relatively few samples across the Pacific did not provide a sound basis for discerning patterns of gene flow among these populations in the same way as the giant clam data. Nevertheless, these data do indicate regional differentiation, and evidence of speciation within ocean basins far from the SE Asian region.

#### **Differentiation between oceans**

There are very few genetic surveys which encompass both the Indian and Pacific Oceans, and those that do have only recently been acquired. All have shown marked genetic differentiation of populations in the Indian Ocean from Pacific populations. Despite the lack of significant differentiation among several populations collected throughout the western Pacific, the one population of coconut crabs collected from Christmas Island in the Indian Ocean was significantly differentiated from all others (Lavery *et al.*, 1996). Similarly, the level of genetic distinction of butterfly fish populations from different oceans was orders of magnitude greater than that between populations within oceans (McMillan and Palumbi, 1995). Major differences in gene frequencies have been observed between populations from different oceans, despite little or no genetic differentiation being observed between populations over large geographical scales within oceans, for the starfish *Linckia laevigata* (Williams and Benzie, 1996, 1997, 1998) and the starfish *Acanthaster planci* (Nishida and Lucas, 1988; Benzie, 1992, unpublished results). Most information has been obtained for *Linckia laevigata*, and it is worth looking at these findings in more detail.

#### *The starfish Linckia laevigata*

Data are available for both allozyme and mtDNA restriction fragment patterns in *L. laevigata* which allowed a deeper interpretation of the genetic data (Fig.2). Data were obtained from more than twenty sites throughout the Indian and Pacific Oceans, providing reasonable coverage of the Indo-Pacific. The complete absence of any spatial differences in gene frequencies throughout the western Pacific (Fig.2), despite the presence of a high degree of polymorphism, suggested either large scale contemporary dis-

