A genetic and morphologic comparison of Macoma balthica from the eastern and western North Atlantic

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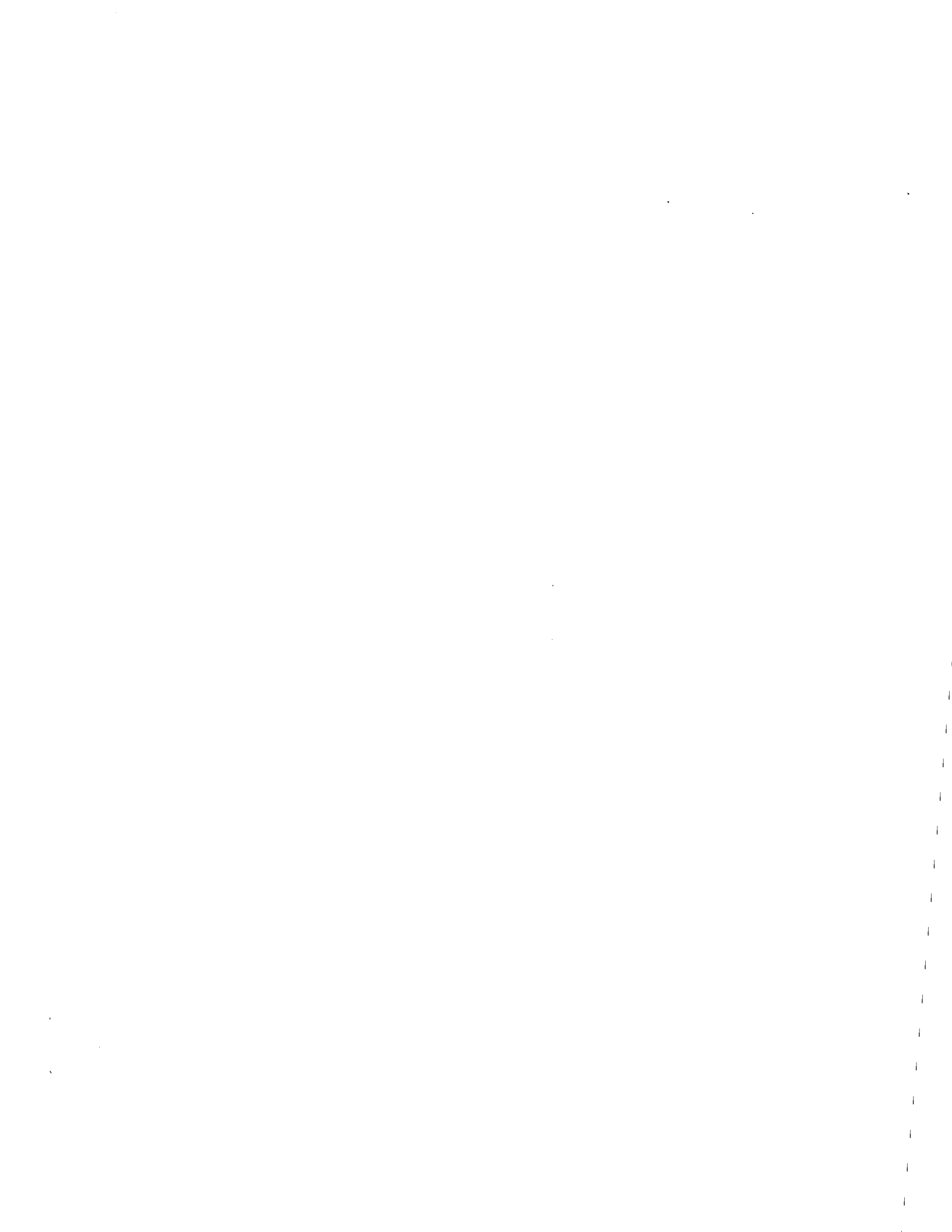*The College of William and Mary in Virginia*　　　　　PH.D.　1984

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A GENETIC AND MORPHOLOGIC COMPARISON OF <u>MACOMA</u> <u>BALTHICA</u>

FROM THE EASTERN AND WESTERN NORTH ATLANTIC

————————

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

————————

by

Brian Walter Meehan

1984

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of the requirements for the degree of

Doctor of Philosophy

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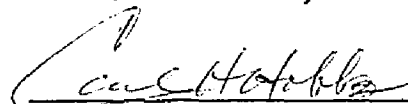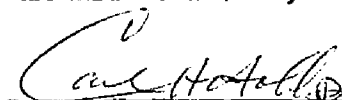
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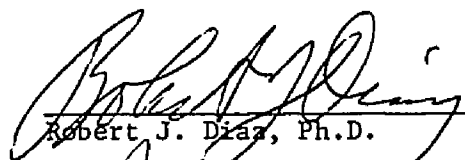Netherlands Institute for Sea Research
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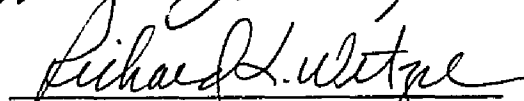Author

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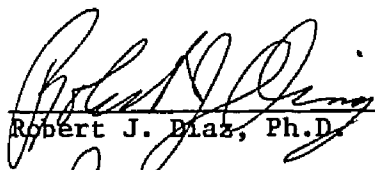Netherlands Institute for Sea Research
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This dissertation is dedicated to the memory

of my mother, Beverly Ann Meehan

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ABSTRACT

Macoma balthica is a Tellinid bivalve that is common
to both marine and estuarine soft-bottom habitats of the
northern hemisphere. To determine if populations on the
eastern and western North Atlantic are conspecific, the
labial palp morphology, shell shape and genetic
composition of these populations were examined.
Previously described differences in the labial palp
morphology do not occur among the populations
investigated. Differences in the shell shape and genetic
composition, determined by enzyme electrophoresis, were
observed between populations from the eastern and western
North Atlantic. Allopatric populations of Macoma
balthica from the eastern and western North Atlantic can
be considered as separate and sibling species.

A GENETIC AND MORPHOLOGIC COMPARISON OF <u>MACOMA</u> <u>BALTHICA</u>

FROM THE EASTERN AND WESTERN NORTH ATLANTIC.

INTRODUCTION

This study was initiated to determine if the eastern
and western North Atlantic populations of _Macoma_
balthica exist as morphologically and genetically
distinct populations. Though population variations of _M._
balthica have been examined by a number of investigators
this study represents the most comprehensive comparison
of _M. balthica_ throughout its North Atlantic
distribution. _M. balthica_ from both the eastern and
western North Atlantic were examined and compared with
regard to labial palp morphology, shell shape and genetic
composition.

Macoma balthica is a Tellinid bivalve that is
common to both marine and estuarine soft-bottom habitats
of the northern hemisphere (Figure 1). In the Pacific
ocean _M. balthica_ occurs along the coast of North America
from Alaska to San Diego, as well as in Japan, where it
has been synonymized with _M. takahokoensis_. There are no
reports of _M. balthica_ from the coastal waters of

