



Note

A genetic dimension to deep-sea biodiversity

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Abstract

Our knowledge of deep-sea biodiversity is based almost entirely on morphological distinctions at the species level. Here, we use haplotype variations in the mitochondrial 16S ribosomal gene to assess biodiversity at the genome level in four deep-sea molluscan morphospecies. Genetic divergence levels among populations of the morphospecies fall within the range of interspecific divergence found in coastal marine and aquatic molluscan genera. Results indicate a rich population structure at the genetic level in deep-sea mollusks, and suggest the possibility that some seemingly coherent morphospecies are composed of cryptic species. © 1999 Elsevier Science Ltd. All rights reserved.

The discovery of high species diversity in the deep-sea benthos by Hessler and Sanders (1967) is perhaps the most startling biogeographic revelation of modern times. It is remarkable to consider that as recently as the middle 1800s, long after the great European voyages of exploration, Earth's largest natural environment was thought to be devoid of life. For nearly a century after the British Challenger Expedition (1872–1876) conclusively demonstrated the existence of life throughout the World Ocean, the great depths were still viewed as a bleak refugium for a sparse assemblage of archaic species. Even the names given to major deep-sea regions, abyssal and hadal, evoke an alien netherworld.

During the last three decades of intense research, these earlier perceptions have been reversed completely. Deep-sea biodiversity is now recognized to be surprisingly rich at both landscape and community levels (Rex et al., 1997). Vast areas of soft-sediment environment are separated by geologically complex and tectonically active regions that harbor a wide variety of novel reducing systems (hydrothermal

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vents and cold seeps), as well as distinctive trench and seamount habitats (Van Dover, 1990). Species diversity varies widely within and among habitats and shows strong variation with depth and latitude (Rex, 1981; Etter and Grassle, 1992; Rex et al., 1993). Precision sampling techniques have revealed diversities averaging 100 species per 0.09 m² at mid-bathyal depths in the temperate North American Basin (Grassle and Maciolek, 1992). While projections of these estimates of diversity to global scales remain controversial (May, 1992; Briggs, 1994), this level of local species coexistence is impressive for marine communities; and it is tremendously higher than previously imagined for the deep sea.

Our understanding of deep-sea species diversity has been based almost exclusively on the morphology of organisms. Very little is known about deep-sea biodiversity at the genetic level, particularly for the small macrobenthos that are the primary constituents of diversity at the community level (Gage and Tyler, 1991). New advances in our ability to sequence DNA from preserved deep-sea material have made it possible, for the first time, to examine genetic population structure on small and large spatial scales (France and Kocher, 1996; Chase et al., 1998a, b). One interesting outcome of this population genetic research is that species diversity may be even higher than estimated by using traditional phenotypic criteria. Here we show that some morphologically coherent populations appear to be composed of genetically distinct populations that may represent cryptic species.

Fig. 1 shows the genetic divergence of haplotypes (distinct DNA sequences) of the mitochondrial 16S ribosomal gene within and among local populations of four deep-sea mollusks, a snail *Frigidoalvania brychia* (Verrill, 1884) and three bivalves *Nuculoma similis* (Rhind and Allen, 1992), *Deminucula atacellana* (Schenck, 1939) and *Malletia abyssorum* (Verrill and Bush, 1898). Sequencing and analytical methods are presented in Chase et al. (1998a, b). All four taxa are well known systematically and are considered to be single species on morphological grounds (Rex et al., 1988; Rhind and Allen, 1992; Allen and Sanders, 1996). They are compared to the divergence among species of coastal marine and aquatic genera of mollusks. The ranges of haplotype divergence found in populations of deep-sea morphospecies overlap the ranges of divergence among well established species. The averages for the shallow-water genera are based on all species within the genus. This is a highly conservative comparison because the shallow-water averages include congeners that are not sister taxa, which has the effect of inflating the mean.

In *F. brychia*, the mean haplotype divergence falls above the mean for whole genera of other gastropods. This is especially remarkable because *F. brychia* populations were collected from a narrow depth range (500–1100 m) separated by only tens of kilometers (Rex et al., 1988). Even populations within single samples covering a kilometer show distinct clades. Populations of *N. similis*, *D. atacellana* and *M. abyssorum* were collected from the western North Atlantic south of New England from depths of 500–2100, 1100–3800 and 2800–5000 m, respectively, on spatial scales of tens to hundreds of kilometers. None of the populations are separated by major topographic features or hydrodynamic regimes. The four putative species from the deep sea (Fig. 1) contain haplotypes that are as genetically different as those of separate species in other molluscan taxa.

Cryptic Species ?

