

# MARINE BIODIVERSITY

Patterns and Processes

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# Chapter 12

## Population genetics and demography of marine species

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### Abstract

The life histories of many marine organisms are characterised by high fecundity, planktonic larvae and a remarkable capacity to colonise remote habitats. These species are commonly viewed as consisting of large, undifferentiated populations that are seldom limited by recruitment. This view leads to the expectation that substantial changes in marine populations generally must be brought about by forces acting over large geographical and temporal scales. However, recent surveys of molecular genetic variation suggest a very different perspective. Sharp geographical discontinuities have been found in the absence of any recognisable barriers to dispersal. These may be interpreted in terms of adaptation to local or regional environments. In many species, low levels of genetic variation or high levels of temporal variance in allele frequencies have indicated surprisingly small genetically effective population sizes. An important question raised by these findings is whether the stability of such populations may be critically dependent on the reproductive success of relatively few individuals. If so, then the potential consequences of habitat or range reduction may be more severe than previously anticipated.

### 12.1 Introduction

The concept of biodiversity unites the variety of life-forms that are the products of evolution with the diversity of habitats and ecosystems in which they are found. These two aspects of biodiversity have traditionally been the subjects of separate disciplines: biosystematics and ecology. However their union is now crucial. The rapid global decline of biological diversity at all levels represents a crisis that neither discipline, by

itself, can adequately address. The developing science of biodiversity must relate ecological processes, which determine patterns of distribution and abundance, to the evolutionary histories of the organisms that undergo these processes. Only by understanding such relationships will it be possible to predict how changes in ecosystems and communities will impact specific taxa and, conversely, how losses or introductions of specific taxonomic groups will impact ecosystem or community function.

The marine realm has presented special problems for both systematists and ecologists (discussed by Ray, 1988). Extended, direct observation of marine organisms in their natural habitats is often difficult, and in some cases, nearly impossible. As a result, many marine environments have barely been explored, and historical information is available for only a few. Furthermore, because of the dynamic nature of oceanographic processes and the extensive movements of organisms in water, marine systems have no true boundaries. It is thus difficult to define small, easily managed units. These problems demand that marine biodiversity be studied and managed in ways that are fundamentally different from those developed for terrestrial systems. Because we know so much less about marine systems, we must find ways to extrapolate what we do know to places we have barely visited, and across time-scales much greater than our history of observation. Management strategies that are concerned with only the most visible (or most valuable) stage of a marine organism's life history are unlikely to succeed. Successful approaches to the study and management of marine biodiversity will probably be more conceptual, integrative and global than those developed for terrestrial systems.

It is to be expected that, in general, strategies for the conservation of biodiversity will be based on well established concepts and principles. My purpose in this chapter is to examine some new findings concerning the population genetics of marine organisms that do not fit within well established views. It is too early to predict whether these new findings will lead to a major shift in the way we think about the population biology of marine organisms. It is also true that much of what they imply has been proposed before, and may even represent views that have claimed adherents for some time. However, in the light of the current biodiversity crisis, the findings that are discussed below have particular significance because they suggest that populations of marine organisms may be far more delicate than is generally perceived.

## **12.2 The significance of population genetics for biodiversity studies**

The importance of genetics to conservation biology has been much debated. Franklin (1980) and Soulé (1980) argued that loss of genetic variation in small refuge populations could threaten their viability and potential for evolutionary adaptation. Based on simple population genetic models, they proposed that a minimum population size of 50 was necessary to prevent inbreeding depression, and a minimum population size of 500 was necessary to prevent loss of evolutionary potential. The inadequacies of such generalisations have led to extensive criticism of genetic criteria for defining minimum viable population sizes (for a review, see Simberloff, 1988). Furthermore, as pointed out by Lande (1988), demographic factors may be more likely to cause the extinction of small populations than lack of genetic variation.

The debate over the role of genetic variation in determining the minimum viable size of a population has had the unfortunate effect of drawing attention away from other, less equivocal, applications of population genetics to conservation biology. Population genetics may be especially helpful in the study of marine biodiversity. A solid conceptual foundation for the study of marine biodiversity must somehow bridge the present gap between ecology and systematics. In principle, population genetics provides such a bridge. Population genetic processes are driven by events that take place in an ecological setting, but lead to evolutionary changes. These events: birth, death and migration, comprise the demography of a population. The evolutionary changes that follow can produce species, as well as higher levels of evolutionary diversity. In turn, adaptations that result from evolutionary change feed back to the ecological level by altering rates of birth, death and migration.