Figure 1. Geographic distribution of <u>Macoma</u> <u>balthica</u> in
the northern hemisphere, stipled areas.
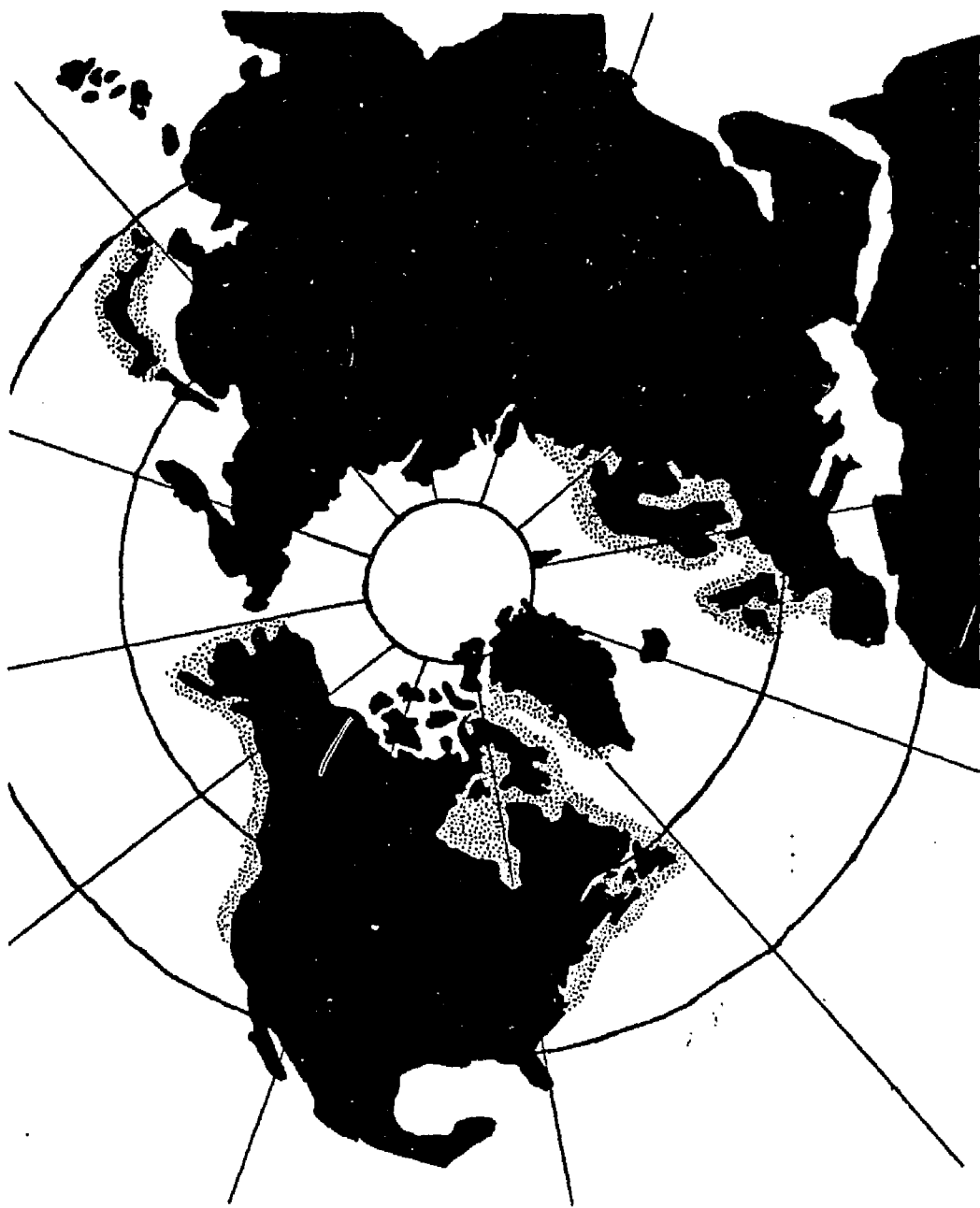
mainland Asia, but it is likely that it exist there as well. In the western North Atlantic this species occurs in coastal waters of western Greenland and the lower Canadian Artic south to North Carolina. In the eastern North Atlantic it occurs from the Bay of Biscay, France, to northern Scandinavia (McErlean, 1967; Castagna and Chanley, 1973; Green, 1973; Abbott, 1974; Chambers and Milne, 1975; McLusky and Allen, 1976; Ankar, 1977; Beukema et al., 1978; Lubinsky, 1980; Madsen, 1983;). According to Abbott (1974) M. balthica rings the Canadian Arctic, thereby connecting Atlantic and Pacific populations; however, Lubinsky (1980) clearly indicates that M. balthica does not make this connection. Such a vast geographic range is not unique among marine fauna, however, there are differences in M. balthica's life history strategies, morphology and habitat type between geographically disjunct locations (Gilman, 1977; Elliot, 1979; and others). Considering the range of M. balthica, these differences among geographically disjunct populations may indicate that geographically wide spread populations are genetically unique.

According to Gilbert (1977), M. balthica in New England have morphologically distinct labial palps relative to populations in Europe (Yonge, 1949). Gilbert suggested that because of the anisomorphic palps of

European and New England M. balthica the current flow
through the mantle cavity of New England M. balthica
occurs in an opposite direction from European M.
balthica. Also, the morphological differences in the
labial palps may be indicative of differences in habitats
and material carried through the incurrent siphon
(Gilbert, 1977; Reid, 1971). Bivalve labial palps are
complex feeding structures which often reflect distinct
feeding niches. For example, Reid and Reid (1969) have
shown that differences in the feeding apparatus
apparently restrict eight different species of Macoma to
specific niches, though M. balthica was not one of the
species examined. Both feeding structures and digestive
processes of molluscs have long been recognized as vital
in the adaptive radiation of the phylum (Purchon, 1977).
The differences in the labial palp morphology between
eastern and western North Atlantic M. balthica may be
indicative of evolutionarily divergent populations.

Differences have also been reported in growth rate,
longevity and maximum size among geographic populations
of M. balthica (Green, 1973) and many factors are thought
to influence these characteristics, including temperature
(Gilbert, 1973; Green, 1973; Lammens, 1967; Reading,
1979), food type and availability (Green, 1973; Elliot,
1979; Hummel, 1983; Nichols and Thompson, 1982), and

habitat characteristics (Gilman, 1979). Of these factors, none acts exclusively to influence life history parameters. The environment is the sum total of the interaction of many separate factors that act synergistically upon organisms (Vernberg, 1975). The different life history strategies of M. balthica occurring in different geographic sites, could be indicative of physiological adaptations to different environments. Gilman (1977) found this to be true for M. balthica populations from different locations along the New England coast. Nicol (1978) found that variations in these same life history characteristics occur in many groups of molluscs that have a large geographic range. Growth rate, longevity and maximum size are difficult to determine and require long-term field investigations. Also, each of these parameters can be influenced by short term environmental variations.

Shell shape has not been previously considered within investigations of the growth aspects of M. balthica. Investigators generally have assumed a constant shell shape among populations, regardless of differences in growth rate and size. Molluscan shell shapes have a strong genetic component which often results in species specific characteristics (Chanley, 1961; Humphrey and Walker, 1982) and variations in shell shape can be influenced by external factors. The shell

shape of an individual is therefore a manifestation of both genetic and environmental forces (Coe, 1948; Dodd, 1964, 1966; Kaufman, 1969; Kennedy et al.,1969). In this regard distinct shell shapes at different locations may reflect different environmental and ecological forces on a single genome, or alternatively, different genomes between locations, or both. Variation in shell shape can present different spatial accommodations for internal organs, influence the suitability to a habitat and affect predator-prey interactions (Kaufman, 1969; Stanley, 1975; Vermeij, 1978; Nicol, 1983). Therefore, different shell shapes of M. balthica between locations may be indicative of divergence by affecting survivorship at different habitats, response to predators and allowing opportunity for reorganization of internal organs. Shell shape is not necessarily a passive characteristic, but may represent a form of adaptive radiation and could be a better criteria to distinguish populations than either growth rate or maximum size.

Differences in the labial palp structure and shell shape of M. balthica between the eastern and western North Atlantic populations could indicate genetic divergence between two allopatric populations (Mayr, 1970; Bush, 1975). A limited portion of the genome of a population can be determined by the examination of

enzymes using electrophoretic techniques (Lewontin, 1974). Because enzymes are immediate products of DNA activity direct observation of enzymes provides indirect information of genetic structure (Avise, 1975; Markert, 1974). The genetic population structure of many organisms has been determined using this technique (see reviews by Ayala, 1975; Burton, 1983; Gooch, 1975; Nevo, 1978). Reid and Dunnil (1969) have utilized gastric and digestive enzymes to distinguish eight Pacific east coast species of Macoma, not including M. Balthica. Green et al. (1983) used enzymes to investigate the relationship between some life history characteristics and genetic population sturcture of an intertidal population of M. balthica. If M. balthica populations on the eastern and western North Atlantic are represented by distinct gene pools, possibly indicated by differences in shell shape and labial palp morphology, this may be manifest as differences in electrophoretically detectable enzyme variations.

MATERIALS and METHODS

Specimens of <u>Macoma</u> <u>balthica</u> were sampled from sites on both the east and west coasts of the North Atlantic (Table 1). Live specimens were transferred to the Virginia Institute of Marine Science or the Netherlands Institute for Sea Research where they were placed in natural sediment or foam rubber in aquaria with flowing seawater. No attempt was made to control or monitor temperature or salinity in the holding system.

Labial palp structure

The labial palps were examined using a dissecting microscope and a scanning electron microscope (SEM). The dissecting microscope was sufficient for gross observation but the SEM was far superior for obtaining detailed photographic records. For observations with the SEM, labial palps of <u>M.</u> <u>balthica</u> were dissected free and washed with a mixture of sputolysin and distilled water

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Table 1. Geographic location and source of studied
          populations of _Macoma_ _balthica_.

