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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. chilensis* Hupe, 1854 from Chile, *M. platensis* 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 zhurmunskii*.

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

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suggests 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, Väinölä 1990).

In the Southern Hemisphere, allozyme characters have been studied in only a very 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, Ferson 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

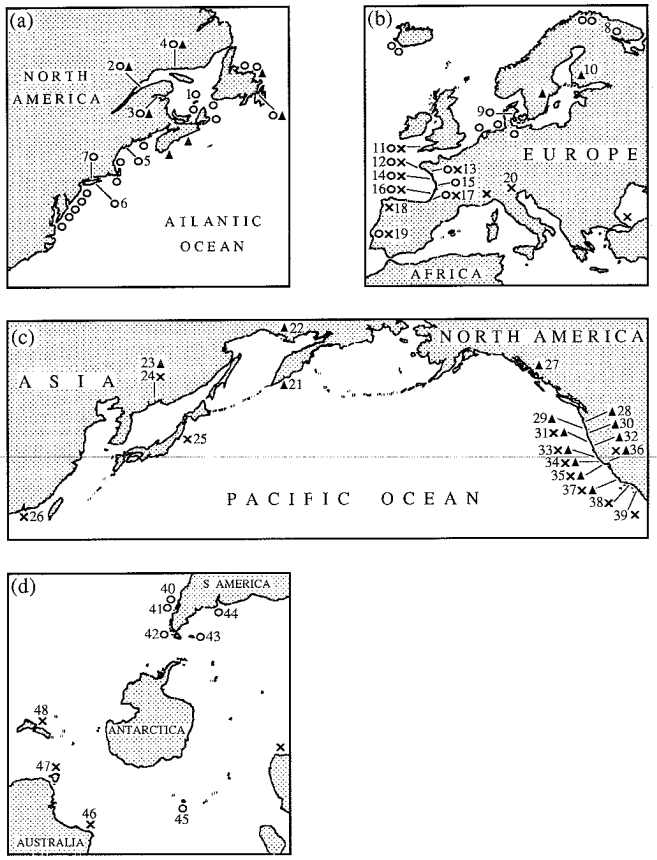

Fig. 1. *Mytilus* spp. Sample locations of mussels used in this study. (a) Eastern North America (b) Europe. (c) North Pacific. (d) Southern Hemisphere. Sample location indicated by numbers corresponding to those in Table 1. Locations without numbers indicate distribution of the species based on other 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*; (×) *M. galloprovincialis*; (▲) *M. trossulus*

Table 1. *Mytilus* spp. Sample locations and sample sizes. Location numbers correspond to those on Fig. 1. Allozyme samples sizes are individuals for which data on all eight enzyme loci were collected. Shell sample sizes are the number of shells for which morphometric characters were measured. The species present are indicated by e, g, and t for *M. edulis*, *M. galloprovincialis* and *M. trossulus*, respectively. Apparent hybrids indicate by e × g, e × t and g × t. Allozyme data used in this paper have previously been reported for the samples from Oregon and California (McDonald and Koehn 1988) and the Soviet Union (McDonald et al. 1990). Allozyme data have been reported elsewhere for mussels from Sanriku, Japan (Wilkins et al. 1983), Sawyers Landing, Oregon (McDonald and Siebenaller 1989), Petersburg, Alaska and San Diego, California (McDonald and Koehn 1988)

Location	Allozymes	Shells	Species
(1) Magdalen Islands, Quebec	24	12	e
(2) Metis, Quebec	21	0	e, e × t, t
(3) Carleton, Quebec	25	0	e, t
(4) Mingan, Quebec	24	0	e, t
(5) Portland, Maine	25	12	e
(6) Shinnecock, New York	24	12	e
(7) Stony Brook, New York	25	25	e
(8) Kandalaksha Bay, USSR	25	12	e
(9) Aarhus, Denmark	11	25	e
(10) Tvarminne, Finland	25	12	t
(11) Rock, England	25	0	e, e × g, g
(12) Ste. Anne la Palud, France	25	0	e × g, g
(13) St. Gildas-de-Rhuys, France	25	0	e, e × g, g
(14) Les Sables d'Olonne, France	25	0	e, e × g, g
(15) Soulac, France	25	0	e
(16) Arcachon, France	24	0	e, e × g, g
(17) Vieux-Boucau, France	25	0	e, e × g, g
(18) Vigo, Spain	23	0	g
(19) Parede, Portugal	25	0	e × g, g
(20) Venice, Italy	25	25	g
(21) Petropavlovsk, USSR	25	0	t
(22) Magadan, USSR	23	12	t
(23) Posjet Bay (intertidal), USSR	19	12	t
(24) Posjet Bay (subtidal), USSR	25	12	g
(25) Sanriku, Japan	0	12	g
(26) Victoria Harbor, Hong Kong	25	12	g
(27) Petersburg, Alaska	0	12	t
(28) Tillamook, Oregon	25	25	t
(29a) Newport, Oregon	25	12	t
(29b) Sawyers Landing, Oregon	0	12	t
(30) Port Orford, Oregon	25	0	t
(31) Crescent City, California	21	0	g × t, t
(32) Eureka, California	25	0	t
(33) Westport, California	25	0	g, g × t, t
(34) Tomales Bay, California	25	0	g, g × t
(35) Muir Beach, California	25	0	g, g × t, t
(36) San Rafael, California	25	0	g, g × t, t
(37) Port San Luis, California	25	0	g, g × t
(38) Los Angeles, California	25	23	g
(39) San Diego, California	0	12	g
(40) Yaldad Bay, Chile	25	12	e
(41) Chiloe, Chile	23	0	e
(42) Punta Arenas, Chile	25	0	e
(43) Falkland Islands	25	12	e
(44) Mar del Plata, Argentina	25	12	e
(45) Kerguelen Islands	22	12	e
(46) Albany, Western Australia	25	11	g
(47) Huon River Estuary, Tasmania	23	12	g
(48) Wellington, New Zealand	25	12	g

3.1.1.1), 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).

