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The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America

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Abstract

Most recent authors have called the bay mussels of the Pacific coast of North America *Mytilus edulis* Linnaeus, 1758. Thirteen samples of *edulis*-like mussels were collected from California, Oregon, and Alaska, USA, in 1985, 1986 and 1987. Electrophoretic evidence from eight loci indicates that these samples consist of two genetically distinct groups, neither of which is similar to *M. edulis* from the Atlantic Ocean. Mussels in southern California are very similar to *M. galloprovincialis* Lamarck, 1819 from the Mediterranean Sea; it is probable that *M. galloprovincialis* was introduced accidentally to southern California. Mussels in Oregon and Alaska are similar to those from the Baltic Sea and parts of eastern Canada; the name *M. trossulus* Gould, 1850 has priority for this taxon. In central and northern California, *M. galloprovincialis, M. trossulus* and their hybrids co-occur. Despite the presence of hybrids between *M. galloprovincialis* and *M. trossulus,* the genetic integrity which they maintain across large areas of the world warrants their recognition as two distinct species.

Introduction

Two species of mussels in the genus *Mytilus* have usually been recognized on the Pacific coast of North America. *M. californianus* Conrad, 1837 inhabits exposed coasts; it is easily distinguished by the radiating ribs on the shell (Soot-Ryen 1955), and since its status as a distinct species has never been in question, it will not be considered further here. The smooth-shelled, "*edulis*-like" mussels of the Pacific coast, which are common in bays and are also present in the intertidal area of some exposed coasts (Suchanek 1978), have gone under a variety of names historically. Gould (1850) described *M. trossulus* from Tillamook, Oregon, USA, distinguishing it from the Atlantic *M. edulis* Linnaeus, 1758 by differences in shell shape, shell color and form of the muscle scars. Gould (1851) also described *M. glomeratus,* based on mussels found on a floating stick in San Francisco Bay, USA. Carpenter (1864) considered *M. trossulus* and *M. glomeratus* to be synonyms of *M. edulis*. Clessin (1889) described *M. septentrionalis* from Banks Island, British Columbia, Canada. In his comprehensive review of the Mytilidae, Lamy (1936) treated *M. trossulus* as a separate species, while *M. glomeratus* and *M. septentrionalis* were considered varieties of *M. trossulus*. Coe (1945) described the subspecies *M. edulis diegensis* from San Diego in southern California. In the most recent comprehensive systematic review of *Mytilus,* Soot-Ryen (1955) considered *M. trossulus, M. glomeratus, M. septentrionalis* and *M. edulis diegensis* all synonyms of *M. edulis*. Scarlato and Starobogatov (1979) described *M. edulis kussakini* from the Pacific coast of the Soviet Union, suggesting that this name might also apply to mussels on the Pacific coast of North America (Scarlato and Starobogatov 1979, Scarlato 1981).

All the above investigators used only morphological characters, which are notoriously variable in mussels (Seed 1968). Recently, allozyme characters have been used to illuminate several areas of mussel taxonomy. For example, similarities at allozyme loci have indicated that the Mediterranean mussel *Mytilus galloprovincialis* Lamarck, 1819 is also present in Japan (Wilkins et al. 1983), South Africa (Grant and Cherry 1985), and the British Isles (Ahmad and Beardmore 1976). In Britain and Ireland, *M. edulis* and *M. galloprovincialis* co-occur, with the proportion of hybrids varying among locations (Skibinski et al. 1978, 1983, Skibinski 1983). Allozymes have also revealed a third form of mussel, present both in some locations in eastern Canada (Type III of Koehn et al. 1984) and in the Baltic Sea (Varvio et al. 1988).

We have surveyed eight enzyme loci in mussels from the Pacific coast of North America and compared these data with Atlantic mussels. Our results indicate that the genetically distinct form of mussel found in eastern Canada and the Baltic Sea is also present from Alaska to central California. The name *Mytilus trossulus* Gould, 1850 has priority