An optimistically long-term strategy for the preservation of biodiversity would strive to balance extinction with speciation. Geographical areas have been identified in which some taxa have recently undergone unusually high rates of speciation. It has been argued that these areas will continue to generate species and, on this basis, should be afforded special protection (Erwin, 1991). However, the conditions that are believed to lead to speciation are not inextricably linked to geography, however much they may be influenced by geographical circumstances. Precursors to speciation such as local adaptation and isolation are population genetic conditions, and as such may be altered by human activities, and are potential objects of management. However, although population

genetic models do a reasonably good job of predicting how much genetic divergence will result from a given set of demographic conditions, they do not predict how much genetic divergence will lead to speciation. It is unlikely that a simple rule will be found that relates some standard measure of genetic divergence to speciation. The magnitude of genetic divergence between congeneric species appears to vary considerably (Avice & Aquadro, 1982). It may be difficult to develop a general understanding of speciation if reproductive isolation depends on specific and idiosyncratic genetic mechanisms, rather than on any overall level of genetic divergence.

The chain of causality can also be followed in the opposite direction, to predict the ecological effects of microevolutionary processes. Two major types of effects are expected: local adaptation and inbreeding depression. While both have been demonstrated in particular cases, it is difficult to reach any generalisation about their importance in natural populations. Theoretical models indicate a range of possibilities that depend on the particular characteristics of a species, its population biology and the nature of genetic variation (e.g. Wright, 1969). Empirical studies are generally biased towards species that are easy to maintain under controlled conditions. Some well entrenched generalisations are based on only a few studies of domesticated mammals and laboratory populations of *Drosophila* (Lande, 1988; Simberloff, 1988). Clearly, the importance of local adaptation and inbreeding depression in marine species needs to be explored.

### 12.3 Gene flow and local adaptation

Throughout its range, a species will experience different environmental conditions, constituting different regimes of natural selection. Transplantation of organisms to a new location may fail if they are not adapted to the conditions they encounter, even though the species may have once flourished at the same location. Furthermore, local adaptation requires that selection is strong enough to counter the homogenising effects of gene flow among populations (Ehrlich & Raven, 1969; Slatkin, 1985). Thus an increase in gene flow between populations may reverse the process of local adaptation, and cause populations to decline.

Natural selection is often viewed as a deterministic process, in which individual alleles are favoured in particular environments where they increase in frequency. This view is basically correct if the effect of each gene is largely independent of others. However, if there are significant

interactions among genes, there may be many different ways for a population to respond to the same set of environmental conditions, with different combinations of genes that work together (Mayr, 1970; Wright, 1977; Hedrick *et al.*, 1978). Which combination is used may depend on the initial genetic composition of the population, but may also be random to some degree. If local adaptation involves combinations of interacting genes, gene flow between populations that are adapted to the same conditions may nonetheless undo local adaptation by mixing incompatible combinations of genes. A consequent reduction in fitness would be considered a form of 'outbreeding depression' (Endler, 1977).

There is no simple test for local adaptation. It is not sufficient to demonstrate spatial or geographical variation in adaptive traits, because most complex traits are subject to direct environmental influence, as well as genetic control. Some form of experimental manipulation is required to control for environmental influences. Typically, a 'common garden' experiment is performed, in which stocks from different sources are reared in a common environment for several generations. However, for practical reasons, this approach can only be used for a few marine species.