A number of authors have either had difficulty in separating allozymes of mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), or have resolved a small number of allozymes (Grant and Cherry 1985, Bulnheim and Gosling 1988, Beaumont et al. 1989, Johannesson et al. 1990). We have found that resolution of MPI allozymes is only good over a narrow range of buffer pH, and that a pH 8.0 buffer system (electrode buffer 150 m*M* tris adjusted to pH 8.0 with citric acid, gel buffer 1:10 dilution of electrode buffer) yields better resolution than the pH 7.5 buffer reported earlier (McDonald and Koehn 1988). The pH of tris buffers varies with temperature, so the best pH to use will depend on the conditions in each laboratory and will need to be determined by experimentation. These trials should include individuals known to have different, closely spaced MPI allozymes, such as *Mytilus galloprovincialis* and *M. trossulus*, since the conditions giving the sharpest bands do not always give the best separation between bands. Good resolution of MPI allozymes also requires running a long gel; we run the bromphenol blue dye marker to the end of a 28-cm long gel. Under these conditions, MPI migrates only a few centimeters from the origin.

Allozyme data were reduced and displayed using principal-component analysis, which finds the orthogonal axes which account for the greatest amount of variation in the multidimensional space. The PRINCOMP procedure of SAS was used (SAS Institute 1982). 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.

Eighteen shell characters (Fig. 2) were measured on mussels from many of the locations for which allozyme studies had indicated the presence of only a single species. Characters were measured in millimeters using either electronic digital calipers or an ocular micrometer fitted to a stereo microscope. To standardize the variables for size, each character (except number of teeth) was log-transformed (using base 10 logs) and divided by the log-transformed length. The shells used for morphometrics ranged from 23 to 80 mm in length and have been deposited in the Natural History Museum, London, accession number BM (NH) 2377.

Canonical variates analysis was used to find linear functions of morphometric variables with coefficients that maximize the distances among *Mytilus edulis*, *M. galloprovincialis* and *M. trossulus* from the Northern Hemisphere. The CANDISC procedure of SAS was used (SAS Institute 1982). The canonical variate for each individual is the sum of each morphometric variable (log-transformed and length-standardized) multiplied by its raw canonical coefficient. These functions were then applied to the samples from the Southern Hemisphere. Functions were also found for each pair of species, since all known overlap areas contain only two species.

Results

Analyses of allozyme data have been reported elsewhere for mussels from the Pacific coast of North America (McDonald and Koehn 1988) and from the Soviet Union (McDonald et al. 1990). Here we add samples from both the North Atlantic and the Southern Hemisphere. Principal component analysis of 71 alleles in 1082 mussels from the Northern and Southern Hemispheres revealed three clusters of individuals (Fig. 3a). The first principal component explained 9% and the second component 8% of the variation among individuals. Each of the remaining 69 principal components explained a relatively small portion of the variation.

In the Northern Hemisphere (Fig. 3b) mussels from Italy, Spain, Portugal, southern California and Hong