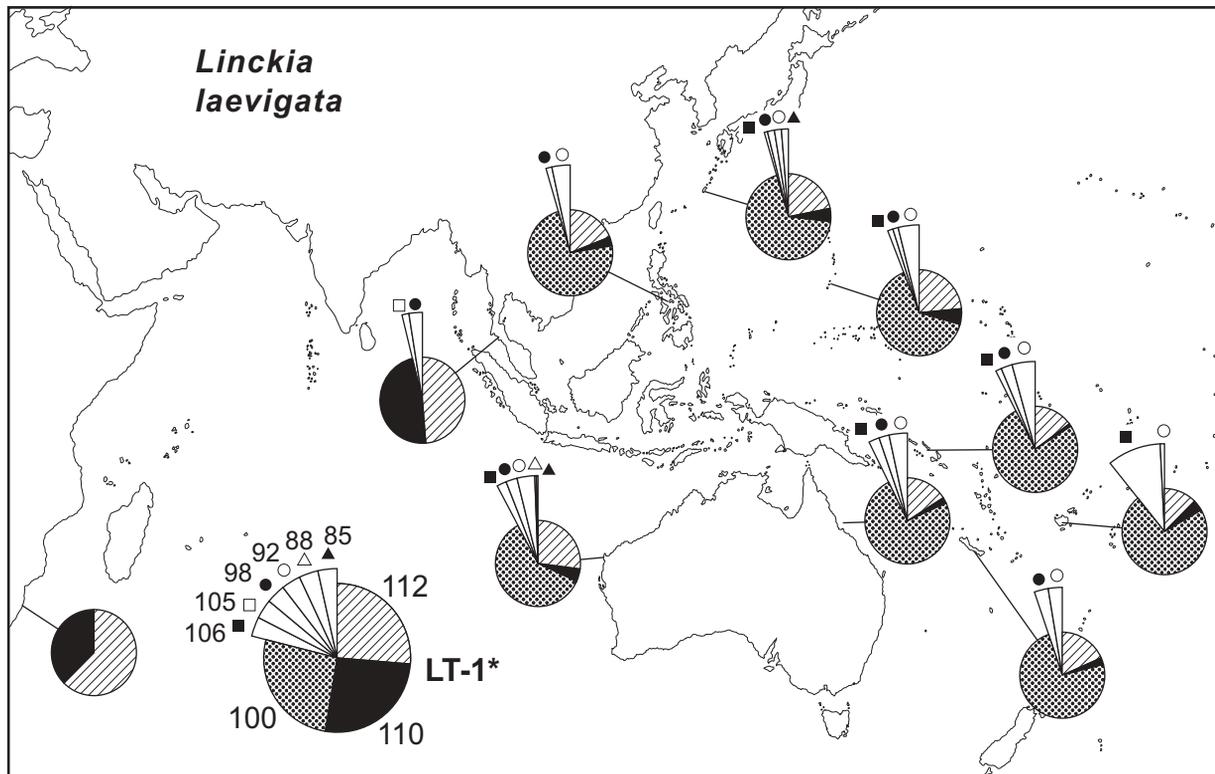


Fig.2. Spatial pattern of allele frequencies at the *LT-1* locus in the starfish *Linckia laevigata* illustrating the marked genetic differentiation of populations in the Indian and Pacific Oceans, but the lack of significant differentiation between populations within each ocean (after Williams and Benzie, 1998). The data also show clearly that the Western Australian population has a genetic constitution similar to that of the Pacific rather than the Indian Ocean.

persal, or that the populations were not at equilibrium. The four-week long larval life of the species might suggest that it could disperse considerable distances, but it was not clear that this period was sufficient to maintain homogeneity throughout the Pacific.

The discovery of some structure in the mtDNA data showed that dispersal was high over short to medium distances and regions where populations were highly connected (such as in the Great Barrier Reef). However, some distinction between the Great Barrier Reef and Fiji populations on the one hand, and Philippines and Western Australian populations on the other, indicated low present-day gene flow between these two groups. These data indicate that the allozymes are not yet at equilibrium and that some other processes (such as balancing selection) are slowing change in allozyme frequencies. The data indicate greater dispersal among populations within oceans in the past than occurs present day.

In contrast, strong and significant differences

were found between the Indian and Pacific Ocean populations (Fig.2). The fact that some differences occurred at several loci (which were not linked, but were segregating independently) indicated that populations had differentiated as a result of genetic drift. The fact that the genetic diversity in each set was high suggested the differences in allele frequencies was not the result of founder effect. The differentiation was thought to occur when gene flow was restricted, probably at times of lowered sea level when land connected much of SE Asia, New Guinea and Australia, almost closing the sea connection between the Indian and Pacific Oceans. These changes are thought to be recent. Phylogenetic analysis of *Linckia* species has shown that *L. guildingi* (distributed throughout the Indo-Pacific and Caribbean) diverged from the other species about 20 Ma, and that the molecular divergence of the Indian and Pacific populations of *L. laevigata* occurred during Pleistocene time (<3 Ma). It is not known whether the genetic differentiation occurred rapidly (125 Ka - 12 Ka) or