The tide-pool copepod, *Tigriopus californicus*, is exceptionally well suited to experimental manipulation. Populations occur in high intertidal rock pools along the west coast of North America. These pools are relatively free of predators, but subject to extremes of temperature and salinity during periods of warm weather and low tide. Burton and co-workers have studied these populations extensively over the past 15 years. Allozyme allele frequencies in tide-pool populations were surveyed on several geographical scales (Burton *et al.*, 1979; Burton & Feldman, 1981). Among a group of tide-pools located on a single rock outgroup, allele frequencies were generally uniform. However, between outcrops, sharp differences in allele frequencies were observed, even in cases where outcrops were separated by less than 500 m. Allele frequencies were also stable through several years of observation, although individual tide-pool populations cycled through extinction and recolonisation. These results indicated that tide-pools within a rock outcrop were linked by gene flow, but little gene flow occurred between tide-pools on different outcrops. This interpretation was confirmed by experiments in which individuals with characteristic allozyme alleles were transferred between populations (Burton & Swisher, 1984). Differences in allele frequencies between outcrops did not appear to constitute any large-scale geographical patterns; along the Californian coast, regional averages of allozyme frequencies were very similar.

By itself microgeographical variation in allozyme frequencies indicates that gene flow is sufficiently restricted to provide the opportunity for local adaptation, but does not imply that local adaptation has actually occurred. Differences in allozyme frequencies can be easily explained as the result of genetic drift, and may have no adaptive significance. Fortunately, the natural habitat of *T. californicus* can be approximated in the laboratory. Matings can be arranged, and progeny reared in small containers. Burton (1987, 1990) crossed animals from either the same population or from populations on different outcrops, raised  $F_1$  progeny, and then intercrossed these  $F_1$  to produce an  $F_2$  generation. In an inter-population cross, haploid combinations of genes derived from each source population are passed on intact to  $F_1$  progeny. However  $F_2$  progeny inherit recombinant genotypes, in which the original haploid combinations of genes have been broken apart. To assess the fitness effects of these crosses, Burton measured the development time of progeny, and rates of mortality under osmotic stress. In a continuously breeding organism such as *T. californicus*, development time should be inversely correlated with fitness. The development times of  $F_1$  progeny were generally between 15 and 17 days, regardless of whether they were the progeny of inter-population or intra-population crosses. In contrast, development times for  $F_2$  progeny of inter-population crosses were typically much longer, indicating a substantial reduction in fitness. Furthermore, in crosses between two of the four populations (SD and AB), most of the  $F_2$  progeny failed to even survive. These declines in fitness did not appear to be the effects of prolonged culture; development times for  $F_2$  progeny of intra-population crosses were either about the same or only slightly longer than their  $F_1$  parents. Thus it appears that interactions between genetic loci play a large role in local adaptation for *T. californicus*.

*Tigriopus californicus* is an excellent model organism for genetic studies, nearly a 'marine *Drosophila*'. However, its tide-pool habitat is unusual, and so we need to consider gene flow and local adaptation in other, more 'typical' marine species. A commonly held view is that for most marine species, dispersal in water provides high levels of gene flow, and, therefore, inter-population divergence and local adaptation are unlikely (Crisp, 1978; Hedgecock, 1986; Utter & Ryman, 1993). Allozyme surveys of both marine fish (Gyllensten, 1985) and invertebrates (Hedgecock, 1986) with nektonic or extended planktonic life-stages have typically found little genetic divergence among populations, a finding consistent with high rates of gene flow. Exceptions have been



found (Burton, 1983) but have not altered the general view, that typical marine species consist of very large, panmictic (randomly breeding) populations, from becoming an established paradigm. This has been especially frustrating for fisheries biologists, who hoped to use genetic markers to identify natural stocks that could be managed separately.

#### 12.4 Molecular markers and unexpected population structure

Recently, surveys of DNA sequence variation in marine animals, along with some new methods for the analysis of allozyme data, have led to some fairly radical reassessments of the established paradigm. Whether or not these new findings prove to be of general significance remains to be seen. To some extent, they represent not so much new ideas as revivals of old ones, such as the idea that the frequencies of allozyme alleles are controlled by natural selection. What is new is that recent technological developments should allow these ideas to be tested with greater rigour than ever before. These studies thus have the potential to force a major reassessment of the prevailing view that marine populations are subject only to large-scale events and processes.

Some of the most interesting new findings concern allozyme variation in the American oyster, *Crassostrea virginica*. This species is of considerable commercial importance, and has been the subject of extensive genetic and physiological studies. Its life history is typical of benthic marine invertebrates. Individual females live for up to 20 years, producing from 10–114 million eggs in a single reproductive cycle (Galtsoff, 1964). A high potential for dispersal is provided by a free-swimming planktonic veliger stage, which drifts in the plankton for 2–3 weeks.

