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Genetic comparison of *Macoma balthica* (Bivalvia, Telinidae) from the eastern and western North Atlantic Ocean

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ABSTRACT: The telinid bivalve *Macoma balthica* is common to both marine and estuarine soft-bottom habitats of the northern hemisphere. To determine if populations in the eastern and western North Atlantic Ocean are conspecific, the genetic composition of these populations was examined. Differences in genetic composition, as determined by enzyme electrophoresis, were observed between populations from the eastern and western North Atlantic. One locus was unique to western North Atlantic populations and 3 others differed in allele composition and frequencies. Allopatric populations of *M. balthica* from the eastern and western North Atlantic can be considered as separate and sibling species.

INTRODUCTION

The tellinid bivalve *Macoma balthica* is common to both marine and estuarine soft-bottom habitats of the northern hemisphere (McErlean 1967, Castagna & Chanley 1973, Green 1973, Abbott 1974, Chambers & Milne 1975, McLusky & Allen 1976, Ankar 1977, Beukema et al. 1978, Lubinsky 1980). In the western North Atlantic Ocean, this species occurs in coastal waters of western Greenland and the lower Canadian Arctic south to North Carolina. In the eastern North Atlantic it occurs from the Bay of Biscay, France, to northern Scandinavia and the White Sea. Such a vast geographic range is not unique among the marine fauna; however, differences in life history strategies, morphology and habitat type (Gilman 1977, Elliot 1979, Meehan 1984) among geographically disjunct populations may indicate that geographically widespread populations are genetically unique.

A limited portion of the genome of a population can be determined by the examination of enzymes using electrophoretic techniques (Brewer 1970, Avise 1975, Markert 1975). The genetic population structure of many organisms has been determined using this technique (see reviews by Ayala 1975, Gooch 1975, Nevo 1978, Burton 1983). Reid & Dunnil (1969) have utilized gastric and digestive enzymes to distinguish 8 Pacific east-coast species of *Macoma*, not including *M. balthica*. Green et al. (1983) used enzymes to investigate the relation between some life-history characteristics and genetic population structure of an intertidal population of *M. balthica*. If *M. balthica* populations on the eastern and western North Atlantic are represented by distinct gene pools, this may be manifested as differences in electrophoretically detectable enzyme variations.

Materials and Methods

Specimens of *Macoma balthica* were sampled from sites on both the east and west coasts of the North Atlantic Ocean (Table 1). Live specimens were transferred to the Virginia Institute of Marine Science (USA) or the Netherlands Institute for Sea Research (The Netherlands) where they were maintained in aquaria with flowing seawater under ambient conditions.

Enzyme variation was examined using horizontal starch gel electrophoresis (Brewer 1970). Samples were prepared for electrophoresis; electrophoretic conditions and detection were described in detail by

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Table 1. *Macoma balthica*. Geographic location and source of studied populations

Population number	Location	Source
1	Sarah's Creek, York River Virginia, USA	Mr. Brian Meehan, Virginia Inst. of Marine Science, Gloucester Point, Virginia
2	Shark River, New Jersey, USA	Ms. Joy Goodsill, Rutgers Univ. Rutgers Shellfish Lab. Port Norris, New Jersey, USA
3	Newark Bay, New Jersey, USA	Dr. Mike McCormick, Montclair State College, Upper Montclair, New Jersey, USA
4	Barn Island Salt Marsh, Barn Island State Park, Connecticut, USA	Dr. Bob Whiltlach, Univ. of Connecticut, Groton, Connecticut, USA
5	Jackson Marine Lab. New Hampshire, USA	Dr. Larry Harris, Univ. of New Hampshire, Durham, New Hampshire, USA
6	Pottery Creek, Passamaquoddy Bay, New Brunswick, Canada	Ms. Leslie Linkletter, Biol. Station, St. Andrews, New Brunswick, Canada
7	Churchill, Hudson Bay, Canada	Dr. Roger H. Green, Univ. of Western Ontario, Ontario, Canada
8	Disko Fjord, Greenland	Dr. G. Hopner Petersen, Zooligisk Museum Kobenhavn, Denmark
9	St. Malo Bay, St. Malo, France	Mr. Franciose Lang, Lab. Maritime, Dınard, France
10	The Wadden Sea, Den Helder, The Netherlands	Dr. Jan J. Beukema, The Netherlands Institute for Sea Research, Texel, The Netherlands
11	Niva Bay, Øresund, Denmark	Mr. Paul B. Madsen, Marine Pollution Lab., Charlettenlund, Denmark
12	University of Helsinki, Zoological Station Tvärminne, Finland	Dr. Sirrka-Lisa Aho-Varvio, Univ. of Helsinki, Helsinki, Finland

