Allozymes and morphometric characters of three species of *Mytilus* in the Northern and Southern Hemispheres

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Abstract. Many authors have considered the common mussels in temperate waters of the Northern and Southern Hemispheres to be a single cosmopolitan species, *Mytilus edulis* Linnaeus, 1758. Others have divided these mussels into several subspecies or species. Samples of mussels were collected from 36 locations in the Northern Hemisphere and nine locations in the Southern Hemisphere. Electrophoretic evidence from eight loci indicates that the Northern Hemisphere samples consist of three electrophoretically distinguishable species: *M. edulis* from eastern North America and western Europe; *M. galloprovincialis* Lamarck, 1819 from the Mediterranean Sea, western Europe, California, and eastern Asia; and *M. trossulus* Gould, 1850 from the Baltic Sea, eastern Canada, western North America and the Pacific coast of Siberia. Mussels from Chile, Argentina, the Falkland Islands and the Kerguelen Islands contain alleles characteristic of all three Northern Hemisphere species, but because they are most similar to *M. edulis* from the Northern Hemisphere, we suggest that they tentatively be included in *M. edulis*. These South American samples are morphologically intermediate between Northern Hemisphere *M. edulis* and *M. trossulus*. Mussels from Australia and New Zealand are similar in allele frequency and morphometric characters to *M. galloprovincialis* from the Northern Hemisphere. Fossil *Mytilus* sp. are present in Australia, New Zealand and South America, which suggests that the Southern Hemisphere populations may be native, rather than introduced by humans. Morphometric characters were measured on samples which the allozyme data indicated contained a single species.Canonical variates analysis of the morphometric characters yields functions which distinguish among our samples of the species in the Northern Hemisphere.

Introduction

Marine mussels in the genus *Mytilus* are present at higher latitudes in all oceans and major seas of the world. This widespread distribution, combined with the effects of local environments on shell shape (Seed 1968), has produced an exceedingly confusing taxonomy for species within the genus. Historically, these species have been given many different names; the common, smooth-shelled mussels have been a particular source of taxonomic confusion. Their taxonomy has been greatly hampered by the paucity of reliable morphological characters; because of environmental influences, it has not been clear whether morphological differences between different locations represent important measures of taxonomic differentiation.

Lamy (1936) comprehensively reviewed the tangled taxonomy and recognized as distinct species *Mytilus edulis* Linnaeus, 1758, *M. galloprovincialis* Lamarck, 1819 from the Mediterranean Sea, *M. trossulus* Gould, 1850 from the Pacific coast of North America, *M. chilenensis* Hupe, 1854 from Chile, *M. platenis* Orbigny, 1846 from Argentina, and *M. planulatus* Lamarck, 1819 from Australia. He described *M. desolationis* from the Kerguelen Islands. Soot-Ryen (1955) considered most of these taxa to be subspecies of *M. edulis*. Powell (1958) described *M. aoteanus* from New Zealand; Fleming (1959) reduced it to *M. edulis aoteanus*. Scarlato and Starobogatov (1979) described two subspecies of *M. edulis* from the Pacific coast of Asia, *M. edulis kussakini* and *M. edulis zhurnanskii*.

*Mytilus californianus* Conrad, 1837 is easily identified by the radiating ribs on the shell (Soot-Ryen 1955); *M. coruscus* Gould, 1861 has a thick shell with small crenulations on the ventral margin near the apex (Kira 1962). Vermeij (1989) noted that the ribs of *M. californianus* are much less prominent in Aleutian Islands specimens than in those further south, and he suggested that *M. californianus* and *M. coruscus* might be a single species with geographic variation in the prominence of the ribs. However, the large DNA sequence divergence between these taxa...
suggested that they are different species (Milyutina and Petrov 1989). Because these mussels are easily distinguished from the *M. edulis* species group, they will not be considered further in this paper.