Population Number	Location	Source
1	Sarahs Creek, York River Virginia, U.S.A.	Mr. Brian Meehan, Virginia Institute of Marine Science, Gloucester Point, Virginia
2	Shark River, New Jersey, U.S.A.	Ms. Joy Goodsill Rutgers University Rutgers Shellfish Laboratory Port Norris, New Jersey
3	Newark Bay, New Jersey, U.S.A.	Dr. Mike McCormick, Montclair State College, Upper Montclair, New Jersey.
4	Barn Island Salt Marsh, Barn Island State Park, Connecticutt, U.S.A.	Dr. Bob Whiltlach, University of Connecticutt, Groton, Connecticutt.
5	Jackson Marine Lab. New Hampshire, U.S.A.	Dr. Larry Harris, University of New Hampshire, Durham, New Hampshire.
6	Pottery Creek, Passamaquoddy Bay, New Brunswick. Can.	Ms. Leslie Linkletter, Biological Station, St. Andrews, New Brunswick, Can.
7	Churchill Hudson Bay, Can	Dr. Roger H. Green University of Western Ontario, Ontario, Can.
8	Disko Fjord Greenland	Dr. G. Hopner Petersen Zooligisk Museum Kobenhavn, Denmark
9	St. Malo Bay, St. Malo, France	Mr. Franciose Lang Laboratorie Haritime, Dinard, 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, Oresund, Denmark	Mr. Paul B. Madsen, Marine Pollution Laboratory, Charlettenlund, Denmark
12	University of Helsinki Zoological Station Tvarminne, Finland	Sirkka-Luisa Aho-Varvio, University Helsinki, Helsinki, Finland

to remove mucus from the surface tissue. Palps were
fixed in 0.1M sodium cacocylate with 1.0% gluteraldehyde.
Conductive properties were imparted upon the tissue using
a modified osmium tetroxide - thiocarbohydrazide - osmium
tetroxide procedure as described by Hyatt (1978) or by
metal coating with gold-platinum in a vacuum evaporator.
In both cases tissues were dehydrated using a graded
alcohol series, stored in acetone, and dried using a
critical point dryer.

For observations with a standard dissecting
microscope, labial palps were exposed by removing one
shell valve and flapping back the mantle and outer palp.
Representatives from all populations were examined using
this method. Only specimens from the Wadden Sea and
Sarah's Creek, locations 10 and 1, respectively, were
examined and photographed with the SEM.

Shell Shape

Previous investigations of Macoma balthica shell
variation have dealt primarily or exclusively with shell
length. For this investigation the height (H), length
(L) and width (W) of shells were measured to the nearest
0.05mm with vernier calipers (Figure 2). Each measure

Figure 2. Illustration of the heigth(H), length(L) and
width(W) dimensions of <u>Macoma</u> <u>balthica</u> used in
the present investigation.
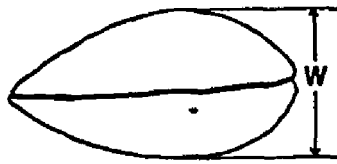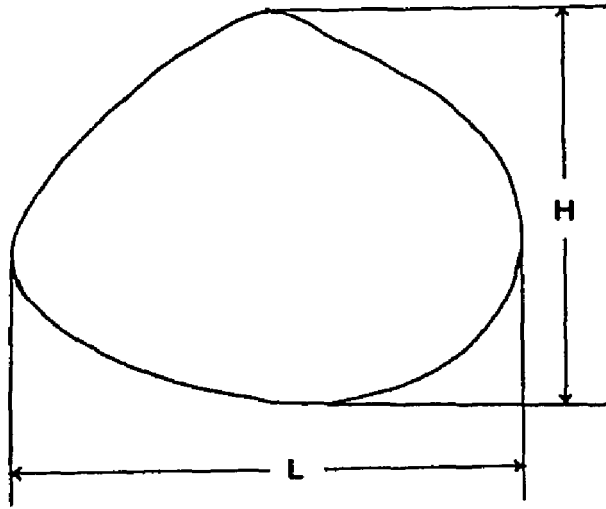
was standardized against the sum of all three
measurements. Standardized data from population samples
were then compared graphically and statistically.
Statistical comparison among all populations was done
using a nonparametric Kruskal-Wallis one way analysis of
variance. Subsequent multiple comparisons between all
pairwise combinations were done following the procedure
outlined by Noether (1971). This procedure allows
multiple comparisons without inflation of the alpha level
of the overall test. The relative similarity of the
shell shapes among the studied populations was determined
using the manahattan distance statistic (Cherry et al.,
1982). This technique is commonly employed in
anthropological investigations in order to give
information on the relative difference or similarity of
shapes (Cherry et al., 1982; Farris, 1972). Height,
length and width parameters, as well as, H:W, L:W and H:L
ratios were used to determine the manahattan distance
values between all pairwise combinations of populations.

Enzyme electrophoresis

Enzyme variation was examined using horizontal
starch gel electrophoresis (Brewer, 1970). Adductor
muscle and digestive gland tissue were dissected from
live individuals and homogenizd in 0.01M Tris with 20%

glycerol, over ice. To remove tissue particulates the homogenates were centrifuged in a refrigerated centrifuge. Filter paper wicks (5 x 5mm) were saturated with supernant, blotted, and inserted into the starch-gel 2.2cm from the cathode edge. Starch gels were 140x140x62mm in dimensions and were made from a mixture of 18.7gm of hydrolysed starch (Connaught Laboratories, LTD., Canada) and 160ml of gel buffer. Studied enzymes, electrophoretic conditions and detection methods are given in Table 2. Each electrophoretic run included an individual of known genotype as a standard.

After electrophoresis, gels were sliced horizontally and the cut surface stained according to methods in Table 2. The fastest migrating allele was designated "A" and slower alleles "B", "C", "D", etc. Photographic records were made of representative runs and those that included rare alleles; relative migration distances were not determined. Data were analysed using the computer software package Biosys-1 (Swofford and 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 homogeniety between populations.

Table 2. Electrophoretic conditions for detection of

Malate dehydrogenase (MDH), Phosphoglucose

Isomerase (PGI), Amino Peptidase (AP) and

Phosphoglucomutase (PGM) in <u>Macoma</u> <u>balthica</u>.

Enzymes(voltage/time)	Buffer and Staining solutions
MDH-1, MDH-2 (250/3hrs.)	Electrode Buffer: 0.135M Tris, 0.0043M Citric Acid. Adjusted to pH. 7.3 with NaOH. Gel Buffer: 1:9 dilution of electrode buffer. Stain: 25 mg NAD, 10 mg MTT, 1 mg PMS, 5 ml substrate Solution, 20 ml 0.1M Tris-HCl, pH 7.0. Substrate solution: 1.34g L-malic acid in 50 ml water, adjusted to pH 7.0 with 2.0M NaH_2CO_3
PGI, AP (250/3hrs.)	Electrode Buffer: Use 100% stock solution A. Stock solution A; 0.03M Lithium hydroxide, 0.19M boric acid, pH 8.1. Stock solution B; 0.05M Tris, 0.008M citric acid, pH 8.4. Gel Buffer: 1:9 mixture of stock solutions A and solution B. PGI Stain: 5 mg sodium fructose-6-phosphate, 5 mg NADP, 5 mg MTT, 2 mg PMS, 10 units glucose-6-phosphate dehydrogenase, 0.5 ml 0.1M $MgCl_2$ 25 ml 0.1M Tris pH 7.0 AP Stain: 25 mg peroxidase, 2 mg amino acid oxidase, 25 mg O-dianisidine HCl, 10 mg leucyl-alanine, 25 ml 0.1M Tris, pH 8.0
PGM (120/3hrs)	Electrode Buffer: 0.10M maleic acid, 0.01M EDTA, 0.01M $MgCl_2$ chloride, pH 7.4. Gel buffer: 1:9 dilution of electrode buffer. Stain: 70 mg glucose-1-phosphate, 5mg NADP, 5mg MTT, 1mg PMS, 10 units Glucose-6-phosphate dehydrogenase, 5ml 0.1M MgCl, 20ml 0.1M Tris pH 7.

RESULTS

Labial palps

The labial palps of Macoma balthica specimens from both Virginia and the Wadden Sea are illustrated in Figures 3 and 4. The labial palps at both of these locations are alike and are representative of all the Macoma balthica examined. For all of the populations the labial palp ridges of Macoma balthica were orientated parallel to the oral groove for the entire length of each labial palp. Yonge (1949), in an earlier report of specimens from Scotland, also reported that the labial palp ridges run parallel to the oral groove (Figure 5). Gilbert (1977) reported that the palp ridges of New England specimens were orientated oblique and perpendicular to the oral groove (Figure 6). The apparent differences in the labial palp morphology reported by Gilbert (1977) cannot be confirmed and there is no evidence to consider the labial palps of eastern and western North Atlantic Macoma balthica dissimilar.