Meehan (1984). Adductor-muscle tissue and digestive diverticular were homogenized in 0.1M tris buffer pH 7.0 with 20 % glycerol and centrifuged at 2000 g for 20 min. Enzymes examined include malate dehydrogenase, phosphoglucose isomerase, phosphoglucomutase, and an aminopeptidase. Phosphoglucose isomerase and aminopeptidase were electrophoresed on a discontinuous lithium hydroxide buffer pH 8.4 (Selander et al. 1969). Phosphoglucomutase was on a maleic acid electrode buffer containing 0.1M tris, 0.1M maleic acid, 0.01M EDTA and 0.01M $MgCl_2$, and adjusted to pH 7.4 with NaOH, the gel buffer was 1:9 dilution of this. Malate dehydrogenase was on a tris-citrate electrode buffer consisting of 0.135M Tris and 0.004M citric acid and adjusted to pH 7.3 with NaOH, the gel buffer was a 1:9 dilution of this. Detection of enzymes was performed following the methods of Shaw & Prasad (1969); leucyl-l-alanine was used as a substrate for the aminopeptidase enzyme. At each locus, the fastest migrating allele was designated 'A', slower alleles as 'B', 'C', 'D', etc. Data were analysed using the computer software package Biosys-1 (Swofford & Selander 1981). For each population, allele frequencies and conformity of genotype frequencies to the Hardy-Weinberg expectations were determined. Comparisons between populations were made using Nei's unbiased genetic identity, cluster analyses (unweighted pair group method), and chi-square tests for homogeneity between populations.

RESULTS

The allele frequencies at studied loci for the populations examined are given in Table 2. Three enzymes were polymorphic in all populations. A population is considered polymorphic if the frequency of the most common allele does not exceed 0.95. Because of difficulties in resolving the aminopeptidase enzyme, it was not included in the analysis of eastern North Atlantic populations. The allele frequencies of each of the investigated loci are discussed below.

Malate dehydrogenase-1 (MDH-1)

The MDH-1 locus was unique to populations in the western North Atlantic Ocean. Two common alleles and 1 rare allele occurred at this locus. The rare allele occurred only at the Shark River population (2).

Table 2. *Macoma balthica*. Sample sizes (n) and allele frequencies at each locus for each population investigated

	Population									
Locus	1	2	3	4	5	6	9	10	11	12
MDH-1										
(N)	49	35	50	30	30	40	64	30	60	60
A	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.663	0.643	0.660	0.617	0.633	0.650	0.000	0.000	0.000	0.000
C	0.337	0.343	0.340	0.383	0.367	0.350	0.000	0.000	0.000	0.000
D	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MDH-2										
(N)	50	35	50	30	30	40	64	30	60	60
A	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000
B	1.000	1.000	1.000	1.000	1.000	0.975	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	1.000	1.000	1.000	1.000
PGI										
(N)	42	35	48	30	30	37	56	30	60	60
A	0.000	0.000	0.000	0.000	0.017	0.027	0.027	0.000	0.000	0.017
B	0.250	0.071	0.031	0.017	0.033	0.027	0.125	0.200	0.150	0.092
C	0.488	0.443	0.583	0.567	0.400	0.351	0.330	0.683	0.525	0.400
D	0.262	0.486	0.354	0.417	0.483	0.595	0.518	0.117	0.317	0.483
E	0.000	0.000	0.031	0.000	0.050	0.000	0.000	0.000	0.008	0.008
F	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
PGM										
(N)	44	35	12	28	30	33	63	30	59	60
A	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.068	0.042
B	0.000	0.000	0.000	0.000	0.000	0.000	0.429	0.200	0.534	0.358
C	0.000	0.000	0.000	0.000	0.000	0.000	0.349	0.483	0.280	0.367
D	0.080	0.200	0.167	0.054	0.017	0.045	0.151	0.283	0.093	0.150
E	0.273	0.414	0.667	0.321	0.467	0.439	0.032	0.033	0.017	0.075
F	0.443	0.371	0.125	0.554	0.333	0.500	0.008	0.000	0.008	0.008
G	0.205	0.014	0.042	0.071	0.167	0.015	0.000	0.000	0.000	0.000
H	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
APP-2										
(N)	47	31	46	28	29	24				
A	0.170	0.339	0.315	0.250	0.397	0.396				
B	0.340	0.403	0.413	0.232	0.397	0.313				
C	0.489	0.258	0.272	0.518	0.207	0.292				

Malate dehydrogenase-2 (MDH-2)

MDH-2 was monomorphic in all populations except the Pottery Creek population (6), which contained 1 fast migrating, relatively rare allele. The western North Atlantic populations are represented by allele 'B', the eastern North Atlantic populations by allele 'C'.