An allozyme survey of American oyster populations along the Atlantic and Gulf of Mexico coasts of North America yielded fairly typical results (Buroker, 1983). Allozyme allele frequencies at most loci were generally uniform over a large geographical range, although 2 of the 21 polymorphic loci appeared to vary with latitude. These findings fit well with the accepted paradigm. Uniformity of allozyme allele frequencies is an expected consequence of high levels of gene flow. Unusual allele frequencies in one population, near Brownsville, Texas, were interpreted as evidence for isolation of this population. Only one locus (*Lap-2*), with allele frequencies that varied with latitude, was proposed to be under selection.

A survey of mitochondrial DNA (mtDNA) variation for essentially the same series of populations yielded a pattern strikingly at odds with

the allozyme data (Reeb & Avise, 1990). Two very divergent groups of mtDNA sequences were found to distinguish Atlantic populations from those in the Gulf of Mexico. The location of the break was on the east coast of Florida, near a known biogeographical boundary. This difference is clearly not due to the greater variability of mtDNA as compared to allozyme loci. Even if detection of mtDNA variation had been limited to the two major forms, the pattern would still be very clear. Several possible explanations for this discrepancy were considered. The difference could be due to the maternal inheritance of mitochondria; the observed pattern would be expected if gene flow between Atlantic and Gulf of Mexico populations was mediated by sperm, but not eggs or larvae. Another possibility was that natural selection, acting on mtDNA, had overcome what appeared to be the substantial gene flow that maintained uniform allozyme frequencies. A third possibility required that Atlantic and Gulf of Mexico populations have been separated for a long time. To achieve the observed level of divergence with typical rates of mtDNA evolution, roughly 1 million years would be required. During that time, selection could have maintained uniform allozyme frequencies, while mitochondrial genomes steadily diverged. Support for the latter explanation came from studies on nuclear DNA polymorphisms. Karl & Avise (1992) examined variation in 'anonymous' nuclear single copy DNA sequences, which for the most part do not appear to encode proteins, and would therefore not be subject to the same forms of selection as protein-encoding allozyme genes. Although these sequences were only moderately polymorphic, they clearly separated Gulf of Mexico and Atlantic populations and therefore corroborated the mtDNA pattern. Thus it appears that in American oysters, selection may have maintained similar allozyme allele frequencies in populations that had been separated for roughly a million years.

The idea that allozyme alleles are subject to selection is hardly novel or obscure. Indeed, from Buroker's (1983) allozyme study of oysters, it was concluded that selection was probably acting at one or two loci. Yet the conclusions reached by Karl & Avise (1992) represent a sharp departure from conventional modes of interpretation. Firstly, while it may be acknowledged that some allozyme loci are under selection, it is often assumed that most are not. Thus, when a number of allozyme loci are surveyed, and most exhibit a similar pattern (i.e. geographical uniformity), selection is not usually invoked to explain this pattern. Only loci that depart from a general pattern are considered candidates for selection. This idea has even been used as the basis for statistical tests

of selection on allozyme loci (eg. Lewontin & Krakauer, 1973). Thus while Buroker (1983) argued that the enzyme locus, *Lap-2*, was under selection that led to geographical variation, Karl & Avise (1992) suggested that nearly all of the other loci surveyed by Buroker were subject to selection that maintained uniformity. Under this interpretation, *Lap-2* may be the only locus that is not under selection.

### **12.5 Geographical and temporal scales**

General invalidation of the 'majority rule' principle for deciding which allozyme loci are not under selection would have broad implications for the interpretation of numerous allozymes surveys (over 1000) that have been conducted. This principle is often used to justify the use of allozyme data to estimate levels of gene flow between populations (Slatkin & Barton, 1989) and to infer historical relationships among populations. Certainly our view of marine populations has been strongly influenced by this principle.