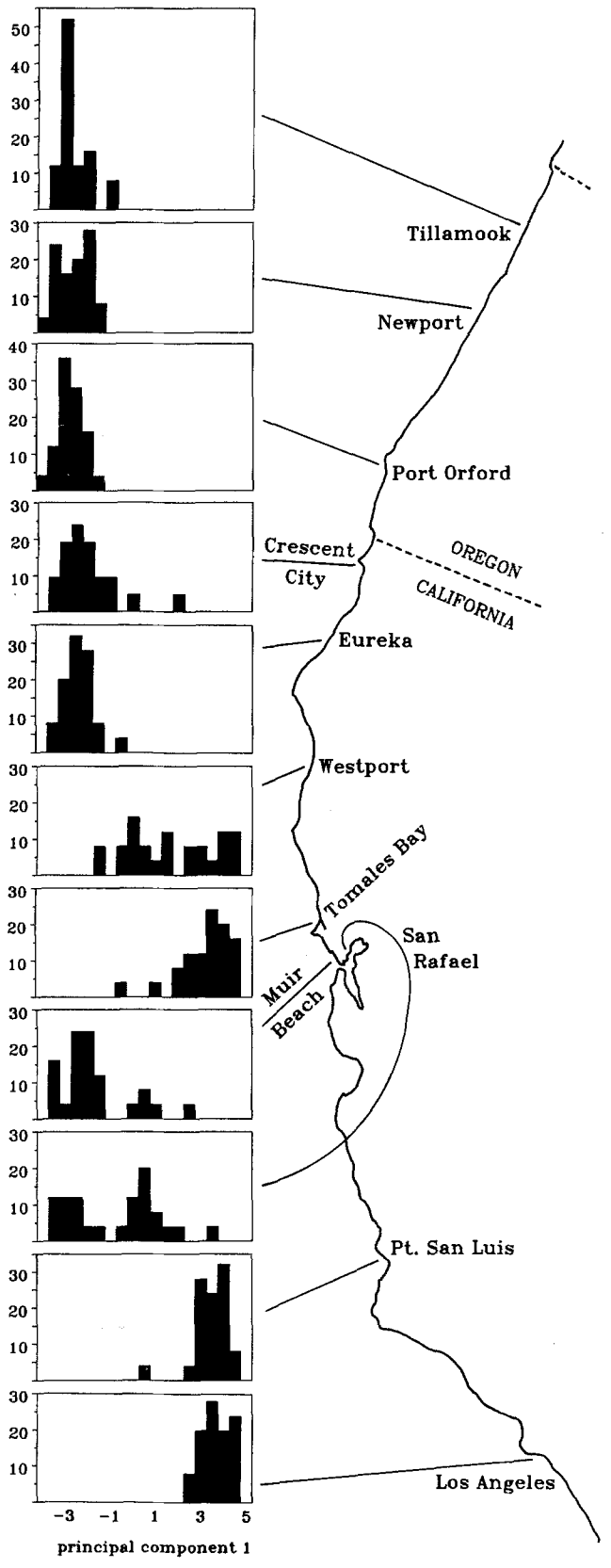

Fig. 1. *Mytilus*. Sample locations on Pacific coast of United States (San Diego, California and Petersburg, Alaska are not shown), and first principal-component values for each sample. All samples except San Diego and Petersburg were included in the analysis, and distribution of values from each sample is shown here

for this taxon. *M. trossulus* co-occurs and hybridizes with *M. galloprovincialis* in central California, but *M. galloprovincialis* is the only *edulis*-like mussel in southern California. We have not found *M. edulis* sensu strictu on the Pacific coast of North America.

Materials and methods

Mytilus spp. were collected in 1985, 1986, and 1987 at 11 locations in California and Oregon, USA (Fig. 1). Sample sizes were 25 mussels from each location except Crescent City, where only 21 mussels were collected. In addition, mussels were collected from San Diego, California and Petersburg, Alaska, USA; because complete data was not obtained on individuals from these locations, these two samples were omitted from most of the data analysis. Mussels were collected from either the intertidal zone or the underside of floating docks, and were returned live to the laboratory. A small piece of hepatopancreas 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 1 to 2 yr of storage at 5 C, facilitating direct comparisons of allozymes from different samples.

Electrophoresis and detection of peptidase-II (AAP, EC 3.4.11.–) and esterase (EST, EC 3.1.1.1) were as in Ahmad et al. (1977). Methods for aminopeptidase (AP, EC 3.4.–.–), aminopeptidase-I (LAP, EC 3.4.11.–), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), octopine dehydrogenase (ODH, EC 1.5.1.11), and phosphoglucomutase (PGM, EC 5.4.2.2) followed Koehn et al. (1976, 1984). LAP is the enzyme coded by the *"Lap-2"* locus of a number of European researchers (e.g. Skibinski et al. 1983); it is the isozyme with the greatest activity using L-leucyl-4-methoxy-β-naphthylamide as substrate. AAP is the enzyme coded by the *"Lap-1"* locus of Skibinski et al. (1983); it has greatest activity with L-alanyl-4-methoxy-β-naphthylamide as substrate. Mannose-6-phosphate isomerase (MPI, EC 5.3.1.8) was detected using the stain of Nichols and Ruddle (1973) and was run on a 28 cm-long gel with a tris-citrate buffer system (electrode buffer 150 m*M* tris, 45 m*M* citric acid, pH 7.5, gel buffer 1 : 10 dilution of electrode buffer). Minor adjustments in running buffer pH were found to be critical for good electrophoretic resolution of MPI allozymes.