Figure 3. Scanning electron micrograph of the labial palp of <u>Macoma</u> <u>balthica</u> from Sarahs Creek, Virginia, U.S.A. (op=outer palp, og=oral groove, ip=inner palp, pr=palp ridge).

ip

pr

og
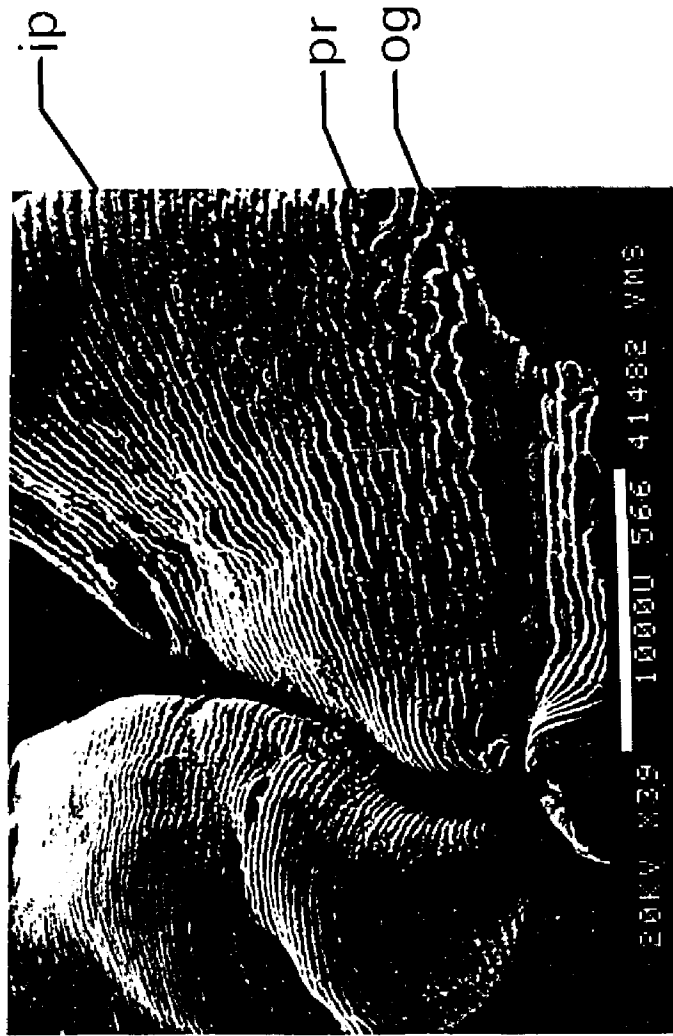
Figure 4. Scanning electron micrograph of the labial

palps of _Macoma_ _balthica_ from the Wadden Sea,

The Netherlands. See legend of Figure 3.

Figure 5.   Labial palps of <u>Macoma</u> <u>balthica</u> from Glasglow,

Scotland, redrawn from Yonge (1949).   See

legend of Figure 3.
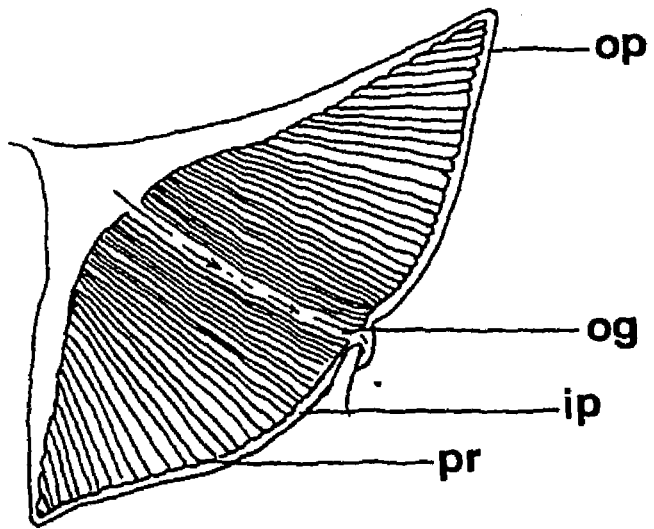
Figure 6. Labial palps of _Macoma_ _balthica_ from New
          England, redrawn from Gilbert (1977). See
          legend of Figure 3.

op

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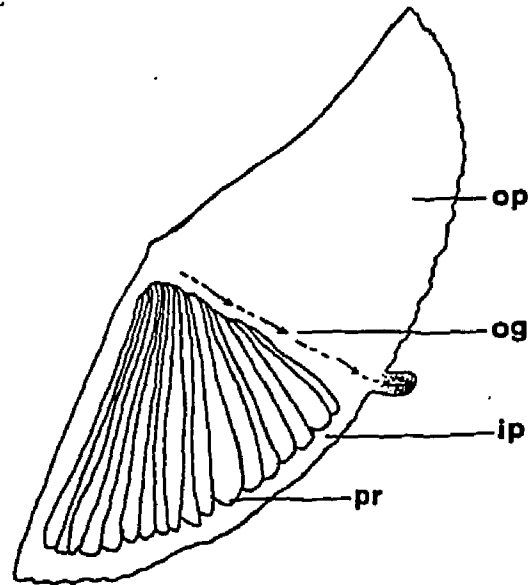
Shell shape

The average shell shapes of nearly all of the Macoma
balthica populations investigated were distinctly and
significantly different from one another and the range of
shell shapes within each population was slight (Tables 3
and 4). The most similarly shaped shells occured among
the Barn Island (4) and Niva bay (11) populations, and
the New Hampshire (5) and Disko Fjord (9) populations.
The only two populations that have average shell shapes
that are not significantly different from one another are
the Barn Island (4) and Neva Bay (11) populations (Table
3). Other populations had non-significant differences of
some but not all shell shape parameters. The average
length and width parameters of the Wadden Sea (10) and
Barn Island (4) populations, the Wadden Sea (10) and Neva
Bay (11) populations and the New Hampshire (5) and Disko
Fjord (8) populations were not significantly different
from one another, but height was significantly different
(Table 3). Moreover, the variation of shell shape for
each population, indicated by the standard deviation of
the hieght, length and width parameters, is very slight
(Table 4). The standard deviation of the mean height,
length and width parameters exceeds 0.009 only for the

Table 3. Results of Kruskal-Wallis non-parametric one
way analyses of variance comparing h, l and w
between all pairwise comparisons of populations
investigated. An h, l or w indicate that a
non-significant difference (P=0.05) occurs at
these parameters between the populations
indicated. Area within the dashed lines
represents comparisons between eastern and
western North Atlantic populations

Population number

	1	2	3	4	5	6	7	8	9	10	11	12
1		*	*	*	*	*	*	*	*	*	*	*
2			*	*	L	*	*	*	*	*	*	*
3				*	*	*	*	*	*	*	*	*
4					H	*	*	*	W	L / W	H / L / W	L
5						*	*	L / W	*	*	H	*
6							W	*	*	*	*	W
7								*	*	*	*	*
8									*	*	*	*
9										*	W	*
10											L / W	L
11												L

Population

number

Table 4. The sample size, mean, standard deviation and
          coefficient of variation of h, 1 and w for
          investigated populations. See Table 1 for
          population locations.

Pop.	number sampled	Mean			Coefficient of variation		
		h(Std.Dev.)	l(Std.Dev.)	w(Std.Dev.)	h	l	w
1	56	.356(.004)	.483(.007)	.162(.008)	1.12	1.45	4.84
2	35	.361(.006)	.466(.006)	.173(.008)	1.66	1.29	3.47
3	48	.362(.006)	.462(.006)	.176(.006)	1.66	1.30	3.41
4	46	.366(.006)	.453(.009)	.182(.008)	1.64	1.99	4.40
5	60	.365(.006)	.463(.006)	.172(.007)	1.64	1.30	4.10
6	119	.370(.007)	.445(.006)	.185(.008)	1.90	1.35	4.32
7	20	.376(.006)	.439(.012)	.185(.013)	1.59	2.73	7.02
8	50	.365(.008)	.463(.006)	.172(.007)	1.64	1.30	4.07
9	128	.359(.017)	.459(.027)	.182(.015)	4.74	5.88	8.24
10	127	.364(.008)	.452(.011)	.184(.015)	2.203	2.43	8.15
11	68	.366(.006)	.453(.007)	.182(.008)	1.64	1.55	4.40
12	75	.362(.009)	.453(.009)	.185(.009)	2.49	1.99	4.87

Wadden Sea (10) and St. Malo (9) populations. This sugests that the shell shape of each of the studied populations is very consistent through age and size.

There was a greater range of shell shapes along the western North Atlantic than along the eastern North Atlantic (Figure 7 and Table 4). The average manahattan distance value between western North Atlantic populations was 9.5, nearly as great or greater than many of the values between eastern and western North Atlantic populations (Table 5). Along the western North Atlantic there was a tendency for populations that were geographically closest together to have the most similar shell shapes (Tables 1 and 5, Figure 7). The shell shapes of the Disko Fjord (8) and the New Hampshire (5) populations were incongruous with this tendency. The two populations that have the most dissimilar shapes are the Sarah's Creek (1) and the Hudson Bay (7) populations, the manahattan distance value between these two populations is 24.649. With the exception of the New Hampshire (5) and Disko Fjord (8) populations, the western North Atlantic populations also tend to follow a north-south gradient. That is, the more southerly _Macoma balthica_ tend to have a longer and flatter shell shape; both width and length vary greater than height (Figures 7, 8 and 9, Table 4). The mean length parameter gradually decreases

Figure 7. Plot of the mean h, l and w of <u>Macoma</u> <u>balthica</u>

from each of the investigated populations.