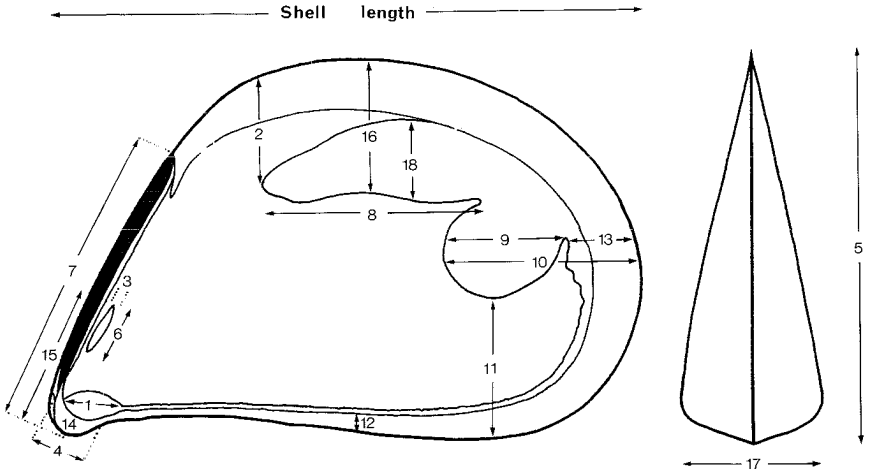

Fig. 2. *Mytilus* spp. Shell characters measured for this study. Numbers correspond to those in Table 3. (1) aam: length of anterior adductor muscle scar. (2) dpr: distance between the anterior end of posterior retractor muscle scar and dorsal shell margin. (3) war: width of anterior retractor muscle scar. (4) hp: length of hinge plate. (5) ht: shell height. (6) lar: length of anterior retractor muscle scar. (7) lig: distance between umbo and posterior end of the ligament. (8) lpr: length of posterior retractor muscle scar. (9) pad: length of posterior adductor muscle scar. (10) padp: distance between anterior edge of posterior adductor muscle scar and posterior shell margin. (11) padv: distance between ventral edge of posterior adductor muscle scar and ventral shell margin. (12) pal: distance between pallial line and ventral shell margin midway along shell. (13) ppad: distance between posterior edge of posterior adductor muscle scar and posterior shell margin. (14) teeth: number of major teeth on hinge plate, excluding any small crenulations which may appear, especially on the posterior ventral face of hinge plate. (15) ular: distance between umbo and posterior end of anterior retractor scar. (16) vpr: distance between ventral edge of posterior retractor muscle scar and dorsal shell margin. (17) wid: shell width. (18) wpr: width of posterior retractor muscle scar

Kong are included in one cluster, which represents *Mytilus galloprovincialis*. The *M. trossulus* cluster includes mussels from Oregon, the Pacific coast of Siberia, and the Baltic Sea. The *M. edulis* cluster includes mussels from Denmark, the White Sea, and the northeastern United States. Locations which were geographically intermediate between the "pure" sites contained a mixture of individuals from two species, usually with some intermediate individuals that were apparently hybrids. In our samples, *M. edulis* and *M. galloprovincialis* co-occur and hybridize in the United Kingdom and France, *M. edulis* and *M. trossulus* in eastern Canada, and *M. trossulus* and *M. galloprovincialis* in northern California.

The Southern Hemisphere mussels formed two clusters in the principal-component analysis (Fig. 3c). The mussels from South America, the Falkland Islands and the Kerguelen Islands ("South American mussels") formed one cluster. These individuals were most similar in their principal-component scores to Northern Hemisphere *Mytilus edulis*. Many individuals, however, were intermediate between Northern Hemisphere *M. edulis*, *M. galloprovincialis* and *M. trossulus*. The reason is apparent from examination of the allele frequencies: many loci of the South American mussels contain alleles that in the Northern Hemisphere are common only in *M. galloprovincialis* or *M. trossulus* (Table 2). In the Northern Hemisphere, *Mpi-92* is found only in *M. galloprovincialis*; this allele is present at most of the South American locations. The *Aap-95* and *Gpi-98* alleles, which in the Northern Hemisphere are common only in *M. trossulus*, are quite common in the South American mussels. *Odh-110*, while present in all three northern species, is most common in northern *M. galloprovincialis*; it is also the most common *Odh* allele in the South American mussels. The *Est-90* allele, which in the Northern Hemisphere is common in *M. galloprovincialis* and *M. trossulus* but rare in *M. edulis*, is the most common *Est* allele in the two samples from central Chile.

Mussels from Australia and New Zealand ("Australian mussels") formed the second Southern Hemisphere cluster, with principal-component scores similar to those for *Mytilus galloprovincialis* from the Northern Hemisphere. There are some differences in allele frequencies between the Northern Hemisphere *M. galloprovincialis* and the Australian mussels, however, most notably at the *Mpi* and *Est* loci (Table 2). The *Mpi-100* allele in the Northern Hemisphere is found only in *M. edulis*, but this allele is present at low frequency in the Huon River and Wellington samples. The *Est-100* allele in the Northern Hemisphere is common only in *M. edulis*, but it is common in the Albany and Huon River samples. There are also differences among the samples from Australia and New Zealand, in particular at the *Ap*, *Odh*, *Est*, and *Aap* loci.

Canonical variates analysis is a multivariate technique in which individuals are first divided into two or more groups using one set of variables. A second, independent set of variables is then analyzed to find linear functions of the variables with coefficients that maximize the distances between groups. We first used the allozyme characters to choose samples of mussels from Northern Hemisphere locations which contained only one species, then measured 18 morphometric characters on shells from those "pure" sites (Table 1). The canonical variates