Data were reduced and displayed using principal-component analysis. For each individual, each allele was treated as a separate variable, with the number of copies of the allele (0, 1 or 2) as the values of the variable. Nei's genetic distance (Nei 1972) among representative populations was reduced to a two-dimensional map using metric multidimensional scaling. The MDSCALE program of the NTSYS package (Rohlf 1985) was used with the linear regression option.

Results

The results of the principal-component analysis of *Mytilus* spp. individuals are shown in Figs. 2 and 3. Large, corre-

lated differences in allele frequency among samples at seven of the eight loci resulted in a first principal component that explained 16% of the variation among individuals. The *Mpi* locus displayed the greatest difference among the samples (Fig. 2). *Mpi-92* was the only allele present in the Los Angeles sample, but the Oregon samples contained only *Mpi-84*, *Mpi-94* and *Mpi-104*. If the rare alleles *Mpi-84* and *Mpi-104* are pooled with *Mpi-94*, individuals in the right peak of Fig. 2 mainly had the *Mpi-92/92* genotype, individuals in the left peak were *Mpi-94/94*, while most mussels with intermediate scores were *Mpi-94/92* heterozygotes. The *Aap* locus was also highly differentiated among samples (Fig. 3). Pooling the alleles for electrophoretically faster allozymes, *Aap-100*, *Aap-105*, *Aap-110* and *Aap-115*, as *Aap-f* and the alleles for slower allozymes as *Aap-s*, most individuals in the right peak of Fig. 3 were *Aap-f/f*, individuals in the left peak were *Aap-s/s*, and intermediate mussels were *Aap-f/s* heterozygotes (Fig. 3).

The first principal component summarized variation in common alleles at seven of the eight loci. *Mpi-92* had the greatest correlation with the first principal component ($r = 0.95$), and at least one allele at each locus except *Est* had r with absolute value greater than 0.59. Higher components did not reveal any obvious patterns. The second principal component, which explained 5% of the variation, was determined largely by the presence or absence of the rare alleles *Est-80*, *Est-95*, *Gpi-107* and *Pgm-86*.

The variation among individuals reflected a geographic pattern (Fig. 1). Mussels from Oregon and northern California constituted the left peak, while southern California mussels constituted mainly the right peak. Most of the mussels with intermediate principal-component scores were from central California. Differences among the central California samples were not associated with any obvious environmental variable. Allele frequencies from San Diego, California, are very similar to those from Los Angeles, and allele frequencies from Petersburg, Alaska, are similar to those from Oregon (Table 1). No individuals from the San Diego and Petersburg samples were electrophoresed for all eight enzymes, and thus they were not included in the principal-component analysis.

A series of representative samples (Table 1) was selected to compare the Oregon and southern California forms with the recognized Atlantic species *Mytilus edulis* and *M. galloprovincialis*, and with the Type III mussels of Koehn et al. (1984). The Los Angeles and Tillamook samples were used to represent southern California and Oregon, respectively. Allele frequencies at Shinnecock, New York, are representative of *M. edulis* from both sides of the North Atlantic (Varvio et al. 1988). The sample from Venice, Italy, represents *M. galloprovincialis* from the Mediterranean. *Mytilus* from the Baltic Sea, at Tvarminne, Finland, are similar to the Type III mussels of Koehn et al. (1984) from eastern Canada (Varvio et al. 1988).