Population numbers correspond to those in

table 1. Figures at the top of the triangle

indicate the change in shape along each of the

axis.
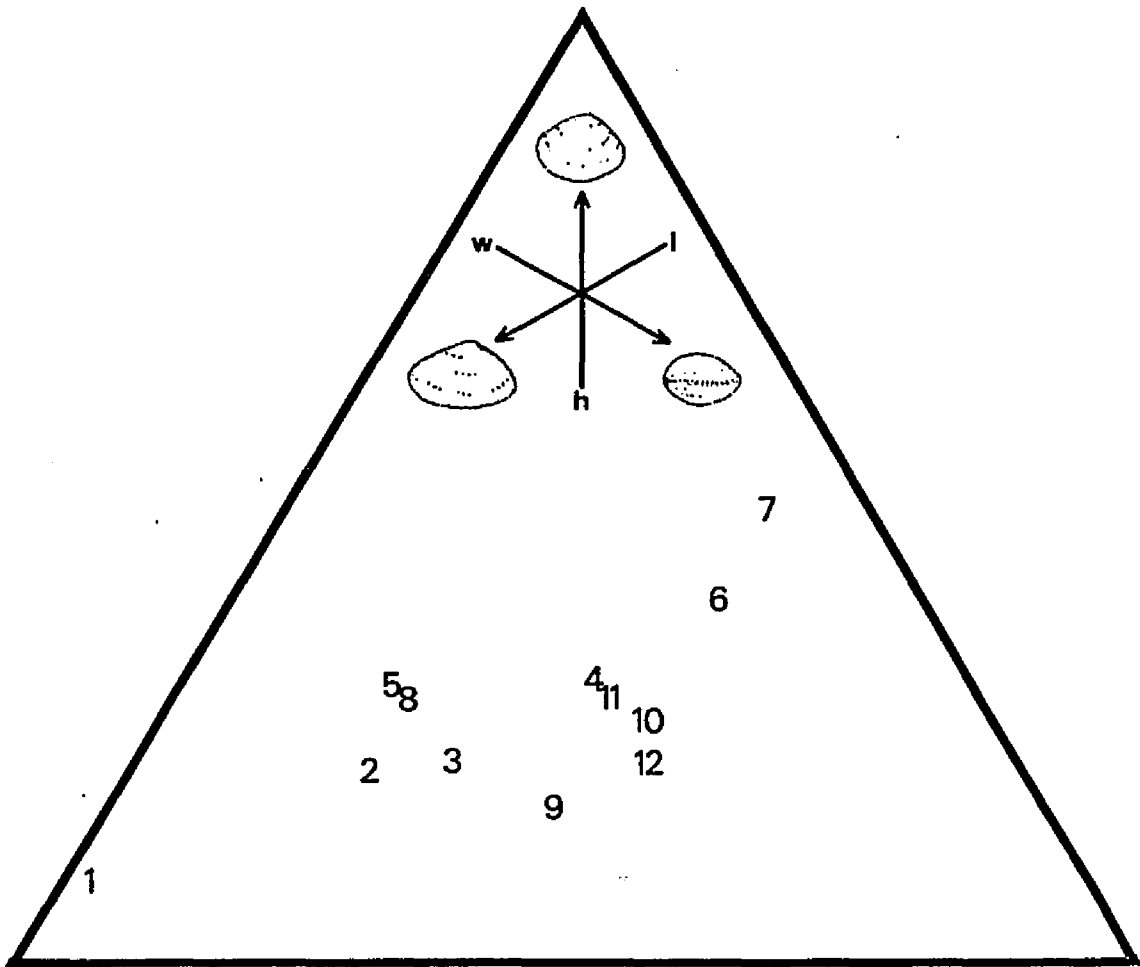
Table 5. Manhattan distance values for all pairwise
comparisons between studied populations.

Pop. No.	2	3	4	5	6	7	8	9	10	11	12
1	10.839	13.286	18.713	11.190	22.694	24.649	9.846	16.970	19.772	18.931	20.287
2		2.449	7.890	2.179	11.886	13.835	2.055	10.667	9.954	8.109	4.472
3			5.442	3.157	9.439	11.39	3.033	4.252	6.506	5.661	7.025
4				7.847	4.104	6.674	7.669	3.155	1.548	0.287	2.970
5					11.536	9.402	0.223	6.900	8.786	7.758	9.671
6						2.941	11.665	6.444	3.333	3.781	3.992
7							7.027	9.381	5.973	6.389	5.938
8								9.416	7.883	10.809	13.954
9									3.111	2.995	3.330
10										1.376	1.615
11											2.844

Figure 8. Photograph of <u>Macoma balthica</u>., lateral view,
from each of the sudied populations, numbers
correspond to population numbers given in
table 1.
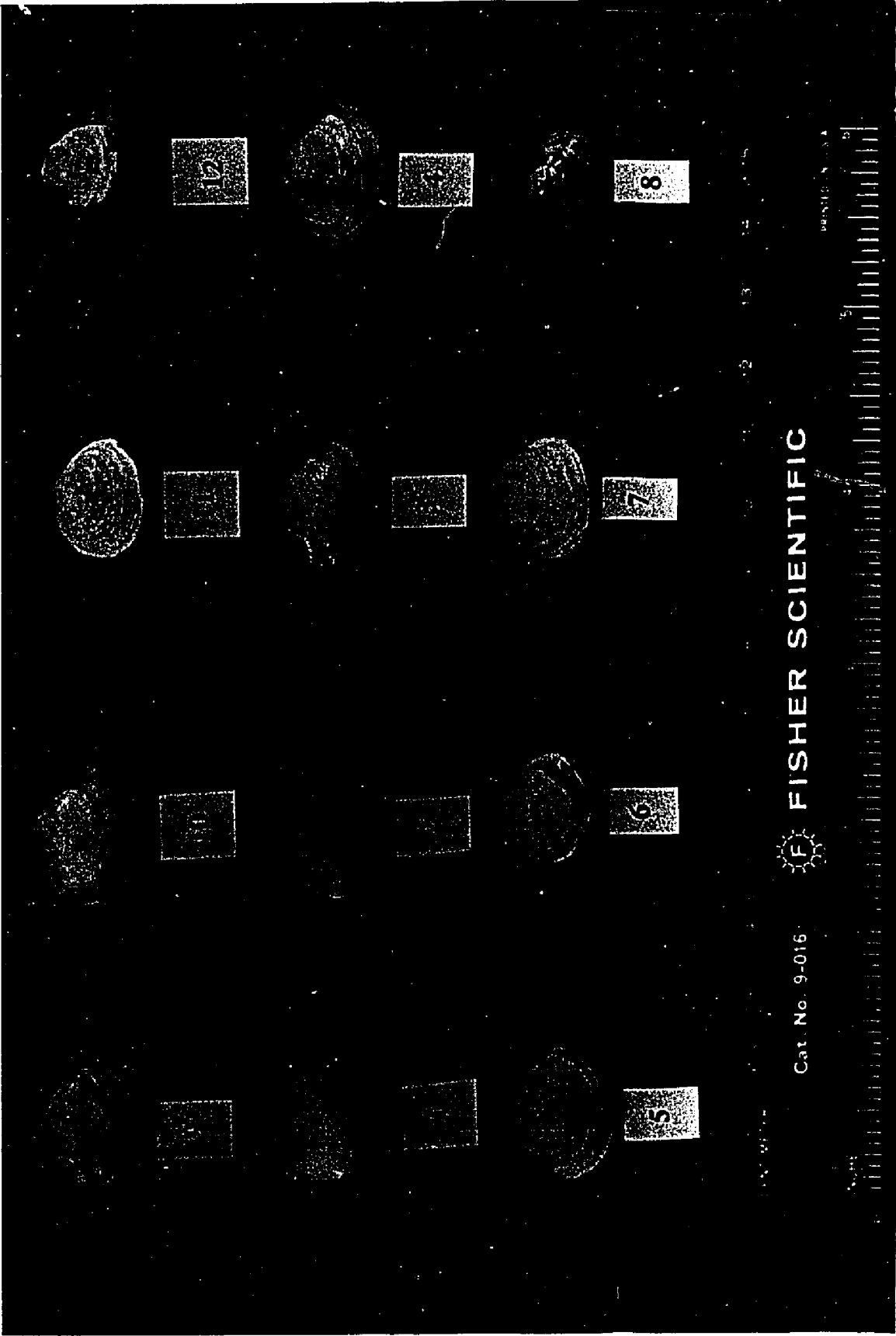
Figure 9. Photograph of <u>Macoma balthica</u>., ventral view,