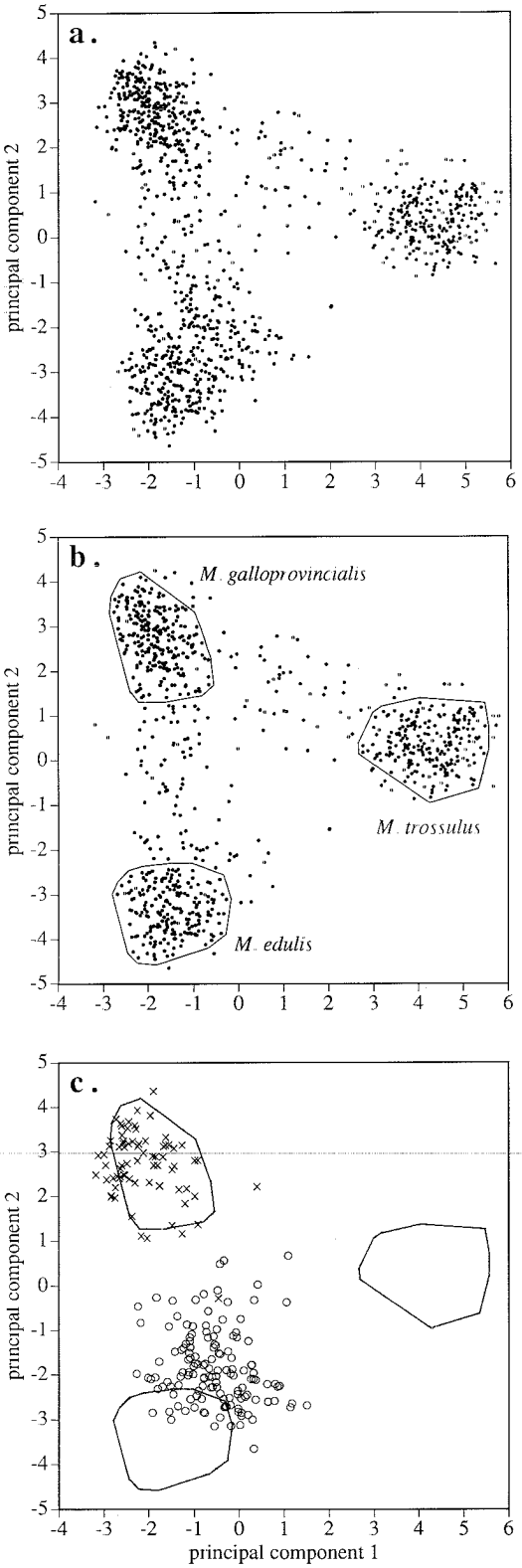

Fig. 3. *Mytilus* spp. (a) First and second principal components of allozyme data for all individuals. (b) Same as (a), except only individuals from the Northern Hemisphere shown. To aid comparison with Southern Hemisphere results, lines have been drawn subjectively around the clusters of individuals. (c) Same as (a), except only individuals from the Southern Hemisphere shown. (o) Mussels from Chile, Argentina, the Falkland Islands and the Kerguelen Islands; (×) mussels from Australia and New Zealand. Outlines of the clusters of Northern Hemisphere individuals repeated

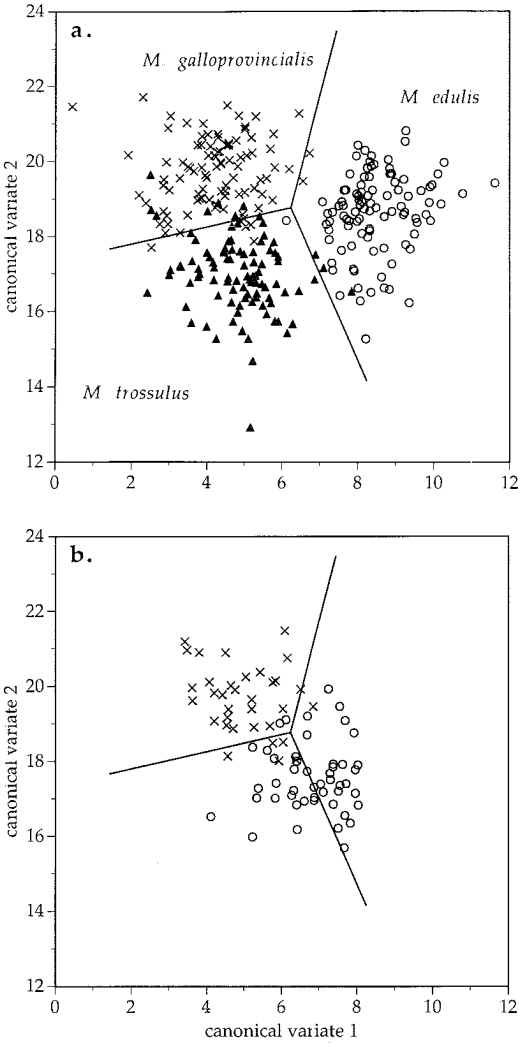

Fig. 4. *Mytilus* spp. (a) First and second canonical variates of morphometric data from individuals from the Northern Hemisphere. (o) *M. edulis*; (×) *M. galloprovincialis*; (▲) *M. torssulus*. To aid comparison with Southern Hemisphere results, perpendicular bisectors of lines connecting the centroids of the species clusters have been drawn. (b) Scores of Southern Hemisphere mussels, using the canonical functions of (a). Lines separating the Northern Hemisphere species clusters are repeated

analysis then found the coefficient for each character that maximized the distances among Northern Hemisphere *Mytilus edulis*, *M. galloprovincialis* and *M. trossulus*. The canonical variate for each individual is the sum of each morphometric variable multiplied by its raw canonical coefficient. The results indicate that there is some overlap in canonical variates, but that most individuals from our samples could be identified using the multivariate function of shell characters (Fig. 4a). In contrast, even the individual characters with the greatest differences among species (e.g. length of the anterior adductor scar and length of the hinge plate) exhibited considerable overlap when taken singly (Fig. 5). Canonical functions were also found for each pair of species, because each of the known areas of geographic overlap, where it would be

Table 2. *Mytilus* spp. Allele percentages in Southern Hemisphere samples and representative Northern Hemisphere samples. Location numbers (in parentheses) correspond to those in Table 1 and Fig. 1. Enzymes coded by these loci are listed in "Materials and methods". Sample sizes given in Table 1