Recently, allozyme characters have been used to clarify the taxonomy of the *Mytilus edulis* species group in the Northern Hemisphere, where three taxa have been identified: *M. edulis*, *M. galloprovincialis* and *M. trossulus* (Bulnheim and Gosling 1988, McDonald and Koehn 1988 and references therein, McDonald et al. 1990). Hybrids have been found at most locations where the ranges of these taxa overlap, which has led to considerable discussion of their taxonomic status (Gosling 1984, McDonald and Koehn 1988, Johannesson et al. 1990, Väinolä 1990).

In the Southern Hemisphere, allozyme characters have been studied in only a few samples of *Mytilus* spp. Levinton and Koehn (1976) compared allele frequencies in samples from Melbourne, Australia, with several locations in the Northern Hemisphere. Unfortunately the three loci they used were ultimately not very useful for distinguishing taxa. Mussels from South Africa are similar in allele frequency to *M. galloprovincialis* from the Mediterranean Sea and southwest England (Grant and Cherry 1985, Beaumont et al. 1989), and historical records suggest that *M. galloprovincialis* was introduced accidentally to South Africa from elsewhere sometime before 1972. *M. "desolationis"* from the Kerguelen Islands were compared with *M. edulis* and *M. galloprovincialis* from the Northern Hemisphere, and they were found to be more similar to *M. edulis* (Blot et al. 1988).

Here we have surveyed eight enzyme loci in mussels from 36 locations in the Northern Hemisphere and nine locations in the Southern Hemisphere. The sample locations were chosen to include areas where separate taxa of *Mytilus* have been recognized, such as Australia, New Zealand, Chile, Argentina, the Kerguelen Islands, the Pacific coast of Siberia, and the Mediterranean Sea. In addition, samples were collected from areas where previous allozyme studies have found large differences in allele frequencies at several loci, such as the Baltic Sea (Bulnheim and Gosling 1988, Varvio et al. 1988) and eastern Canada (Koehn et al. 1984). While a number of samples were collected in areas where species overlap and hybridize, such as northern California, western Europe and eastern Canada, our broad geographic survey was not designed to include the intensive small-scale sampling which is needed to determine the geographic and ecological ranges of the species and the extent of their hybridization.

While allozyme characters are the primary means of distinguishing among *Mytilus edulis*, *M. galloprovincialis* and *M. trossulus*, it would be useful to be able to identify the species using shell characters. Previous comparisons of shell characters between *M. edulis* and *M. galloprovincialis* have concentrated on sites where both species and their hybrids co-occur (Lewis and Seed 1969, Seed 1972, 1974, 1978, Verduin 1979, Pern et al. 1985, Beaumont et al. 1989). Because shell characters of mussels are influenced by the environment (Seed 1968), it would be necessary to sample mussels from a wide variety of habitats to determine whether morphometric characters can reliably discriminate among species. Such a study would also have to include extensive sampling from areas of overlap and hybridization. To determine whether such an intensive investigation would be worthwhile and to determine which characters would be most informative, we have first used allozyme characters to choose locations which contain only a single species. We then used a multivariate analysis of 18 morphometric characters to find the weighting of characters which maximizes the distances among the species.

Materials and methods

*Mytilus* spp. were collected from 1985 to 1988 at 36 locations in the Northern Hemisphere and nine locations in the Southern Hemisphere (Table 1, Fig. 1). A small piece of digestive gland was used for the initial electrophoretic analyses; the remainder of the tissue was lyophilized for use in subsequent work. All enzymes could be resolved in lyophilized samples following 2 to 3 yr of storage at 5°C, facilitating direct comparisons of allozymes from different samples.

Electrophoretic methods are given in McDonald and Koehn (1988) for peptidase-II (AAP, EC 3.4.11.-), esterase (EST, EC

![Fig. 1. Mytilus spp. Sample locations of mussels used in this study. (a) Eastern North America. (b) Europe. (c) North Pacific. (d) Southern Hemisphere. Sample location indicated by numbers corresponding to those in Table 1. Locations without numbers indicate distribution of the species based on other publications (Koehn et al. 1984, Grant and Cherry 1985, Bulnheim and Gosling 1988, Varvio et al. 1988). For distribution of species in the British Isles, see Skibinski et al. (1983). Symbols indicate the species present at each location: (O) M. edulis; (x) M. galloprovincialis; (A) M. trossulus](image-url)