from each of the sudied populations, numbers

correspond to population numbers given in

table 1.
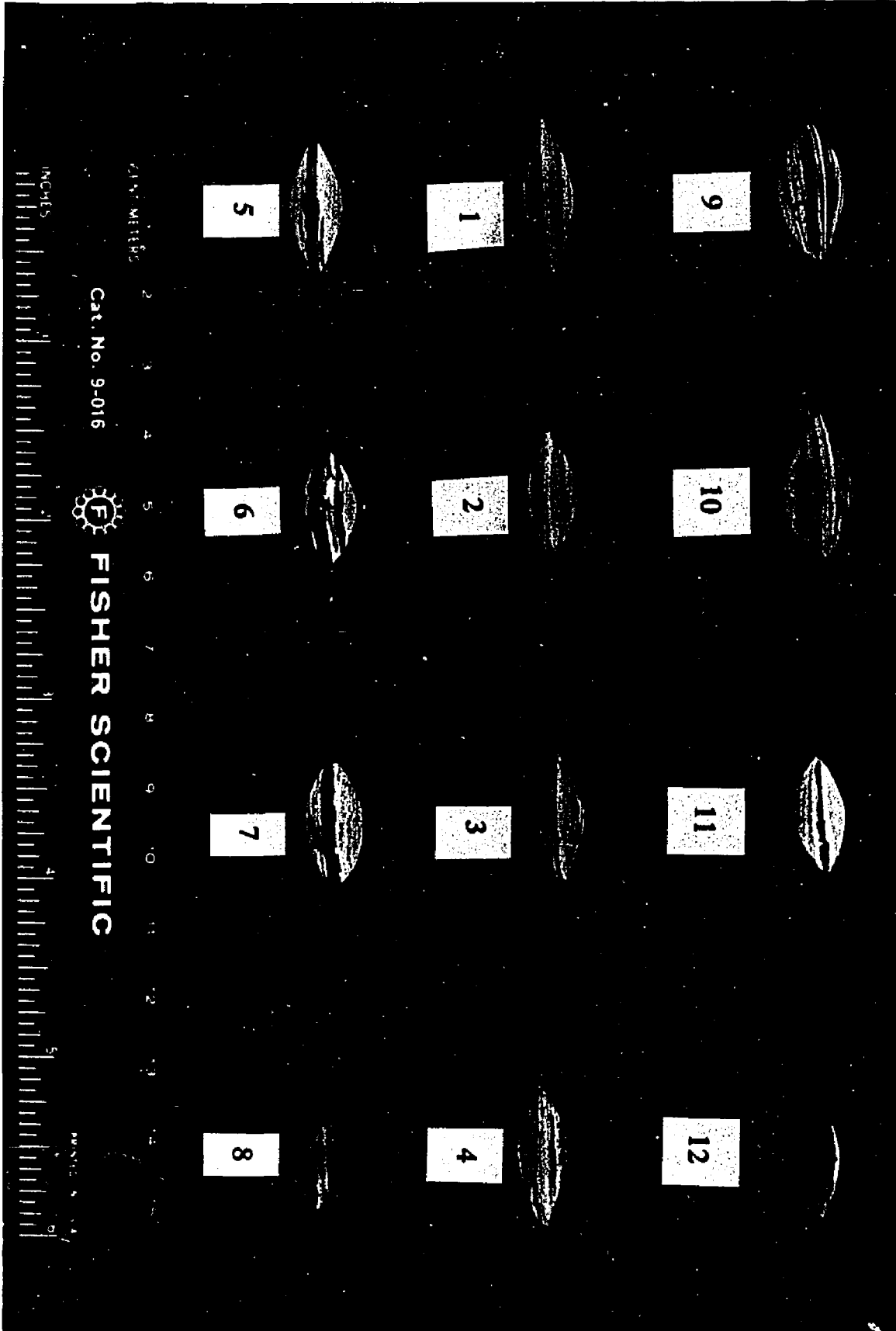
Cat. No. 9-016   (F) FISHER SCIENTIFIC

from 0.483 for the Sarah's Creek (1) population to 0.439
for the Hudson Bay (7) population. The mean width
parameter increases from 0.162 for the Sarah's Creek (1)
population to 0.185 for the Pottery Creek (6) population.
The actual differnce in shell shapes caused by these
differences in the length and width parameters is
illustrated in Figures 8 and 9.

Definitive differences between the average shell
shapes of Macoma balthica from the eastern and western
North Atlantic were not very apparent. Generally, the
shell shapes of Macoma balthica on the eastern North
Atlantic are wider then the western North Atlantic
populations (Figures 7, 8 and 9). Other distinctions
were less apparent. The coefficient of variation values
(Table 4) are slightly greater for eastern North Atlantic
populations, indicating that, at a particular location,
the shell shapes for these populations are slightly more
variable. Shell shapes of eastern North Atlantic
populations are also much more similar between
populations then those for the western North Atlantic.
The average manhattan distance value between populations
on the eastern North Atlantic was 2.54. The shell shapes
of M. balthica on the eastern North Atlantic seem less
related to latitude and there is no obvious relationship
between similarity of shape and geographic proximity
between populations.

Enzyme electrophoresis

The allele frequencies at studied loci for the populations examined are given in Table 6 and Figures 10, 11 and 12. Four enzymes, representing five loci, were investigated, three were polymorphic in all of the populations. A population is considered polymorphic when 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. Variations in allele frequencies did occur among both eastern and western North Atlantic populations. The allele frequencies of each of the investigated loci are presented below.

Malate dehydrogenase-1 (MDH-1)

The MDH-1 locus was expressed only by populations in the western North Atlantic. Two common alleles and one rare allele occured at this locus. The rare allele occured only at the Shark River population (2).

Malate dehydrogenase-2 (MDH-2)

MDH-2 was monomorphic at all of the populations except the Pottery Creek population, which contained one fast migrating relatively rare allele (Table 6). Other

Table 6. Sample sizes (n) and allele frequencies

at each locus for each population investigated.

Table 6

LOCUS	Population									
	1	2	3	4	5	6	7	8	9	10
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				