Species (location)	Locus	*Aap*										*Est*					
		80	85	90	95	100	105	110	115	120	125	80	90	95	100	105	110
Southern *M. edulis*	(40)	0	2	0	34	62	2	0	0	0	0	0	30	0	70	0	0
	(41)	0	0	2	26	67	2	2	0	0	0	0	59	0	41	0	0
	(42)	0	0	2	46	44	4	4	0	0	0	0	8	0	90	0	2
	(43)	0	0	4	70	26	0	0	0	0	0	0	0	0	100	0	0
	(44)	0	0	0	52	48	0	0	0	0	0	0	0	0	100	0	0
	(45)	0	0	0	76	24	0	0	0	0	0	0	0	0	100	0	0
Southern *M. galloprovincialis*	(46)	0	0	0	2	4	4	8	64	18	0	2	74	0	24	0	0
	(47)	0	0	0	0	2	0	15	54	25	4	2	48	0	48	2	0
	(48)	0	0	0	4	16	10	36	20	8	6	0	100	0	0	0	0
Northern *M. edulis*	(6)	0	0	4	8	84	4	0	0	0	0	2	2	0	92	0	4
Northern *M. galloprovincialis*	(20)	0	0	0	2	4	10	26	52	6	0	0	100	0	0	0	0
M. trossulus	(28)	2	6	36	48	6	0	2	0	0	0	4	90	6	0	0	0

Species (location)	Locus	*Ap*								*Mpi*							
		90	95	100	105	108	117	120	125	84	90	92	94	96	100	104	110
Southern *M. edulis*	(40)	0	0	54	42	4	0	0	0	0	4	18	0	0	78	0	0
	(41)	0	0	52	33	11	4	0	0	0	4	20	0	0	76	0	0
	(42)	0	8	72	18	2	0	0	0	0	4	8	0	6	82	0	0
	(43)	0	4	70	22	4	0	0	0	0	0	0	0	0	100	0	0
	(44)	0	6	58	30	6	0	0	0	0	2	4	0	0	88	0	6
	(45)	0	0	86	12	2	0	0	0	0	0	2	0	2	96	0	0
Southern *M. galloprovincialis*	(46)	0	0	6	14	56	18	4	2	0	0	100	0	0	0	0	0
	(47)	0	0	19	23	56	2	0	0	0	0	96	0	0	4	0	0
	(48)	0	6	54	22	18	0	0	0	0	0	94	0	0	6	0	0
Northern *M. edulis*	(6)	16	6	38	40	0	0	0	0	0	10	0	0	0	88	0	2
Northern *M. galloprovincialis*	(20)	0	0	18	42	22	10	4	4	0	0	100	0	0	0	0	0
M. trossulus	(28)	2	8	62	22	4	2	0	0	6	0	0	92	0	0	2	0

Species (location)	Locus	*Gpi*										*Lap*				
		86	89	93	96	98	100	102	105	107	110	92	94	96	98	100
Southern *M. edulis*	(40)	0	0	0	0	92	6	2	0	0	0	2	14	82	2	0
	(41)	0	0	0	2	85	13	0	0	0	0	2	13	80	4	0
	(42)	0	8	2	4	64	22	0	0	0	0	0	38	62	0	0
	(43)	0	0	0	12	28	52	4	0	2	2	2	30	68	0	0
	(44)	0	10	0	16	32	42	0	0	0	0	2	26	72	0	0
	(45)	0	4	0	6	52	38	0	0	0	0	0	10	90	0	0
Southern *M. galloprovincialis*	(46)	0	2	0	0	0	98	0	0	0	0	0	2	94	4	0
	(47)	2	4	0	6	0	85	0	0	2	0	0	12	79	8	0
	(48)	0	0	0	6	2	92	0	0	0	0	2	4	74	10	10
Northern *M. edulis*	(6)	0	4	2	12	0	54	4	0	24	0	0	44	19	35	2
Northern *M. galloprovincialis*	(20)	0	0	0	0	0	92	0	6	2	0	0	0	46	42	12
M. trossulus	(28)	0	6	24	0	56	2	10	2	0	0	6	50	28	12	4

Table 2 (continued)

Species (location)	Locus	*Odh*						*Pgm*						
		80	90	98	100	110	120	86	89	93	100	106	111	114
Southern *M. edulis*	(40)	2	12	2	0	82	2	0	0	2	88	10	0	0
	(41)	0	7	0	0	93	0	0	0	0	80	20	0	0
	(42)	0	8	0	12	80	0	0	0	0	82	18	0	0
	(43)	2	0	0	60	38	0	0	0	4	54	42	0	0
	(44)	0	2	0	70	28	0	0	0	6	56	38	0	0
	(45)	0	16	0	25	59	0	0	0	0	90	10	0	0
Southern *M. galloprovincialis*	(46)	0	36	0	8	56	0	0	10	6	62	22	0	0
	(47)	2	57	7	0	35	0	0	0	29	69	2	0	0
	(48)	0	4	20	4	66	6	0	0	22	72	6	0	0
Northern *M. edulis*	(6)	0	4	0	84	12	0	0	4	14	82	0	0	0
Northern *M. galloprovincialis*	(20)	0	6	0	34	60	0	6	0	14	50	28	2	0
M. trossulus	(28)	2	10	26	50	12	0	0	0	0	10	32	52	6

especially interesting to study morphometrics, involves only two species (Fig. 6). Standardized canonical coefficients (Table 3) represent the amount that the canonical variate changes for each change of one standard deviation in the individual character, and therefore the characters with the highest standardized coefficients contribute the most to the canonical function.