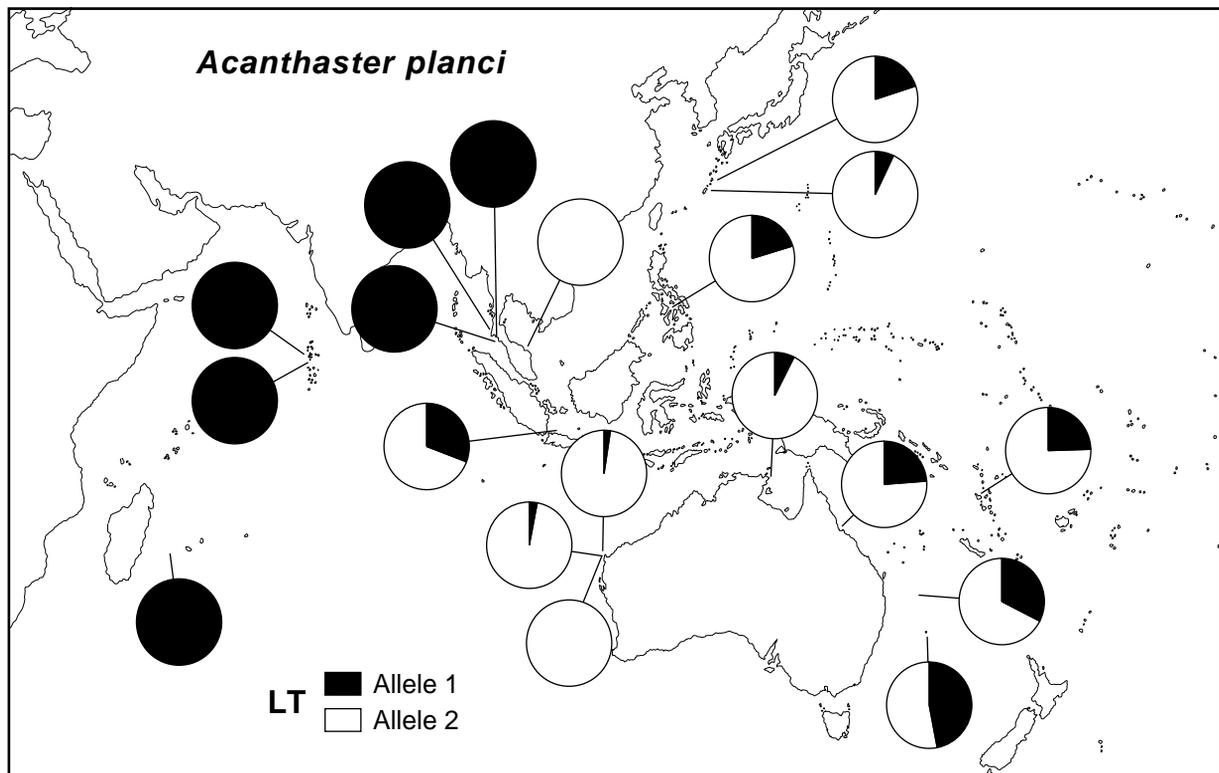


Fig.3. Spatial pattern of allele frequencies at the *LT* locus in the crown-of-thorns starfish, *Acanthaster planci*, illustrating the major genetic differentiation of populations in the Indian and Pacific Oceans, but the lack of significant differentiation between populations within each ocean (Benzie, unpublished data). The data also show clearly that the Western Australian populations have a genetic constitution similar to that of the Pacific rather than the Indian Ocean.

accumulated over several periods of lowered sea level known to have occurred in the last 3 myr.

It is important to note that the Western Australian populations of *L. laevigata* had a similar genetic constitution (allozyme and mtDNA) to the Pacific populations even though they are situated in the Indian Ocean. Oceanographic, micropalaeontological and sedimentological data provide evidence that these populations have been isolated from others in the Indian Ocean by upwelling to the west of the Australian coast (Fleminger, 1986; Wells and Wells, 1994; Wells *et al.*, 1994). It is speculated that they received (or that the populations were originally founded by) recruits from the SE Asian region through the Indonesian throughflow rather than from the east coast of Australia via the Torres Strait and the Northern Australian coast (Godfrey *et al.*, 1993; Gordon and Fine, 1996). It is pertinent to note that data from an unrelated starfish *A. planci* also shows a similar geographic pattern of allozyme variants (Fig.3).

The taxonomic composition of a number of marine faunal groups such as sponges (Berquist and Kelly-Borges, 1995) is also consistent with a connection of Western Australia with the Pacific rather than the Indian Ocean.

The distribution of mtDNA genotypes suggested that gene flow had resumed between the Indian and Pacific Ocean populations in the region of the Indonesian archipelago (Williams and Benzie, 1997). However, data within this region were limited to one population and further work will be required to determine 1) whether there is widespread introgression, 2) whether some hybrid zone has been established or 3) whether gene flow is now highly restricted. While there are a variety of colour morphs in *L. laevigata*, populations in the Pacific (and Western Australia) are predominantly blue while those in the Indian Ocean are violet or salmon pink in colour. It is pertinent to note that the crown-of-thorns starfish in the Pacific (and in Western Australia) are grey-purple to brick red in colour whereas those from the In-

dian Ocean are blue-purple to pink (Benzie, 1992), and the colour groups have very different allozyme frequencies (Benzie, unpublished data) (see Fig.3). No mtDNA data are yet available, but the concurrence in spatial pattern of genetic differentiation in two unrelated starfish suggests the pattern may be general to other marine invertebrates.