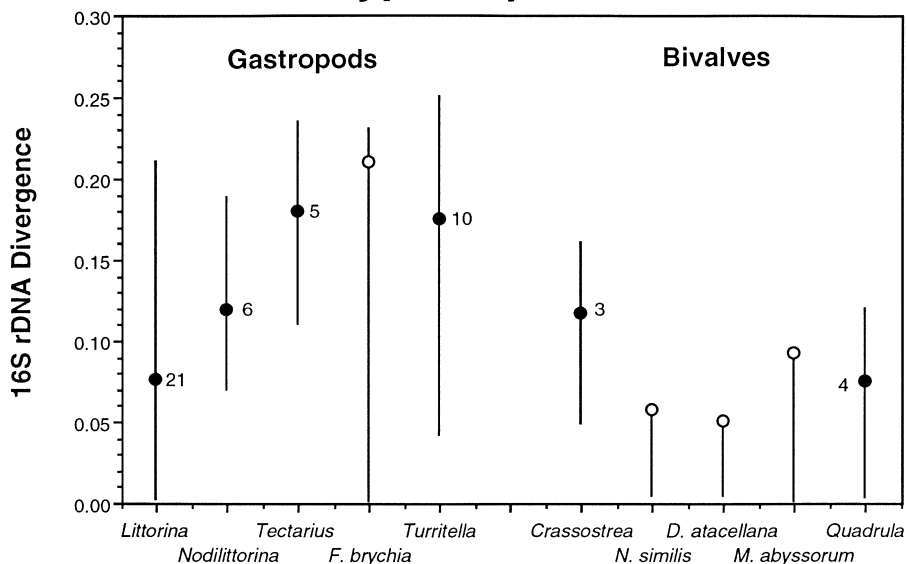


Fig. 1. Average levels of sequence divergence (pairwise distances) in the 16S rDNA gene (196 bp) among aquatic and shallow-marine congeneric species compared to deep-sea species collected from the western North Atlantic at depths ranging from 500–5000 m. Open and solid circles represent deep-sea and shallow-water species, respectively. The bars for the shallow-water genera represent the ranges in divergence among well-studied species, both morphologically and genetically, and are based on data from ÓFoighil et al. (1995), Reid et al. (1996) and Lydeard et al. (1996). Shallow-water representatives include the gastropod genera *Littorina*, *Nodilittorina*, *Tectarius* (periwinkles) and *Turritella*; and the bivalve genera *Crassostrea* (oysters) and *Quadrula* (freshwater mussels). The circles indicate mean divergence. The number beside each mean indicates the number of congeneric species included in the average. The circles for deep-sea species (*Frigidoalvania brychia*, *Nuculoma similis*, *Deminucula ataccellana*, *Malletia abyssorum*) are the average divergences among haplotypes from different clades. The bars for the deep-sea species indicate levels of divergence among all haplotypes. The deep-sea species were collected with an epibenthic sled (Hessler and Sanders, 1967) or box corer (Hessler and Jumars, 1974). *Frigidoalvania brychia* populations are upper bathyal (457–1102 m) from Woods Hole Benthic Stations 96, 105, 207 and 87 (Rex et al., 1988), and 346 (39°54.1'N, 70°10.7'W); *Nuculoma similis* populations are upper to mid bathyal (530–2180 m) from Woods Hole Benthic Stations 105, 207, 128 and 73 (Allen and Sanders, 1996) and Atlantic Continental Slope and Rise Stations N12, N2 and N8 (Maciolek et al., 1987); *Deminucula ataccellana* populations are mid to lower bathyal (1102–3834 m) from Woods Hole Benthic Stations 87, 73, 103, 115, 62, 340, 77, and 85 (Rhind and Allen, 1992; Allen and Sanders, 1996) and 209 (39°46.8'N, 70°50.7'W); and *Malletia abyssorum* populations are lower bathyal to abyssal (2864–4870 m) from Woods Hole Benthic Stations 72, 77, 85, 84, 80 and 123 (Allen and Sanders, 1996). The material was fixed in formalin and then preserved in alcohol (see Chase et al., 1998 a, b for details of DNA sequencing procedures).

Cryptic species are widespread in coastal marine taxa (Knowlton, 1993) and are also known in hydrothermal vent bivalves (Vrijenhoek et al., 1994). Their occurrence in the highly diverse soft-sediment community, especially on these relatively small spatial scales, adds an entirely new genetic dimension to our understanding of

deep-sea biodiversity and has important implications for understanding the structure and function of this ecosystem. It raises the possibility that estimates of species diversity on local scales could be revised significantly upward. The central problem in deep-sea ecology, since the pioneering work of Hessler and Sanders (1967), has been to explain how so many ecologically similar species could coexist in such a seemingly uniform habitat (Grassle and Maciolek, 1992; Rex et al., 1997). If cryptic species prove to be common elements of deep-sea communities, this higher level of coexistence presents an even more formidable challenge to basic ecological theory.

So little is known about genetic variability within deep-sea species, particularly at the DNA level, that cryptic taxa might not be the only plausible interpretation for the patterns of intraspecific genetic variation that we report here. For example, unexpectedly high levels of cladistic diversity might be explained, in part, by the retention of ancestral polymorphisms within morphotypes, radical differences in the rate of sequence evolution within and between species, or periods of episodic selection on mtDNA haplotypes marking maternal lineages (Rand et al., 1994; Stewart et al., 1996). Whatever the mechanisms are that allow or generate this variability, there exists considerable and previously unrecognized genetic diversity on small spatial scales.

The ability to assess directly the genetic structure of populations will make it possible to study the evolutionary origin of the deep-sea fauna. The very basic problems of how or where speciation and adaptive radiation have taken place in this immense environment, and how these historical processes may have shaped geographic patterns of species diversity remain virtually unstudied. The most essential evidence required to understand these phenomena is just beginning to emerge. The high genetic biodiversity and pronounced population structure on small spatial scales (Fig. 1) make it seem likely that, in addition to ecological causes, dynamic evolutionary divergence may help explain the extraordinarily high diversity found in some deep-sea soft-sediment communities.

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