Buroker's (1983) interpretation of allozyme variation in the American oyster is consistent with the paradigm of large, panmictic marine populations. However, the distributions of variation in mitochondrial (Reeb & Avise, 1990) and nuclear DNA (Karl & Avise, 1992) imply the presence of an impenetrable wall across what appears to be a nearly continuous habitat. The completeness of this boundary (which is most apparent in the mitochondrial data) implies that whenever oyster larvae are carried across it, they fail to become established. Even if it is argued that two cryptic species are involved, a high degree of local adaptation is implied.

The paradigm of large, panmictic marine populations, implies that regional patterns of variation must be shaped by major oceanographical events that isolate populations for long periods of time. Population genetics theory shows that the rate of genetic drift should be inversely proportional to the breeding size of a population (Fisher, 1930; Wright, 1931). It follows that larger populations require more time to diverge by genetic drift (Crow & Aoki, 1984), and require less inter-population migration to prevent divergence (Wright, 1965). Thus it might be expected that regional patterns of allozyme diversity reflect major events that have taken place in the Pleistocene, or earlier. Such events would provide the degree of isolation and the amount of time required to generate major regional patterns.

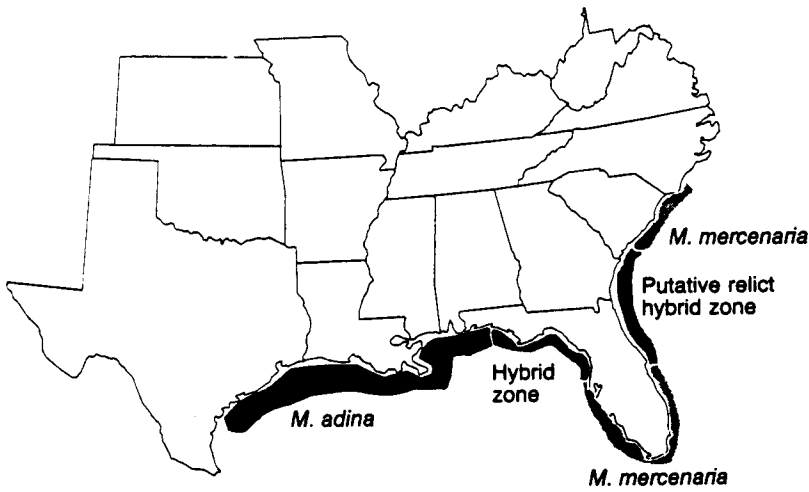


Fig. 12.1. Geographical ranges of *Menippe adina* and *M. mercenaria*, and two putative hybrid zones.

### 12.6 Historical versus ecological explanations for geographical variation in stone crabs

This historical view guided an initial investigation of regional patterns of diversity in the stone crab, *Menippe* (Schneider-Broussard, 1993; Schneider-Broussard & Neigel, 1996). Two species of stone crab are recognised from the Atlantic and Gulf of Mexico coasts of North America (Fig. 12.1). *Menippe mercenaria* ranges from North Carolina south to peninsular Florida. *Menippe adina*, recently recognised as a distinct species, occurs in the western Gulf of Mexico (Williams & Felder, 1986). These two species differ in a number of characteristics, including frequencies of allozyme alleles, colouration patterns and physiology (Bert, 1986; Williams & Felder, 1986). However, crabs with intermediate characteristics are found along the western coast of Florida, in what is considered to be a broad hybrid zone (Bert, 1986; Williams & Felder, 1986; Bert & Harrison). This distribution can be explained as the result of allopatric speciation and secondary contact at the hybrid zone. However, a second apparent hybrid zone on the Atlantic coast is more difficult to explain, because it is completely embedded within the range of *M. mercenaria* (Bert, 1986). Allozyme alleles and phenotypic characteristics of *M. adina* appear to have introgressed into *M. mercenaria* without any obvious direct route. This pattern suggests

that some ancient, large-scale event must have allowed entry of *M. adina* into the Atlantic. Bert & Harrison (1988) proposed that this event was the opening of the Suwanee Straits, a waterway across northern Florida that most probably appeared during times of extremely high sea level in the Miocene (12 million years (my) before present (bp)) and Pliocene (3.5 my bp).