These findings are particularly relevant to SE Asian biogeography because they provide evidence for strong genetic differentiation, consistent with vicariant origins in oceans on either side of the SE Asian region, even within widespread marine species with long larval lives. The divergence in allopatry appears to occur in less than 3 Ma, or perhaps as little as tens of thousands of years. The lack of equilibrium in genetic structure indicates far greater dispersal among populations within oceans in past times, but less between oceans. These data provide further support for views that speciation of marine taxa did not occur within a centre of origin (SE Asia), but from successive isolation of populations outside this region (Wallace *et al.*, 1991; Pandolfi, 1992, 1994; Wallace, 1997). Cladistic biogeographic analysis of corals has suggested species arose from successive isolation of populations consistent with major geologic events in the Indo-Pacific, rather than spreading out from the Indo-Malay region after arising within that region (Pandolfi, 1992, 1994). Wallace (1997) presents further evidence demonstrating that patterns of endemicity of *Acropora* corals are consistent with a significant level of speciation within either the Indian or Pacific Oceans followed by the spread of these taxa into the SE Asian region. Several siganid fish species distributions support this same interpretation (Woodland, 1983). The genetic structure of butterfly fish (McMillan and Palumbi, 1995) and coconut crabs (Lavery *et al.*, 1996) also show little variation within the Indian or Pacific Oceans but marked genetic differences between oceans.

## Discussion

SE Asia has long been recognised as having high levels of marine biodiversity. The many hypotheses which have been advanced to explain the biogeography of tropical marine organisms have been summarised by Rosen (1988) and each falls into one of two major models. In the first, species are thought to originate in a centre of high diversity, and then spread to peripheral ar-

eas and is known as the dispersal model. In the second, species are thought to form by divergence of populations divided by a geographic barrier, and is known as the vicariance model. In the vicariance model there is no requirement to have highly diverse centres of origin.

The principal reasons for suggesting the SE Asian region is the centre of origin of coral species is the high diversity within the region, and the reduction in diversity east and west. In the case of corals, the average age of higher taxonomic units (families, genera) also decreases moving outwards from the SE Asian region and this fact has been used to support the dispersal model (Stehli and Wells, 1971). However, Pandolfi (1992) has shown that some of the most derived coral species that show the greatest degree of endemism are at the periphery of Indo-Pacific coral distributions. This implies that many species must have originated far from the SE Asian centre of diversity. Jokiel and Martinelli (1992) have demonstrated in a simple model how speciation in the isolated peripheral areas of the Pacific still leads to an accumulation of species diversity in the western margin of the ocean at the tropics because of ocean circulation patterns. More recently the patterns of endemism of *Acropora* coral species Wallace (1997) and sponges (Kelly-Borges and Valentine, 1995) are consistent with vicariant divergence of populations in the two ocean basins, rather than within the SE Asian region.

The limited genetic data available are of interest because they suggest that patterns of genetic variation within species today are not at equilibrium, and that they are the result of historical events. The patterns of genetic diversity in giant clams indicate that dispersal from SE to NW is consistent with major ocean currents inferred at times of low sea level, and that dispersal among sites within oceans was greater in the past than now. Major genetic discontinuities between populations in the Indian and Pacific Oceans indicate divergence in allopatry at times of low sea level, and provide evidence for the origin of species in the two oceans rather than in the SE Asian region. The domination of patterns of variation explained by low sea levels should not be surprising given that sea levels have been lower than present day levels for much of the Pleistocene.

It is important to note that there is almost no data on the genetic structure of species within the SE Asian region. Potts (1985) and McManus (1985) suggested that sea level changes played an important role in creating isolated

populations by cutting off local sea basins within the SE Asian region. It is likely that changing sea levels have influenced speciation of marine organisms by this means within the region, particularly those with taxa with low dispersal potential.

A review of the limited data available cannot be conclusive, therefore, but does invite speculation that present patterns of genetic variation have resulted from highly pulsed dispersal of marine taxa in the Indo-Pacific, related to global climate change and major geological events, and that regional speciation outside the Indo-Malay region has been greater than thought in the past. Movement of species originating in the Indian and Pacific Oceans into the Indo-Malay archipelago may have played a more important role in producing diversity in that region than traditionally recognised.

It will be necessary to develop specific predictions of the spatial patterns of genetic variation expected under different biogeographic hypotheses so that these can be explicitly tested. This will be a challenging task as many of the theories have identical biogeographical predictions (Pandolfi, 1992). Some approaches have been suggested by Palumbi (1997) which predict that older genotypes are likely to be found where species originate, but he also indicates that differences in population size and extinction rates in the central Pacific (lower population size and higher extinction rates) compared to the western Pacific (higher population sizes and lower extinction rates), might mask this pattern. Nevertheless, further application of molecular genetic tools to examine the structure of species within the SE Asian region will provide an important means of advancing our understanding of the origin and maintenance of biodiversity in the region.

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