Phosphoglucose isomerase (PGI)

PGI was represented by as many as 6 alleles in 1 population. Allele 'F' at the New Hampshire population (5) was the only allele unique to the western North Atlantic for this locus. Generally, allele 'B' was more common in the eastern North Atlantic and allele 'E' was more common in the western North Atlantic. In the Sarah's Creek population (1) allele 'B' occurs at a much higher frequency (seemingly at the expense of allele 'D') than in other western North Atlantic populations.

Phosphoglucomutase (PGM)

Of the 8 alleles representing this locus, 3 ('D', 'E', 'F') were shared among nearly all populations studied. Two distinct alleles ('G', 'H') occurred in the western North Atlantic populations, and 3 distinct alleles ('A', 'B', 'C') occurred in the eastern North Atlantic populations. Allele 'F' was common in the western North Atlantic but it occured at very low frequencies in the eastern North Atlantic. Allele 'H' occurred only in the

New Hampshire population at low frequency. Alleles unique to the eastern North Atlantic represent 60 % or more of all alleles present at this locus.

Aminopeptidase (AP)

Because this locus was scored only for the western North Atlantic populations an amphi-Atlantic comparison was not possible. This locus contained 3 alleles shared among all the western North Atlantic populations studied.

The allele frequencies at each of the populations studied agree with Hardy-Weinberg expectations, except in the Tvärminne (12) and Sarah's Creek (1) populations. The deviation from Hardy-Weinberg equilibrium for the PGI locus in the Tvarminne (12) population could be caused by a combination of sample size and presence of some rare alleles (Table 2). When the rare alleles at the PGI locus of the Tvärminne (12) population are pooled into a single group, the allele frequencies are in strong agreement with Hardy-Weinberg expectations. The allele frequencies at all of the polymorphic loci for the Sarah's Creek population (1) are in disagreement with Hardy-Weinberg expectations. Also, the MDH-1 and the PGI loci of the Sarah's Creek (1) population showed a strong difficiency of heterozygotes. The Sarah's Creek population is located very near the southern distributional limit of *Macoma balthica*. Perhaps, the departures from the Hardy-Weinberg equilibrium and the heterozygote difficiencies are a reflection of this (i.e. marginal habitat). As a marginal habitat, this population may be partially isolated and it may be subject to extraordinary strong selection at these loci.

With regard to all the loci examined, the populations studied on each side of the North Atlantic are very similar to one another (Table 3), but not homogeneous (Table 5). The average genetic identity among western North Atlantic populations is 0.975, among eastern North Atlantic populations 0.971. In contrast, eastern and western North Atlantic populations are quite different from one another (Fig. 1; Tables 3 and 4). The average genetic identity between eastern and western North Atlantic populations is 0.169. The most striking difference between eastern and western North Atlantic populations occurs at the MDH loci (Table 2). Along the western North Atlantic this enzyme system is coded for by 2 loci, MDH-1 and MDH-2; on the eastern North Atlantic only the MDH-2 locus is present.

DISCUSSION

The slight variations in allele frequencies within the populations studied were not unexpected. Variations in allele frequencies along microgeographic and macrogeographic ranges are common in marine bivalves and are often associated with environmental and habitat differences (Koehn & Mitton 1972, Koehn et al. 1973, Levinton 1972, Mitton et al. 1973, Singh & Zouros 1978, Theisen 1978, Koehn 1983). Green et al. (1983) found that the genetic heterozygosity of 2 intertidal populations of *Macoma balthica* increased slightly with increased distance above mean low water. It is likely that the variations in allele frequencies within each of the populations studied are caused by environmental and habitat differences. Unique alleles among eastern or western North Atlantic populations are at such low frequencies that they do not significantly differentiate populations, and it could be that they have simply remained undetected in other populations.