Figure 10. The cummulative frequency of the PGM alleles

at each of the populations investigated.
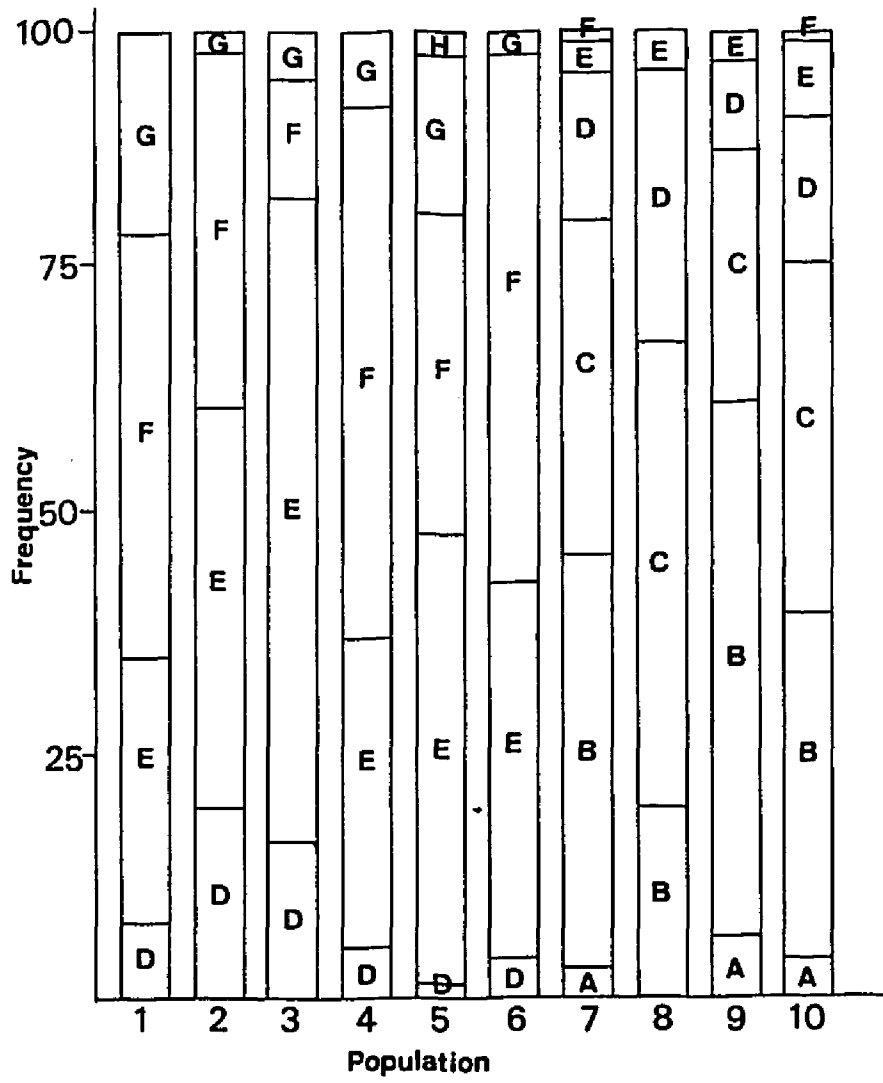
Figure 11. The cummulative frequency of the PGI alleles
at each of the populations investigated.
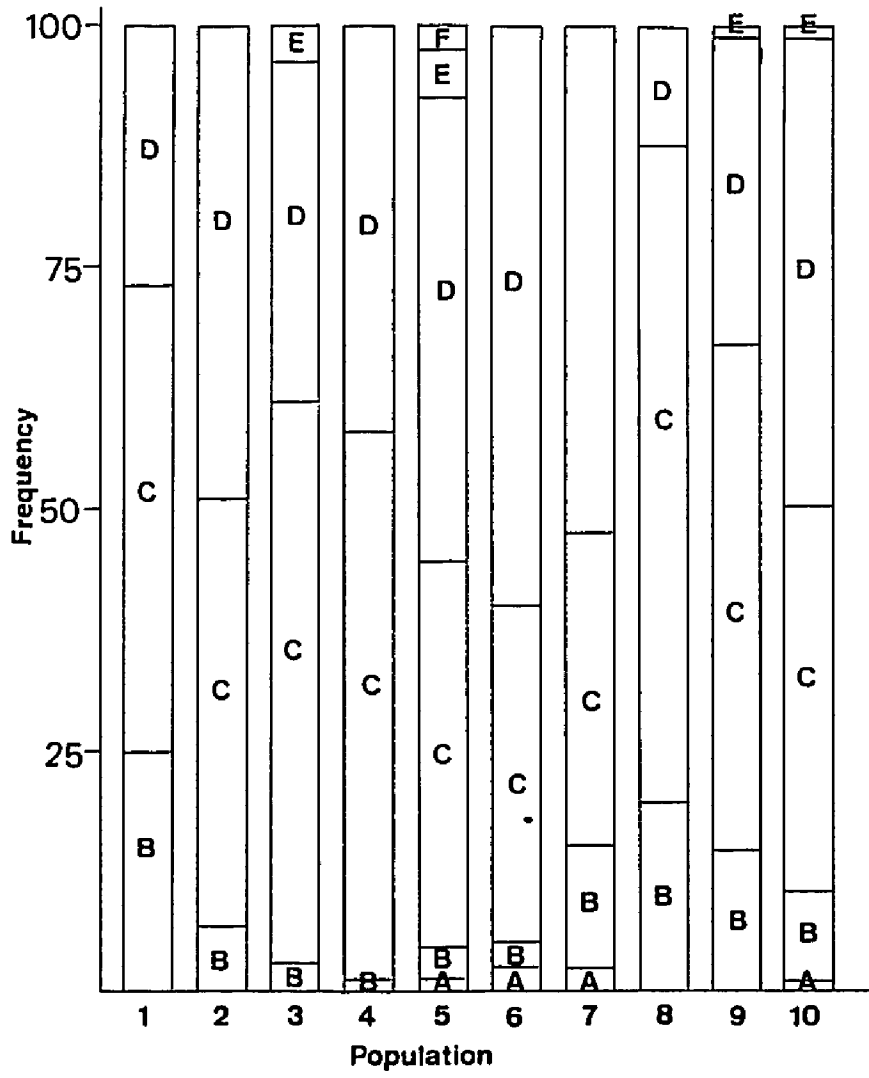
Figure 12. The cummulative frequency of the AP alleles
at each of the populations investigated.
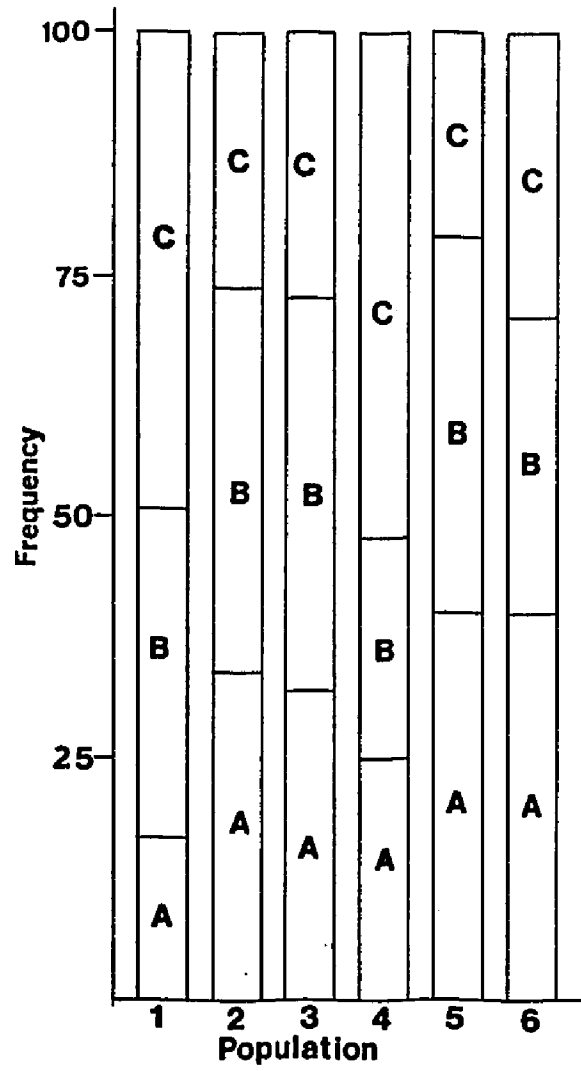
populations contained alleles unique to either the eastern or western North Atlantic. The western North Atlanic populations are represented by allele "B" and the eastern North Atlantic by Allele "C".

Phosphoglucose Isomerase (PGI)

PGI was represented by as many as six alleles in any one population. All six alleles for this locus were present in the New Hampshire population (5). The Tvarminne population (12) contained five alleles. Allele "F" at the New Hampshire population was the only allele unique to the western North Atlantic for this locus. Comparing eastern and western North Atlantic populations, it is difficult to discern any distinct pattern in the allele frequencies for this locus. Generally, allele "B" was more common on the eastern North Atlantic and allele "E" was more common on the western North Atlantic. At the Sarah's creek population allele "B" occurs at a much higher frequency, seemingly at the expense of allele "D", than in other western North Atlantic populations.

Phosphoglucomutase (PGM)

This locus exhibited more alleles then any of the other loci examined. Of the eight alleles representing this locus three ("D", "E", "F") were shared among nearly all the studied populations. Two distinct alleles ("G", "H") occurred in the western North Atlantic populations

and three distinct alleles ("A","B","C") occurred in the eastern North Atlantic populations. Allele "F" was common on the western North Atlantic but it occured at very low frequencies on the eastern North Atlantic. Allele "H" occurred only in the New Hampshire population at low frequency. The alleles that are unique to the eastern North Atlantic represent 60% or more of all the alleles that are present at this locus.

Aminopeptidase (AP)

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

The allele frequencies at each of the populations studied agree with Hardy-Weinberg expectations at each of the populations except the Tvarminne (12) and Sarah's Creek (1) populations (Table 7). The deviation from Hardy-Weinberg equilibrium for the PGI locus at the Tvarminne (12) population could be caused by a combination of the sample size and the presence of some rare alleles (Table 6). When the rare alleles at the PGI locus of the Tvarminne (12) population are pooled into a

Table 7. Chi-square test for deviation from Hardy-
Weinberg law for the Sarah's Creek (1) and
Tvarmine (12) populations, calculated from
allele frequencies using Biosys-1 (Swofford and
Selander, 1981), significant deviations occur
at $P < 0.05$.