When the functions from the canonical variates analysis of the Northern Hemisphere mussels were applied to the Southern Hemisphere samples, Southern Hemisphere *Mytilus edulis* were morphologically intermediate between northern *M. edulis* and *M. trossulus* (Fig. 4b). The southern and northern *M. galloprovincialis*, in contrast, were quite similar to each other.

Discussion

Recent authors have often divided the *Mytilus* spp. of the Southern Hemisphere into five taxa: *Mytilus chilensis* in Chile, *M. platensis* in Argentina, *M. desolationis* in the Kerguelen Islands, *M. planulatus* in Australia, and *M. aoteanus* in New Zealand. These taxa have been considered either full species or subspecies of *M. edulis*. Principal-component analysis of allozyme data on mussels from these areas revealed only two clusters of individuals, one consisting of mussels from South America, the Falkland Islands and the Kerguelen Islands, and the other consisting of mussels from Australia and New Zealand. This result is based on only nine samples, including samples from at or near the type localities of the five previously recognized taxa. Further samples from more locations might reveal additional groups, but based on the present set of samples only two taxa of *Mytilus* have been demonstrated in the Southern Hemisphere.

The South American mussels are electrophoretically similar to Northern Hemisphere *Mytilus edulis*, but alleles characteristic of Northern Hemisphere *M. galloprovincialis* and *M. trossulus* were also found at high frequency at some loci. Except for the rare *Mpi-96* allele, no allele was present in the South American mussels that was not also present in the Northern Hemisphere. Our results are consistent with those of Blot et al. (1988), who found that mussels from the Kerguelen Islands were more similar to northern *M. edulis* than to northern *M. galloprovincialis*. The analysis of morphometric characters places the South American mussels between Northern Hemisphere *M. edulis* and *M. trossulus*. Blot et al. (1988) concluded that *M. desolationis* from the Kerguelen Islands warranted recognition as a distinct semispecies within a *M. edulis* superspecies. The differences between South American mussels and Northern Hemisphere *M. edulis* are considerably smaller than the differences among Northern Hemisphere *M. edulis*, *M. galloprovincialis* and *M. trossulus*. We therefore feel that mussels from South America, the Falkland Islands and the Kerguelen Islands should be included tentatively in *M. edulis*. Data from additional enzyme loci, from other characters such as mitochondrial DNA, and from additional locations will be needed to determine more precisely the relationship between Northern and Southern Hemisphere *M. edulis*.

The mussels from Australia and New Zealand were quite similar in allele frequencies and shell characters to *Mytilus galloprovincialis* from the Northern Hemisphere. They were also similar in morphology. We therefore conclude that the mussels from Australia and New Zealand should be included in *M. galloprovincialis*.

One reason for the similarity between Northern and Southern Hemisphere *Mytilus* spp. could be human introduction of Northern Hemisphere mussels to the Southern Hemisphere. *M. galloprovincialis* was accidentally introduced to Japan (Wilkins et al. 1983), Hong Kong (Lee and Morton 1985), South Africa (Grant and Cherry 1985), and southern California, USA (McDonald and Koehn 1988). In each case the allele frequencies of the introduced populations are almost identical to those of *M. galloprovincialis* from the Mediterranean Sea. The absence of *Mytilus* sp. mussels from aboriginal shell mid-

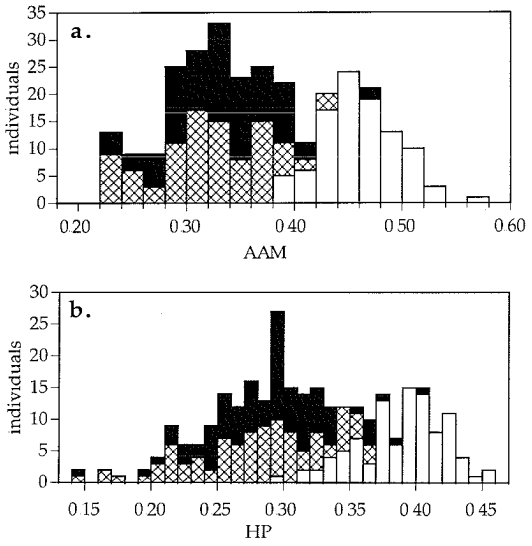

Fig. 5. *Mytilus* spp. (a) Distribution of the log-transformed, length-standardized size of anterior adductor muscle scar (AAM) in the Northern Hemisphere samples. Open bars: *M. edulis*; crosshatched bars: *M. galloprovincialis*; filled bars: *M. trossulus*. (b) Distribution of the log-transformed, length-standardized size of hinge plate (HP) in the Northern Hemisphere samples.