Nei's genetic distance (Nei 1972) was computed for each pair of samples. The distances are not comparable with those found among other groups of organisms, because we did not use a random sample of loci, but instead used loci

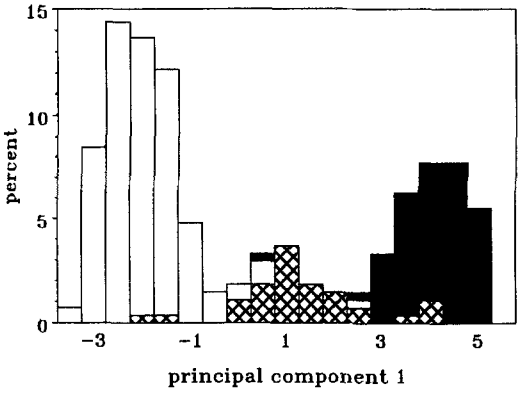

Fig. 2. *Mytilus*. Distribution of first principal-component values of *Mpi* genotypes in the 11 samples shown in Fig. 1, combined. For this figure only, *Mpi-84* and *Mpi-104* are pooled with *Mpi-94*. Filled bars represent individuals with *Mpi-92/92* genotype, crosshatched bars individuals with *Mpi-94/92* genotype, and open bars individuals with *Mpi-94/94* genotype

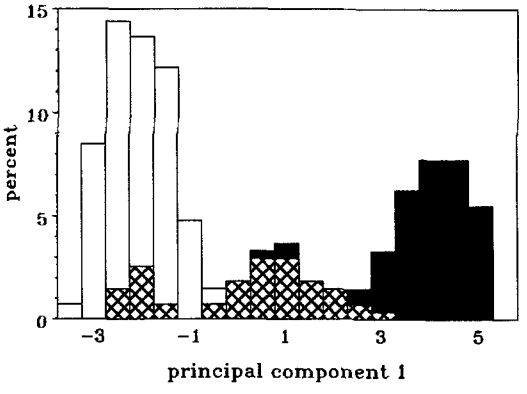

Fig. 3. *Mytilus*. Distribution of first principal-component values of *Aap* genotypes in 11 samples shown in Fig. 1, combined. Filled bars represent *Aap-f/f*, crosshatched bars *Aap-f/s*, and open bars *Aap-s/s*. *Aap-f* includes *Aap-100*, *Aap-105*, *Aap-110* and *Aap-115*, and *Aap-s* includes the remaining four alleles

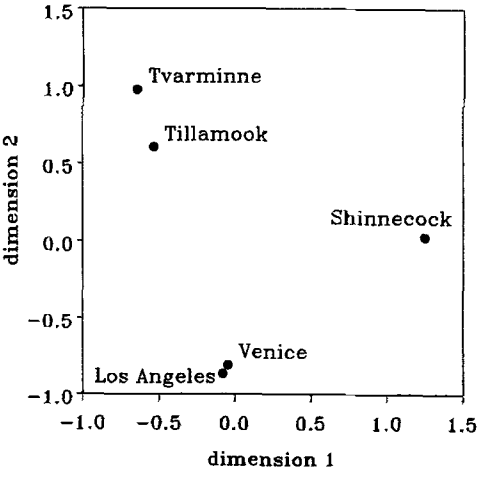

Fig. 4. *Mytilus*. Results of multidimensional scaling of Nei's genetic distance among samples listed in Table 1

Table 1. *Mytilus*. Allele percentages in representative samples. Enzymes coded by these loci are listed in "Materials and methods". The Shinnecock, New York, sample represents *M. edulis* (*Me*). *M. galloprovincialis* (*Mg*) is represented by samples from Venice, Italy, and Los Angeles, California. *M. trossulus* (*Mt*) is represented by samples from Tillamook, Oregon and Tvarminne, Finland. Sample sizes are 25 individuals, except for the *Lap* locus from Shinnecock, which includes 24 individuals. Allele frequencies for *M. galloprovincialis* from San Diego, California, and *M. trossulus* from Petersburg, Alaska, are also listed. Sample sizes for these two sites range from 23 to 64, except that the *Aap* locus from Petersburg includes only 8 individuals

	Aap									*Est*					*Ap*									*Lap*				
	80	*85*	*90*	*95*	*100*	*105*	*110*	*115*	*120*	*80*	*90*	*95*	*100*	*110*	*90*	*95*	*100*	*103*	*105*	*108*	*117*	*120*	*125*	*92*	*94*	*96*	*98*	*100*
Shinnecock (*Me*)	0	0	4	8	84	4	0	0	0	2	2	0	92	4	16	6	38	0	40	0	0	0	0	0	44	19	35	2
Venice (*Mg*)	0	0	0	2	4	10	26	52	6	0	100	0	0	0	0	0	18	2	40	22	10	4	4	0	0	46	42	12
Los Angeles (*Mg*)	0	0	0	0	4	4	52	40	0	4	96	0	0	0	0	0	22	2	36	18	6	12	4	0	0	62	36	2
San Diego (*Mg*)	–	–	–	–	–	–	–	–	–	0	100	0	0	0	0	0	22	1	38	21	12	5	0	0	4	69	23	4
Tillamook (*Mt*)	2	6	36	48	6	0	2	0	0	4	90	6	0	0	2	8	62	0	22	4	2	0	0	6	50	28	12	4
Tvarminne (*Mt*)	0	0	8	92	0	0	0	0	0	0	78	22	0	0	10	0	84	0	6	0	0	0	0	0	20	16	2	62
Petersburg (*Mt*)	0	31	6	63	0	0	0	0	0	2	96	0	1	2	1	21	54	0	22	2	0	0	0	8	51	34	6	1