We used mtDNA to estimate the time of separation between *M. mercenaria* and *M. adina* (Schneider-Broussard, 1993; Schneider-Broussard & Neigel, 1996). In many taxa, mtDNA evolves more rapidly than nuclear DNA (Vawter & Brown, 1986), and in some instances rates of mitochondrial DNA evolution have been calibrated with paleontological data (Avise *et al.*, 1987). We chose to examine sequence variation in the mitochondrial large subunit ribosomal RNA gene (often referred to as the '16 S' gene), because rates of evolution in this sequence have been calibrated for other decapod crustaceans (Cunningham *et al.*, 1992).

In comparing mtDNA sequences from two species, it is possible that some of the divergence seen actually accumulated before speciation, as genetic variation within the ancestral species (Neigel & Avise, 1986). Thus estimates of divergence time should be based on the most similar pairs of sequences from two species. In our study, we included samples of *M. mercenaria*, *M. adina* and putative Atlantic hybrids. We expected to see evidence for two types of relationship between sequences (Fig. 12.2). Firstly, we expected to find sequences that were separated at or prior to the time of speciation. The most similar of these would be used to estimate the date of the speciation. In addition, we expected Atlantic hybrids to have sequences that were originally derived from *M. adina*, but somewhat divergent from modern *M. adina* sequences because of the long isolation of these relict hybrids from *M. adina* in the Gulf of Mexico. These sequences would be used to estimate the date of hybridisation.

The results of our mitochondrial DNA studies are illustrated in Fig. 12.3. Although we found some differences among DNA sequences, the most similar sequences from *M. adina* and *M. mercenaria* were identical. The same sequence was also found in individuals from the presumed Atlantic hybrid zone. It appears that the present distributions of genetic variation in *Menippe* were not generated over millions of years, as had been supposed. The existence of an Atlantic hybrid zone was particularly difficult to explain, as there is no geological evidence of a recent opening of the Suwanee Straits.

*Menippe adina*  
(Gulf of Mexico)

*Menippe mercenaria*  
(Atlantic)

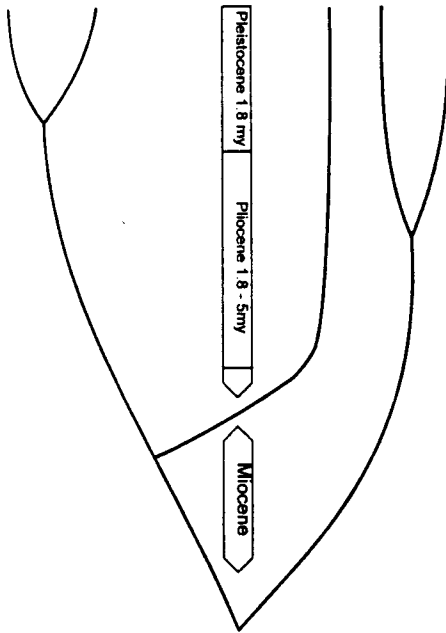


Fig. 12.2. Predicted relationships among ancestral and introgressed mitochondrial DNA sequences, based on secondary contact during a late Pliocene opening of the Suwanee straits.

The possibility of natural selection on allozyme alleles suggests a very different interpretation of genetic variation in *Menippe*. '*M. adina*-like' alleles may be maintained by contemporary conditions in populations along the Atlantic coast, rather than remaining there as historical relicts. Contemporary current patterns could transport larvae from *M. adina* to Atlantic populations at frequent intervals (Schneider-Broussard, 1993). Thus the observed geographical pattern may have no historical basis. This is not to say that historical events had no role in the initial separation of *M. mercenaria* and *M. adina*. A very recent separation might not have provided enough time for divergence of mtDNA sequences. However, long-distance dispersal of large numbers of larvae would tend to quickly erase historical patterns, once barriers to dispersal were removed. In contrast, the constant availability of a genetically diverse pool of larvae would allow selection to generate new, and potentially more complex, geographical distributions.