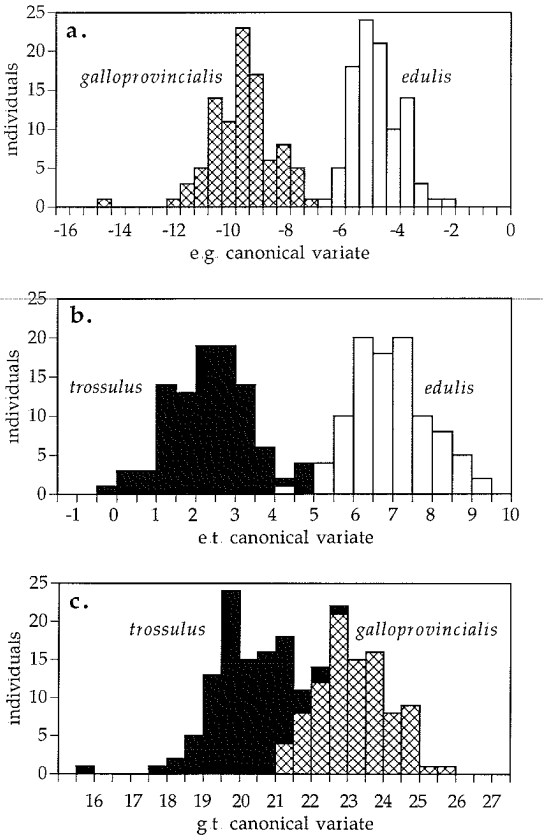

Fig. 6. *Mytilus* spp. Distributions of canonical variates for pairs of species from the Northern Hemisphere. Bar patterns as in Fig. 5. (a) *M. edulis* and *M. galloprovincialis*; (b) *M. edulis* and *M. trossulus*; (c) *M. galloprovincialis* and *M. trossulus*

Table 3. *Mytilus* spp. Canonical coefficients of the morphometric characters. Characters described in Fig. 2. In each column, the first number is the raw canonical coefficient and the number in parentheses below the standardized canonical coefficient. Characters whose standardized coefficients have a greater absolute value contribute more to the canonical function. Coefficients are given for the first and second canonical variate for the three-species analysis ("Can 1" and "Can 2"), and the two-species canonical variates for *M. edulis-M. galloprovincialis* ("Can e.g."), *M. edulis-M. trossulus* ("Can e.t."), and *M. galloprovincialis-M. trossulus* ("Can g.t.")

Character	Can 1	Can 2	Can e.g.	Can e.t.	Can g.t.
(1) aam	12.04	1.65	13.12	15.01	−3.71
	(0.94)	(0.13)	(1.08)	(1.15)	(−0.18)
(2) dpr	−0.59	−4.56	3.15	−9.31	0.68
	(−0.04)	(−0.28)	(0.19)	(−0.59)	(0.04)
(3) war	3.20	4.02	2.70	5.80	6.36
	(0.30)	(0.38)	(0.24)	(0.56)	(0.54)
(4) hp	10.60	−3.47	10.26	9.57	−3.40
	(0.69)	(−0.23)	(0.71)	(0.60)	(−0.16)
(5) ht	−1.07	34.75	−23.36	−2.90	50.53
	(−0.02)	(0.75)	(−0.44)	(−0.06)	(1.15)
(6) lar	0.44	−2.10	0.85	−2.88	2.39
	(0.03)	(−0.15)	(0.06)	(−0.21)	(0.19)
(7) lig	10.08	−9.90	14.75	−2.53	−11.18
	(0.33)	(−0.32)	(0.45)	(−0.08)	(−0.37)
(8) lpr	−4.25	−13.16	−1.29	−7.64	−12.18
	(−0.18)	(−0.57)	(−0.06)	(−0.31)	(−0.53)
(9) pad	−1.74	0.20	−0.30	5.13	−1.04
	(−0.09)	(0.01)	(−0.01)	(0.27)	(−0.05)
(10) padp	−2.13	−4.21	−1.27	−14.94	−0.03
	(−0.06)	(−0.12)	(−0.03)	(−0.48)	(0.00)
(11) padv	1.75	−2.66	−1.08	9.79	−13.71
	(0.08)	(−0.13)	(−0.05)	(0.50)	(−0.59)
(12) pal	7.35	1.03	6.84	6.87	−1.12
	(0.46)	(0.06)	(0.42)	(0.46)	(−0.06)
(13) ppad	−5.34	1.51	−2.43	−3.72	−2.36
	(−0.22)	(0.06)	(−0.10)	(−0.17)	(−0.10)
(14) teeth	0.11	−0.11	0.16	0.00	−0.10
	(0.12)	(−0.13)	(0.19)	(0.01)	(−0.10)
(15) ular	−6.75	9.37	−11.87	8.82	4.12
	(−0.34)	(0.48)	(−0.49)	(0.45)	(0.24)
(16) vpr	−4.60	1.53	2.02	5.87	−3.03
	(−0.25)	(0.08)	(0.11)	(0.31)	(−0.16)
(17) wid	3.34	7.82	−0.33	5.92	11.11
	(0.14)	(0.32)	(−0.01)	(0.23)	(0.44)
(18) wpr	−1.79	9.43	−8.57	−0.67	8.63
	(−0.14)	(0.73)	(−0.57)	(−0.05)	(0.73)

dens in South Africa, and from early museum collections in South Africa and Japan, is further evidence that present populations of *M. galloprovincialis* were introduced (Wilkins et al. 1983, Grant and Cherry 1985). In contrast, there are some differences in allele frequency between Southern Hemisphere *M. galloprovincialis* and their Northern Hemisphere conspecifics. Fossils and subfossils of *Mytilus* sp. have been found in New Zealand (Fleming 1959, Fleming and Suggate 1964), New South Wales and Victoria (Donner and Jungner 1981), South Australia (Hope et al. 1977), and Tasmania (Colhoun et al. 1982,

Kerrison and Binns 1984). This suggests that the Southern Hemisphere *M. galloprovincialis* are native rather than introduced. Similarly, *Mytilus* sp. have been found in pre-Columbian shell middens in Argentina (Johnson 1976) and Quaternary deposits in Uruguay (Sprechemann 1978), and there are substantial differences in allele frequency between southern and northern *M. edulis*. This also suggests that the South American mussels are native, rather than introduced. It is however possible, although we think it is unlikely, that the Southern Hemisphere fossils represent native *Mytilus* species that have been displaced by accidentally introduced Northern Hemisphere mussels.