	Gpi									*Odh*					*Mpi*								*Pgm*						
	86	*89*	*93*	*96*	*98*	*100*	*102*	*105*	*107*	*80*	*90*	*98*	*100*	*110*	*84*	*86*	*90*	*92*	*94*	*100*	*104*	*110*	*86*	*89*	*93*	*100*	*106*	*111*	*114*
Shinnecock (*Me*)	0	4	2	12	0	54	4	0	24	0	4	0	84	12	0	0	10	0	0	88	0	2	0	4	14	82	0	0	0
Venice (*Mg*)	0	0	0	0	0	92	0	6	2	0	6	0	34	60	0	0	0	100	0	0	0	0	6	0	14	50	28	2	0
Los Angeles (*Mg*)	0	0	0	0	0	86	0	10	4	0	6	0	22	72	0	0	0	100	0	0	0	0	2	6	16	44	24	8	0
San Diego (*Mg*)	0	0	0	1	0	92	0	6	0	0	6	0	28	65	0	0	0	100	0	0	0	0	0	5	11	54	24	4	2
Tillamook (*Mt*)	0	6	24	0	56	2	10	2	0	2	10	26	50	12	6	0	0	0	92	0	2	0	0	0	0	10	32	52	6
Tvarminne (*Mt*)	0	0	4	0	94	0	2	0	0	0	4	0	88	8	0	10	0	0	90	0	0	0	0	0	0	4	2	86	8
Petersburg (*Mt*)	5	0	19	0	71	6	0	0	0	0	11	32	47	10	4	0	0	0	95	0	2	0	0	0	3	12	36	39	10

known to be useful in discriminating *Mytilus* taxa. The set of pairwise distances was reduced to a two-dimensional map using metric multidimensional scaling. The results (Fig. 4) summarize what is apparent from a casual inspection of the data. The southern California mussels were nearly identical to *Mytilus galloprovincialis* from the Mediterranean, while the Oregon mussels were similar to those from the Baltic, albeit with some differences in allele frequency.

Discussion

We address three questions concerning the *Mytilus* of the Pacific coast of North America: (1) How many forms of smooth-shelled, *edulis*-like mussels are present on the Pacific coast? (2) what name has priority for each form? (3) what taxonomic rank should each form have? The principal-component analysis of the allozyme data divided the individuals into three clusters. One cluster contained almost all the southern California mussels, which differed greatly in allele frequency at most loci from Oregon mussels and which were genetically indistinguishable from Mediterranean *M. galloprovincialis*. Oregon mussels mainly fell into a second cluster on the principal-component analysis; they resembled Baltic Sea mussels, and therefore also resembled the Type III mussels of Koehn et al. (1984) from eastern Canada (Varvio et al. 1988). The middle cluster consisted largely of individuals that were heterozygous for alleles that distinguish southern California mussels from Oregon mussels. Hence, there are two genetically distinct groups in western North America, with central and northern California containing a complex mixture of "pure" Oregon and "pure" southern California forms, with their hybrids. The situation is thus similar to that in Europe, where pure *M. edulis* is present on the Atlantic coast of Scandinavia (Varvio et al. 1988), pure *M. galloprovincialis* is present in the Mediterranean, but in Britain and Ireland both taxa occur, with varying proportions of mixing and hybridization (Skibinski et al. 1978, 1983, Skibinski 1983).