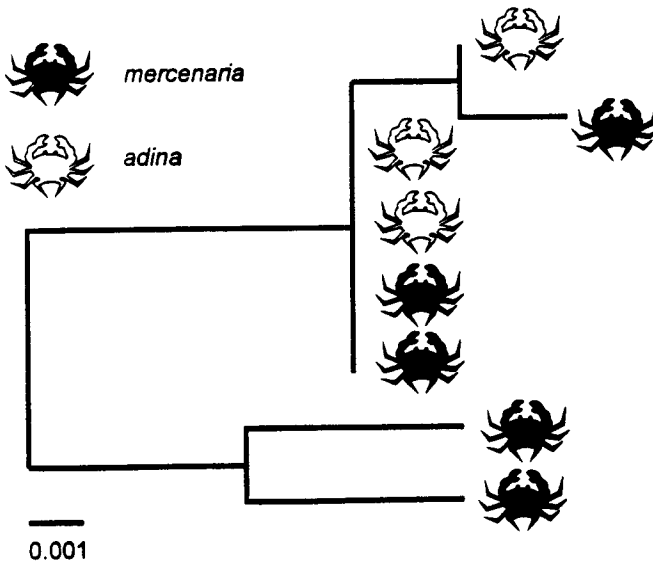


Fig. 12.3. Modified Kimura distance phenogram of *Menippe* mitochondrial large subunit ribosomal DNA sequences. The bar represents 0.001 units.

The idea that highly fecund organisms could be subject to intense selection was proposed by Williams (1975). In his 'Elm-Oyster' model, enormous numbers of genetically variable progeny allowed selection to limit success to only those that were extremely well adapted to current environmental conditions. A contrasting view would be that larval success is mostly a matter of luck, of being carried along by currents to food but not predators, and, ultimately, to a suitable habitat. However, there may be room for both luck and genetics, if the number of larvae is large enough to sustain reductions by both. If this is the case, then large numbers of larvae do not represent a surplus, but rather the raw material for local adaptation.

### 12.7 Inbreeding and effective population size

The second microevolutionary process with direct ecological effects is inbreeding. Inbreeding may occur at several levels within a population. Many plants and lower animals are capable of a most extreme form of inbreeding, self-fertilisation. Self-fertilisation may occur under conditions in which mating with other individuals is not possible; for example, when population density is extremely low. A more general

form of inbreeding occurs when matings occur between related individuals. Finally, genetic drift can be considered to be a form of inbreeding. Genetic drift is the random change in gene frequencies that occurs because each generation represents a limited statistical sample of the genetic diversity present in the preceding generation. As a result of genetic drift, a population's gene pool will tend to represent a decreasing portion of the original founders. This effect is most severe in small populations, in which the limited statistical sample represented by each generation is subject to large sampling errors. As genetic diversity is lost from a small population, the effect becomes the same as if individuals were mating between close relatives. In sufficiently large populations, genetic variation generated by mutation is sufficient to balance the loss of diversity from genetic drift.

A general consequence of all forms of inbreeding is an increase in the proportion of homozygous loci among inbred progeny. This increase in homozygosity can in turn cause a reduction in fitness, referred to as inbreeding depression. There are at least two genetic mechanisms that can explain inbreeding depression (reviewed by Charlesworth & Charlesworth, 1987). One is an increase in the proportion of genetic loci that are homozygous for rare, recessive alleles with deleterious effects. These alleles are not eliminated from large populations because they generally occur in heterozygous combinations with other alleles, which thus shield them from selection. If a population suddenly decreases in size, or if mating occurs between related individuals, these alleles will more frequently combine as homozygotes that express their deleterious effects. The other genetic mechanism that can explain inbreeding depression is a decrease in the proportion of genetic loci that are heterozygous for pairs of alleles that confer greater fitness as heterozygotes than either would as a homozygote. Sickle cell anaemia is a well-known example of heterozygote superiority. The sickle cell allele of the human haemoglobin locus confers resistance to malaria as a heterozygote, but severe anaemia as a homozygote. While the difference between these two mechanisms of inbreeding depression may appear subtle, they are quite different with respect to the potential for a population to resist or recover from inbreeding depression. If inbreeding occurs gradually, recessive deleterious alleles can be purged from a population by selection. Elimination of these deleterious alleles will both reduce the severity of inbreeding depression as well as make the population somewhat resistant to further inbreeding depression. However, if loss of heterozygosity is responsible for inbreeding depression,



gradual inbreeding will not prevent the loss of alleles. Once allelic diversity is lost, it can only be restored by immigration or mutation.