The presence of the MDH-1 locus in the western North Atlantic, as well as many alleles unshared at common loci between eastern and western North Atlantic populations, strongly indicates that the eastern and western North Atlantic populations of *Macoma balthica* are genetically distinct. As a general descriptor, genetic similarity values indicate that eastern and

Table 3. *Macoma balthica*. Matrix of Nei's unbiased identity coefficients calculated from allele frequencies using Biosys-1 (Swofford & Selander 1981)

Population	1	2	3	4	5	6	7	8	9	10
1	·····	0.974	0.937	0.985	0.974	0.956	0.143	0.177	0.158	0.156
2		·····	0.978	0.992	0.997	0.996	0.182	0.173	0.169	0.195
3			·····	0.946	0.977	0.945	0.165	0.194	0.172	0.188
4				·····	0.988	0.989	0.167	0.177	0.173	0.183
5					·····	0.996	0.164	0.140	0.152	0.178
6						·····	0.178	0.131	0.153	0.187
7							·····	0.937	0.986	1.000
8								·····	0.959	0.954
9									·····	0.987
10										·····

western North Atlantic populations of *M. balthica* are not conspecific. Often, genetic similarity values greater than 0.9 are associated with conspecifics, and values less than 0.9 occur between subspecies or species (Avise 1975). Skibinski et al. (1980) examined the genetic similarity among the mussels *Mytilus edulis*, *M. galloprovincialis* and *Modiolus modiolus*. Genetic similarity between the *Mytilus* species was less than 0.9, between the genera *Mytilus* and *Modiolus* less than 0.25. Buroker et al. (1979a, b) found that the genetic similarity among 5 species of *Crassostrea* was less than 0.8, that among conspecific populations greater than 0.9.

Genetic differentiation, determined by electrophoresis of enzymes, between populations only implies genetic isolation; post-settling selection can create the same differences. However, *Macoma balthica* has a restricted ability to migrate and it is unlikely that gene flow occurs between eastern and western North Atlantic populations. As a true infaunal bivalve, *M. balthica* is highly adapted to, and dependent upon,

Table 4. *Macoma balthica*. Summary of genetic differences between populations in the eastern and western North Atlantic Ocean inferred by enzyme electrophoresis

Locus	Differences between eastern and western North Atlantic populations
MDH-1	Locus unique to western North Atlantic populations
MDH-2	Alleles unique to each side of the North Atlantic
PGI	One unique, rare allele; large differences in allele frequencies of shared alleles
PGM	Two unique alleles in the western North Atlantic and 3 unique alleles in the eastern North Atlantic

Table 5. *Macoma balthica*. Summary of chi-square values and associated P-values for the analyses of heterogeneity of allele frequencies among the populations studied

Locus	Alleles	Chi-square	D.F.	P
		Western North Atlantic Ocean		
MDH-1	3	6.183	10	0.79964
MDH-2	2	9.792	5	0.08136
PGI	6	87.353	25	0.00000
PGM	5	66.469	20	0.00000
Totals		169.797	60	0.00000
		Eastern North Atlantic Ocean		
PGI	5	42.823	12	0.00002
PGM	6	36.916	15	0.00130
Totals		79.739	27	0.00000

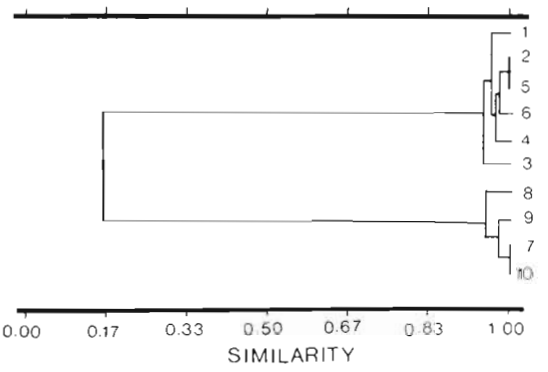

Fig. 1. *Macoma balthica*. Population phenogram calculated from Nei's unbiased genetic identity (1978), using Biosys-1 (Swofford & Selander 1981)

its habitat; as an adult it has only a limited ability for survival outside the sediment. *M. balthica* must depend on a passive mode of dispersal utilizing its planktonic larvae. There are 4 primary factors for successful transoceanic transport of teleplanic larvae: direction and speed of available ocean currents, distance between populations, maximum duration of larval development, and larval behavior (Burton & Feldman 1982, Colebrook 1982, Scheltema 1972a, 1978). The planktonic larval period of *M. balthica* is approximately 2 mo long (Lammens 1967, Ankar 1980, Gilbert 1979). It is generally possible for molluscs to postpone metamorphosis from a planktonic to a benthic state (e.g. Bayne 1965, Seed 1976); there are no indications that *M. balthica* is an exception to this rule. As absolute larval longevity values are unknown, it will be assumed that *M. balthica* can delay metamorphosis for as long as 1 mo, assuming a maximum planktonic larval duration of 90 d. Laboratory experiments with *Mytilus edulis* (Bayne 1965) indicate that metamorphosis can be delayed up to 40 d at 10°C, and 2 d at 20°C.