The mussels from southern California are similar in allele frequencies to *Mytilus galloprovincialis* from the Mediterranean, a species that apparently has been introduced to several geographically widespread areas with relatively warm waters. In Japan, mussels biochemically and morphologically similar to *M. galloprovincialis* are now present. Mussels were apparently absent from Honshu before the early 1930's, and it thus seems likely that *M. galloprovincialis* was introduced to Japan (Wilkins et al. 1983). *M. galloprovincialis* apparently was also introduced to South Africa sometime before 1972 (Grant and Cherry 1985) and to Hong Kong sometime before 1982 (Lee and Morton 1985). Coe (1946) noted that *"M. edulis diegensis"* was collected in San Diego, California, as early as 1907, but increased greatly in abundance in the early 1940's. Our southern California samples are nearly identical genetically with *M. galloprovincialis* from Venice (Fig. 4). The morphological similarity of southern California mussels to Mediterranean *M. galloprovincialis* has already been noted by Seed (1972). We are presently attempting to distinguish the three genetic groups of *Mytilus* using multivariate analysis of morphometric characters. Preliminary results indicate that the three genetic groups of mussels differ morphometrically, and these results also confirm the morphological similarity of southern California mussels to Mediterranean *M. galloprovincialis* (R. Seed, R. K. Koehn and J. H. McDonald unpublished data). Many marine species have been introduced to California (Carlton 1975), and it now appears that *M. galloprovincialis* can be added to that list.

Mussels electrophoretically similar to *Mytilus* from Oregon are also found in southern Alaska (Table 1), the Pacific coast of the Soviet Union (J. H. McDonald, R. K. Koehn, and A. I. Pudovkin unpublished data), parts of eastern Canada (the Type III of Koehn et al. 1984), and the Baltic Sea (Varvio et al. 1988). The genetic similarity among these mussels from widespread geographic regions, and the distinctiveness of this group of mussels from *M. edulis* and *M. galloprovincialis*, requires formal taxonomic recognition. Over 30 species, subspecies and varieties of *edulis*-like mussels have been described as new (Lamy 1936, Soot-Ryen 1955). One way to determine which of these names has priority for the Oregon mussels would be to compare the morphology of Oregon mussels with that of the type specimen of each nominate taxon. This would be impractical for several reasons: the morphological differences between *M. edulis* and *M. galloprovincialis* are slight (Seed 1972, Gosling 1984), and distinguishing the Oregon mussels is likely to be equally difficult; mussels exhibit a large amount of environmentally caused variation in morphology (Seed 1968); many of the early taxa were based on unusual individuals; and some of the type specimens are lost. Rather than compare the Oregon mussels with type specimens, we compared them with samples taken at or near the type localities of each nominate taxon. We used only allozyme characters, which yield a much clearer discrimination among *M. edulis*, *M. galloprovincialis* and the Oregon mussels than do morphological characters. This does require the assumption that the modern sample includes the taxon upon which each early name was based, which may not always be true, given the history of introductions of *Mytilus* and the vagueness of most early type localities.

Lamy (1936) lists 17 synonyms for *edulis*-like mussels described up to 1850. Eight of these species (*Mytilus edulis* Linnaeus, 1758, *M. pellucidus* Pennant, 1777, *M. vulgaris* Da Costa, 1778, *M. galloprovincialis* Lamarck, 1819, *M. abbreviatus* Lamarck, 1819, *M. hesperianus* Lamarck, 1819, *M. retusus* Lamarck, 1819, and *M. elegans* Brown, 1827) were described from Europe, outside the Baltic Sea *M. edulis* and *M. galloprovincialis* are the only *Mytilus* species now recognized from this area. [The type locality for *M. edulis* Linnaeus, 1758 is the North Atlantic. If it becomes evident that the type specimen of *M. edulis* was actually collected in the Baltic Sea and therefore represents a taxon different from most European mussels (Varvio et al. 1988), it will be necessary to apply for permission to declare a neotype. The alternative, giving a name other than *M. edulis* to northern European mussels from outside the Baltic,

would cause considerable confusion]. Four species have been described from Australia (*M. angustanus* Lamarck, 1819, *M. corneus* Lamarck, 1819, *M. planulatus* Lamarck 1819, and *M. ungularis* Lamarck, 1819) and one species from Uruguay (*M. platensis* Orbigny, 1842); samples from near the type localities of these species do not have allele frequencies resembling the mussels from Oregon (J. H. McDonald and R. K. Koehn unpublished data). *M. borealis* Lamarck, 1819, and *M. notatus* de Kay, 1843, were described from New York, and thus are probably synonyms of *M. edulis*. *M. minganensis* Mighels, 1844 was described from Mingan, Quebec, Canada. Both *M. edulis* and the Type III mussels of Koehn et al. (1984) co-occur at Mingan (J. H. McDonald and R. K. Koehn unpublished data). Unfortunately, the type specimen of *M. minganensis* was destroyed in a fire (Johnson 1949). The brief description of *M. minganensis* is inadequate to distinguish the species, and thus it seems best to consider *M. minganensis* to be a *nomen dubium*.