One of the most common criticisms of the 50/500 rule advocated by Franklin (1980) and Soulé (1980) is that it must be applied to the genetically effective size of a population (denoted  $N_e$ ), which determines the rate of genetic drift, rather than the census size, or total number of individuals ( $N$ ). Only breeding individuals contribute to  $N_e$ , and if a few individuals are much more successful at breeding than others,  $N_e$  will be closer to their number. Thus in general,  $N_e$  tends to be smaller than  $N$ . For terrestrial vertebrates with limited fecundity,  $N_e$  and  $N$  are usually at least of the same order of magnitude, and may be nearly equal (e.g. Nunney & Elam, 1994). However, in highly fecund species, including many plants and marine organisms,  $N_e$  may be orders of magnitude lower than  $N$  (e.g. Orive, 1993).

The best way to estimate  $N_e$ , and thus the rate at which genetic variation is lost, is from detailed pedigree information (e.g. Wright, 1965). However, such information is generally only available for captive populations. An alternative approach is to observe some effect of genetic drift, and derive a value of  $N_e$  consistent with that observation. This approach is complicated by the fact that there are several distinct manifestations of genetic drift, and each corresponds to a different definition of  $N_e$  (Ewens, 1982).

The variance effective size of a population is based on the variance in allele frequencies over time that is caused by genetic drift. Thus by measuring fluctuations in allele frequencies over time, and assuming they are caused by drift, it is possible to estimate variance effective population size for the period of observation. Such data must be analysed and interpreted carefully. One approach is described by Waples (1989). Hedgecock *et al.* (1992) have applied this method to populations of several marine species, including American oysters. The results are quite startling. Estimates of  $N_e$  for natural populations of American oysters in the upper Chesapeake Bay were as low as 5–50. Taken at face value, this implies that a very large and geographically extensive population is sustained by relatively few individuals. The potential importance of this finding is apparent by asking the question: what if these individuals had been removed from the population; would others have taken their place, or would the population have declined?

Another approach to estimating  $N_e$  is based on the expected relationship between the amount of genetic variation in a population, and the product of effective population size and mutation rate:  $N_e$  (for a review,

see Neigel, 1996). Using known mutation rates for mtDNA, it is possible to estimate  $N_e$  from a sample of mtDNA sequences taken from a population. Because this approach is based on levels of genetic variation that have developed over evolutionary time, the parameter estimated is sometimes referred to as 'evolutionary effective population size', although it may also be considered an estimate of inbreeding effective population size. Estimates of  $N_e$  based on mtDNA for American eels, *Anguilla rostrata*, and hardhead catfish, *Arius felis*, are two or three orders of magnitude lower than estimates of the current breeding size of their respective populations (Avisé *et al.*, 1988). One possible explanation for this discrepancy is that populations of these species have only recently reached their present sizes, and thus estimates of  $N_e$  reflect a history of smaller populations. However, another possibility is that these populations are sustained by the progeny of relatively few individuals.

Whether it is luck or genetic superiority that limits reproductive success to a small proportion of a population, very small effective population sizes will lead to a loss of genetic variation. In large populations, the loss of genetic variation from genetic drift is compensated for by mutation. However, in small populations, mutations occur too infrequently to replenish variation, and most genetic variation will be lost within  $4N_e$  generations. The detrimental effects of reduced genetic variation, inbreeding depression and loss of adaptive potential, are probably not serious for populations with effective sizes of several thousand (Lande, 1988). However, estimates of  $N_e$  for marine species suggest that corresponding total numbers of individuals must be much larger, perhaps by several orders of magnitude. Thus if the geographical range of a once widespread marine species becomes restricted to a few reserves or protected habitats, a rapid loss of genetic diversity may result.

A major question in conservation biology is: how much genetic diversity can a species lose, without risking extinction? In game populations that will be carefully managed in parks or zoos, slight inbreeding depression or loss of adaptive potential may be offset by the elimination of other threats, such as drought or predation (Simberloff, 1988). However, it is unlikely that many marine species, with their complex life histories and exacting requirements, will be managed in captivity. Can marine populations that are compromised by loss of genetic variation be sustained under natural conditions? If recent interpretations of allozyme studies are taken at face value, the potential for adaptation that is provided by a genetically diverse pool of planktonic larvae may be indispensable for survival.

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