Our study is an attempt to sketch the broad distribution patterns of *Mytilus* species. Like most previous geographic surveys of allozymes in *Mytilus*, we have not sampled a range of mussel habitats in each geographic area. More intensive sampling can add many important details about the distribution of these species. In the British Isles, beaches exposed to wave action are dominated by *M. galloprovincialis*, while more protected areas a short distance away are dominated by *M. edulis* (Gosling and Wilkins 1981, Skibinski et al. 1983, Skibinski and Roderick 1991). A sample from an intertidal beach at Posjet Bay, USSR, contained only *M. trossulus*, while mussels from a floating dock a few meters away were all *M. galloprovincialis* (McDonald et al. 1990).

There have been several attempts to find a single morphological character that would consistently discriminate between *Mytilus edulis* and *M. galloprovincialis* (Lewis and Seed 1969, Seed 1972, 1974, Verduin 1979, Ferson et al. 1985, Beaumont et al. 1989). These studies have found varying amounts of overlap between the species for each character, but the fact that many samples were from locations now known to include hybrids has made it uncertain whether character overlap was due to the presence of hybrids between species or variation within each species. Here, we analyzed individuals from locations for which allozyme characters indicated the presence of only a single species. Characters which have previously been considered useful for distinguishing *M. edulis* and *M. galloprovincialis*, such as length of the anterior adductor muscle scar and length of the hinge plate, contributed most to the canonical variates analysis. In these "pure" samples, there was considerable overlap between species in even the most informative of the individual characters. However, canonical variates analysis of 18 characters yielded functions which distinguished the pure samples of the species quite well. Much further research will be needed to determine whether the morphometric differences described here persist in areas of overlap and hybridization, and whether the differences are genetic, environmental, or produced by genetic-environmental interaction. This study did not include some characters which have previously been considered useful for distinguishing *M. edulis* and *M. galloprovincialis*, such as mantle color, ligamentary angle, and the position of the point of maximum shell width (Lewis and Seed 1969, Seed 1972, 1974, Verduin 1979, Beaumont et al. 1989). It is possible that addition of these characters might yield even better discrimination among species of *Mytilus*.

Whether *Mytilus edulis*, *M. galloprovincialis* and *M. trossulus* should be considered separate species has been the subject of considerable discussion, centering on the status of *M. galloprovincialis* as a distinct species from *M. edulis* (Seed 1978, Gosling 1984, McDonald and Koehn 1988, Johannesson et al. 1990, Väinölä 1990). One reason for the reluctance to consider these taxa separate species is that where their ranges overlap, hybridization often occurs (Seed 1974, 1978, Skibinski et al. 1978, 1983, Skibinski 1983, McDonald and Koehn 1988, Skibinski and Roderick 1991). However, there are many examples from plants and animals, including marine invertebrates (Dillon and Manzi 1989, Kwast et al. 1990), of hybridization between groups that are taxonomically recognized as distinct species. Despite hybridization and massive potential for dispersal via a planktonic larval stage which lasts several weeks, each of the three taxa of *Mytilus* maintains a distinct set of alleles, with fairly homogeneous allele frequencies across vast distances. We feel that this genetic distinctness warrants taxonomic recognition at the species level. Failing to recognize these taxa would confuse, rather than aid, the understanding of their biology.

Recognizing *M. edulis*, *M. galloprovincialis* and *M. trossulus* as distinct species clarifies the interpretation of some biological observations on mussels. For example, Milyutina and Petrov (1989), in a systematic study of mytilids using DNA-DNA hybridization, were puzzled by the large amount of intraspecific variation they found within *M. edulis*. Their results are much clearer once it is realized that their samples of "*M. edulis*" from Posjet Bay and the Barents Sea are probably *M. trossulus*. As another example, mussels are commonly used as biomonitors of marine pollution. However, individuals of *M. trossulus* accumulate about 50% more of many elements than *M. edulis* from the same location (Lobel et al. 1990). Taxonomy should receive more careful consideration in the design and interpretation of biomonitoring studies.

Far more interesting than the taxonomic rank that should be assigned to these taxa are the biological mechanisms that keep them distinct despite hybridization. Promising areas for further research include measurement of survival, growth rate and physiological parameters in natural hybrids (Skibinski 1983, Gardner and Skibinski 1988) and laboratory hybrids (Lubet et al. 1984), comparison between species of reproductive characters such as spawning time (Seed 1971, Gardner and Skibinski 1990) and sperm morphology (Drozdov and Reunov 1986, Hodgson and Bernard 1986, Crespo et al. 1990), and examination of mitochondrial DNA (Skibinski 1985, Edwards and Skibinski 1987, Fisher and Skibinski 1990, Hoeh et al. 1991) and nuclear DNA (Milyutina and Petrov 1989).

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