The type locality of *Mytilus trossulus* Gould, 1850 was "Killimook, Puget Sound, Oregon." Killimook was one of many early variant spellings of the modern-day Tillamook, Oregon (Holman, 1910). In 1850, "Oregon" included the present state of Washington, site of Puget Sound. Tillamook is not in Puget Sound; it is not clear whether Gould meant to indicate that *M. trossulus* was found in both Killimook and Puget Sound, or whether he mistakenly believed Killimook to be in Puget Sound. One of the samples in our study was collected in Tillamook Bay; it is electrophoretically typical of the other Oregon samples, and very similar to Baltic Sea mussels and to the Type III mussels (Koehn et al. 1984) from eastern Canada. Thus, the name *M. trossulus* Gould, 1850 has priority for this geographically widespread taxon.

The final question is what taxonomic rank to assign to *Mytilus edulis*, *M. galloprovincialis* and *M. trossulus*. There has been much discussion of the taxonomic ranks of *M. edulis* and *M. galloprovincialis* (reviewed in Gosling 1984). One reason why some have been reluctant to consider *M. edulis* and *M. galloprovincialis* as two distinct species has been the absence of a character, either morphological or electrophoretic, which would unequivocally assign each individual to one or the other species. We have found that *Mpi* is diagnostic in almost all allopatric populations of *M. edulis*, *M. galloprovincialis* and *M. trossulus*. A combination of the other loci with large differences in allele frequency would also discriminate the taxa quite well in allopatric populations. Preliminary results suggest that multivariate analysis of morphometric characters will also discriminate among the three taxa better than previous methods using single characters (R. Seed, R. K. Koehn and J. H. McDonald unpublished data). Where the geographical ranges of these taxa overlap, or where introductions have brought them into secondary contact, the allozyme characters often indicate that both mixing and hybridization occur.

The second reason that some have been reluctant to consider *Mytilus edulis* and *M. galloprovincialis* as distinct species is the presence of hybrids where the taxa co-occur. There is no generally accepted maximum amount of hybridization which two taxa can exhibit and still be considered separate species. Any decision in this systematic gray area is bound to be somewhat arbitrary, especially when, as with *M. edulis* and *M. galloprovincialis* in Britain, the amount of hybridization varies among locations (Skibinski et al. 1978, 1983, Skibinski 1983). Taxonomy has two goals: to aid information retrieval, which requires taxonomic stability, and to reflect evolutionary relationships, which may necessitate taxonomic revision with each new hypothesis or set of characters. For over 150 yr, most of the many physiological, biochemical, and ecological works published on *Mytilus* have recognized *M. edulis* and *M. galloprovincialis* as distinct species. To start treating *M. galloprovincialis* as a subspecies or a variety of *M. edulis*, based on occasional hybridization, would cause considerable confusion, especially if some workers accepted the change while others did not. We therefore feel that the taxonomic rank of species is appropriate for *M. edulis* and *M. galloprovincialis*, while recognizing that determining whether they are biological species will require both further research into the nature of their biological interactions and acceptance of an operational definition of biological species. The relationship of *M. trossulus* with *M. edulis* and with *M. galloprovincialis* resembles the relationship of *M. edulis* with *M. galloprovincialis*. *M. trossulus* has unique *Mpi* alleles, and nearly unique alleles at several other loci, in allopatric populations. Where the range of *M. trossulus* overlaps *M. edulis* or *M. galloprovincialis*, both mixing and hybridization occur. Because *M. trossulus* is as different from *M. edulis* and *M. galloprovincialis* as they are from each other, it should be considered a taxonomically distinct species, while again recognizing that the biological processes which maintain the differences among these three species require much further investigation.

Systematics and distribution

Only names used for mussels from the Pacific coast of North America are given here. Many papers which simply indicate that *Mytilus edulis* is present on the Pacific coast are not listed.

Mytilus galloprovincialis Lamarck, 1819

Mytilus edulis diegensis Coe, 1945 (Coe 1945, p. 28; 1946, p. 85–104).
Mytilus edulis Linnaeus, 1758 [Soot-Ryen 1955, p. 19–23, p. 26–27 (in part)].