The water currents that would operate as vectors for transoceanic larval transport for *Macoma balthica* are illustrated in Fig. 2. Using estimates of velocity for transport along these currents (Scheltema 1966), the time required for passive travel from the western to eastern Northern Atlantic ranges from 150 to 300 d. It is apparent that the North Atlantic Ocean currents are not suitable as vectors for direct exchange of planktonic larvae between eastern and western North Atlantic populations.

Another possible mechanism for maintenance of a contiguous range is by utilizing Iceland and Greenland as stepping stones. Berger (1973, 1977) and Kraeuter (1974) suggested that Greenland and Iceland operated in the past as stepping stones for the colonization of the North American coast by *Littorina littorea*. It is unlikely that Greenland and Iceland operate as

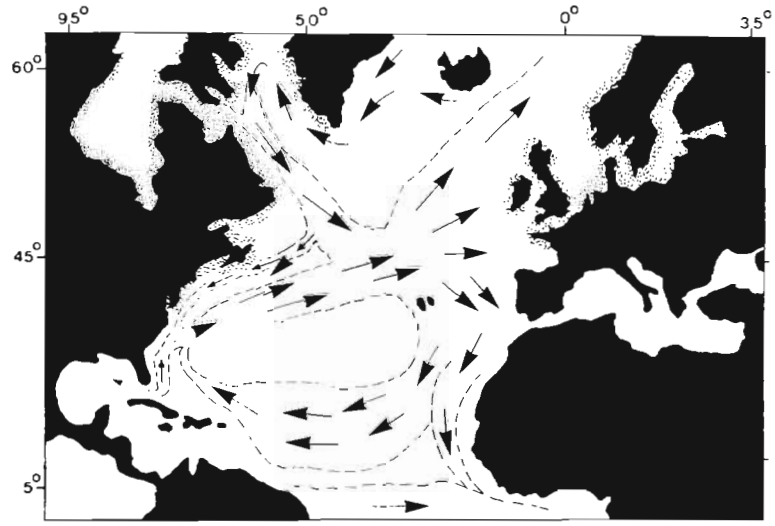

Fig. 2. Distribution of *Macoma balthica* (stippled areas) and major ocean currents in the North Atlantic Ocean

stepping stones for *Macoma balthica*. This species occurs only on western Greenland (Madsen pers. comm.) and it is not present in coastal or near-shore waters of Iceland (Sparck 1937). A mild modification of this stepping-stone model invoking continental drift may be the most likely model for explaining the establishment of *M. balthica* in its North Atlantic range.

A few sporadic fossil records of *Macoma balthica* exist for as far back as 60 million yr (Moore 1969). Perhaps *M. balthica* established its amphi-Atlantic distribution during post-genesis of the Atlantic basin, and as the Atlantic broadened by continental drift (Kennett 1982, Hallam 1983), transoceanic exchange of larvae was continually reduced. With this hypothesis, also used to describe the distribution of a number of other species (Sterrer 1973, Vermeij 1978), the tectonic plates can be regarded as slow-moving biotope carrying rafts (Pielou 1979). Therefore, for a considerable length of time, while *M. balthica* was passively extending its range, it was continually inhabiting the same environmental regions and filling the same niches. This transition to allopatry would not involve the invasion of a 'new' habitat; it also would not require any change or adaptive radiation (Schvarts 1977, Stanley 1977). Though *M. balthica* may have once existed as a conspecific population throughout the North Atlantic, possibly as a result of the phenomenon of plate tectonics, it now exists as 2 allopatric populations which are slowly diverging according to the potential of each.

CONCLUSION

The evidence presented here suggests that *Macoma balthica* in eastern and western North Atlantic waters should be considered as separate and sibling species. They are morphologically similar, but geographically isolated and genetically distinct (Mayr 1970). It is recommended that future research in this direction be applied towards interbreeding eastern and western North Atlantic populations, determining the extent of the presence of *M. balthica* on Greenland and the Faeroe Islands, and extensive genetic analysis of both populations, with emphasis on the northern distributional reaches. Also, investigations concerning *M. balthica* should be conducted with caution, when utilizing the world-wide literature concerning this bivalve.

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