Diagnosis. Soot-Ryen (1955) describes the morphology of Pacific coast *"Mytilus edulis,"* which includes *M. galloprovincialis* and *M. trossulus*. At present the three *edulis*-like mussels can only be distinguished reliably using allozyme characters. These characters are migration distances relative to known allozymes, and thus identifying an unknown sample of mussels will require comparison with mussels from a

location known to contain a single species. Relative to the common allozymes in *M. trossulus*, in *M. galloprovincialis* the common AAP allozymes migrate faster, while the common MPI allozyme migrates slower. Relative to the common allozymes in *M. edulis*, in *M. galloprovincialis* the common AAP, EST and MPI allozymes migrate slower. Relative to the common allozymes in *M. edulis*, in *M. trossulus* the common AAP, EST and MPI allozymes migrate slower, while the common PGM allozymes migrate faster. Some AP, GPI, and ODH allozymes are also nearly unique to one of the three species (Table 1).

Type locality. Mediterranean Sea, near Martigues, France.

Type specimen. Muséum National d'Histoire Naturelle, Paris.

Habitat. In bays, estuaries, and exposed coasts, attached to hard substrates from mid-tide level to several meters subtidally.

Distribution. Southern California; Japan (Wilkins et al. 1983); Hong Kong (Lee and Morton 1985); South Africa (Grant and Cherry 1985); Mediterranean Sea; Atlantic coast of Europe north to the British Isles, where *Mytilus galloprovincialis* and *M. edulis* co-occur (Ahmad and Beardmore 1976, Skibinski et al. 1978, 1983, Skibinski 1983). In central California, *M. galloprovincialis*, *M. trossulus*, and their hybrids are present. The *"M. edulis"* found in Baja California, Mexico (Soot-Ryen 1955) is probably *M. galloprovincialis*.

Remarks. The populations of *Mytilus galloprovincialis* in southern California, Japan, Hong Kong, and South Africa were apparently introduced.

Mytilus trossulus Gould, 1850

Mytilus trossulus Gould, 1850 (Gould 1850, p. 344; 1852, p. 450; 1856, pl. 41, figs. 567, 567a; 1862, p. 94; Lamy 1936, p. 107–108).
Mytilus glomeratus Gould, 1851 (Gould 1851, p. 92–93; 1862, p. 214).
Mytilus edulis Linnaeus, 1758 [Carpenter 1864, p. 643; Soot-Ryen 1955, p. 19–23, p. 26–27 (in part)].
Mytilus septentrionalis Clessin, 1889 (Clessin 1889, p. 58, pl. 8, fig. 1).
Mytilus edulis kussakini Scarlato and Starobogatov, 1979 [Scarlato and Starobogatov 1979, p. 109 (in part); Scarlato 1981, p. 245–246 (in part)].

Diagnosis. At present *Mytilus trossulus*, *M. galloprovincialis* and *M. edulis* can only be distinguished reliably using allozyme characters, as described for *M. galloprovincialis*.

Type locality. Tillamook, Oregon.

Type specimen. The type specimen apparently is lost (Johnson 1964). The description (Gould 1850) and figure (Gould 1856) clearly are of an *edulis*-like mussel; therefore, unless a second taxon of *edulis*-like mussel is found at Tillamook, it is not necessary to declare a neotype.

Habitat. In bays and estuaries, attached to hard substrates from mid-tide level to several meters subtidally. On exposed coasts, sometimes occurring with *Mytilus californianus* in the intertidal area (Suchanek 1978).

Distribution. Northern California, Oregon, southern Alaska; the Pacific coast of the Soviet Union (J. H. McDonald, R. K. Koehn and A. I. Pudovkin unpublished data); parts of eastern Canada, where *Mytilus edulis* and *M. trossulus* co-occur (Koehn et al. 1984); the Baltic Sea (Varvio et al. 1988). In central California, *M. trossulus*, *M. galloprovincialis*, and their hybrids are present. Samples from Washington and British Columbia have not been typed electrophoretically, but mussels in this region are probably also *M. trossulus*.

Remarks. The type locality for *M. glomeratus* Gould, 1851 is San Francisco, California. At present, both *M. trossulus* and *M. galloprovincialis* occur in the San Francisco area. Because it is unlikely that *M. galloprovincialis* had been introduced to California by 1851, *M. glomeratus* is probably a synonym of *M. trossulus*. The type locality for *M. septentrionalis* Clessin, 1889 is Banks Island, British Columbia. Because *M. trossulus* is found both to the north, in Petersburg, Alaska, and to the south in Oregon, it is likely that *M. septentrionalis* is a synonym of *M. trossulus*.

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