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P
Sarah's Creek population						
MDH-1						
	B-B	25	21.556			
	B-C	15	21.888			
	C-C	9	5.556			
				4.852	1	0.028
PGI						
	B-B	6	2.625			
	B-C	3	10.250			
	B-D	6	5.500			
	C-C	15	10.006			
	C-D	8	10.738			
	D-D	4	2.881			
				13.138	3	0.004
PGM						
	D-D	0	0.278			
	D-E	1	1.909			
	D-F	5	3.102			
	D-G	1	1.432			
	E-E	5	3.273			
	E-F	12	10.636			
	E-G	1	4.909			
	F-F	4	8.642			
	F-G	14	7.977			
	G-G	1	1.841			
				13.626	6	0.034
Tvarminne population						
PGI						
	B-B	1	1.200			
	B-C	9	8.200			
	B-D	1	1.400			
	C-C	15	14.008			
	C-D	2	4.783			
	D-D	2	0.408			
				8.120	3	0.044
PGM						
	B-B	0	1.200			
	B-C	5	5.800			
	B-D	6	3.400			
	B-E	1	0.400			
	C-C	8	7.008			
	C-D	8	8.217			
	C-E	0	0.967			
	D-D	1	2.408			
	D-E	1	0.567			
	E-E	0	0.033			
				6.500	6	0.370

single group the allele frequencies are then in strong
agreement with Hardy-Weinberg expections (Table 8). The
allele frequencies at all of the polymorphic loci for the
Sarah's Creek population (1) are in disagreement with
Hardy-Weinberg expectations. Some allele frequencies at
the PGM and PGI loci of the Sarah's Creek population were
also dissimilar to other western North Atlantic
populations (Table 6). At the PGI locus allele "G" was
present at a much higher frequency and allele "D" at a
lower frequency. At the PGM locus allele "G" occured at
a much higher frequency and allele allele "C" at a lower
frequency. Also, the MDH-1 and the PGI loci of the
Sarah's Creek (1) population show a strong deficiency of
heterozygotes (Table 9). The Sarah's Creek population is
located very near the southern limit of M. balthica's
range, perhaps the departures from the Hardy-Weinberg
equilibrium and the heterozygote deficiencies are a
reflection of this (ie. marginal habitat). As a marginal
habitat, this population may be partially isolated and it
may be subject to extraordinary strong selection, perhaps
at these loci.

With regard to the loci examined, the studied
populations on each side of the North Atlantic are very
similar to one another (Table 10), but not homogeneous
(Table 11). The average genetic identity among western
North Atlantic populations is 0.975 and among eastern

Table 8. Chi square test fo deviation from Hardy-
          Weinberg law for the Tvarminne (12) population
          with the rare alleles pooled.

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P
PGI	HOMOZYGOTES FOR MOST COMMON ALLELE	15	14.008			
	COMMON/RARE HETEROZYGOTES	11	12.983			
	RARE HOMOZYGOTES AND OTHER HETEROZYGOTES	4	3.008	0.700	1	0.403
PGM	HOMOZYGOTES FOR MOST COMMON ALLELE	8	7.008			
	COMMON/RARE HETEROZYGOTES	13	14.983			
	RARE HOMOZYGOTES AND OTHER HETEROZYGOTES	9	8.008	0.526	1	0.468

North Atlantic populations is 0.971. A genetic identity of one indicates that the two populations are identical. In contrast, eastern and western North Atlantic populations are quite different from one another (Figure 13 and Tables 11 and 12). 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 6). Along the western North Atlantic this enzyme system is coded for by two loci, MDH-1 and MDH-2, and on the eastern North Atlantic only the Mdh-2 locus is present.

Table 9. Observed heterozygotes, heterozygotes expected

by Hardy-Weinberg law and fixation index (F)

for the Sarah's Creek (1) population.

Calculated from allele frequencies in table 1,

using Biosys-1 (Swofford and Selander, 1981).

Population	LOCUS	OBSERVED HETEROZYGOTES	EXPECTED HETEROZYGOTES	FIXATION INDEX (F)	D
SGK.					
	MDH-1	15	21.888	0.315	-0.315
	PGI	17	26.488	0.358	-0.358
	PGM	34	29.966	-0.135	0.135

Table 10. Matrix of Nei's unbiased genetic distance and
similarity coefficients calculated from allele
frequencies using Biosys-1 (Swofford and
Selander, 1981). Unbiased genetic identity
above diagonal and unbiased genetic distance
below diagonal.

POP.	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	0.026	*****	0.978	0.992	0.997	0.996	0.182	0.173	0.169	0.195
3	0.066	0.023	*****	0.946	0.977	0.945	0.165	0.194	0.172	0.188
4	0.015	0.008	0.056	*****	0.988	0.989	0.167	0.177	0.173	0.183
5	0.026	0.003	0.023	0.012	*****	0.996	0.164	0.140	0.152	0.178
6	0.045	0.004	0.056	0.011	0.004	*****	0.178	0.131	0.153	0.187
7	1.941	1.706	1.803	1.789	1.806	1.729	*****	0.937	0.986	1.000
8	1.732	1.752	1.641	1.731	1.964	2.034	0.065	*****	0.959	0.954
9	1.843	1.777	1.758	1.754	1.882	1.880	0.015	0.042	*****	0.987
10	1.858	1.637	1.673	1.697	1.728	1.676	0.000	0.047	0.013	*****

Table 11. Summary tables of chi-square values and
associated P-values for the analyses of
heterogeniety of allele frequencies among
studied populations.

Locus	Alleles	Chi-square	D.F.	P
Western North Atlantic				
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				
PGI	5	42.823	12	0.00002
PGM	6	36.916	15	0.00130
Totals		79.739	27	0.00000

Table 12. Summary of genetic differences between
           populations on the eastern and western North
           Atlantic infered by enzyme electrophoresis

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

Figure 13.   Population phenogram calculated from
              Nei's unbiased genetic identity (1978) using
              Biosys-1 (Swofford and Selander (1981).

SIMILARITY

0.00	0.17	0.33	0.50	0.67	0.83	1.00
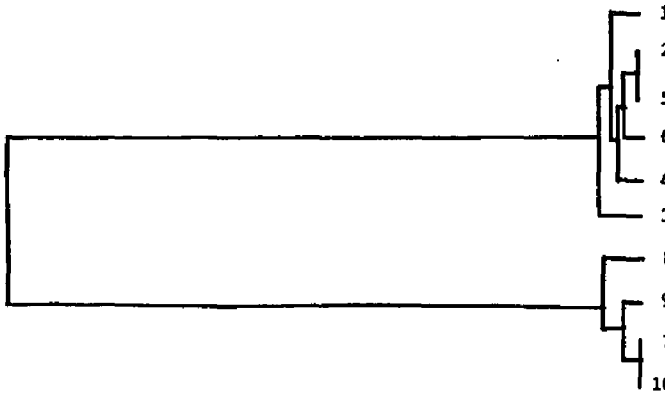
0.00	0.17	0.33	0.50	0.67	0.83	1.00

DISCUSSION

Labial Palps

The labial palps of Macoma balthica were re-examined
to better describe and compare previously reported
differences between eastern and western North Atlantic
populations. The differences in the labial palps as
described by Yonge (1949) and Gilbert (1977) implies
differences in feeding between the New England and
Scottish Macoma balthica. According to Gilbert (1977),
this arrangement of the palp ridges accommadated the
palps for sorting and movement of food particles and
assisted Macoma balthica as an effective deposit feeder.
Re-examination of the labial palps of both the eastern
and western North Atlantic M. balthica indicate that
they were both the same as reported by Yonge (1949). In
the present investigation Macoma balthica specimens were
not examined from the exact same location that Gilbert
obtained her specimens. However, they were examined from
other locations in New England, both north and south of
Gilbert's. The description of the labial palps given by
Gilbert (1977) may be erroneous. In any case, the labial
palps of M. balthica cannot be used as a morphological

character to distinguish between eastern and western North Atlantic populations.

Shell Shape

Bivalve shell shape and structure can be influenced by both physical and chemical components of a habitat (Digby, 1968; Dodd, 1964, 1966; Lutz and Rhoads, 1977). In particular habitats there are optimum shell shapes which are often shared among the bivalves within that habitat (Kaufman, 1969; Nicol, 1978; Stanley, 1970, 1975; Vermeij, 1978). For example, smooth compressed shells with reduced hinges, smooth inner valve margins and relatively small adductor muscles are characteristics shared among rapid, deep burrowing bivalves. Many shallowly buried infaunal bivalves contain radial or concentric ribs and complex hinge dentition which stabilize the animal in the sediment and prevents the valves from shearing upon one another, respectively (Vermeij, 1978). Though shell shape and habitat characteristics are closely coupled, habitat induced variations in shell shape are bounded by the limits imposed by the genetic composition of a species. Shell shape is genetically restricted (Kennedy, et al., 1969); otherwise, bivalve shells would be amorphous, complying to the demands dictated by habitat characteristics.

Closely related bivalves living in similar habitats might be expected to have similar shell shapes (Nicol, 1983). A bivalve will possess the most advantageous shell shape for survival at a particular habitat within its perceptive and genetic capabilities. It is likely that the variety of shell shapes of M. balthica are habitat induced, within the limits of its genetic composition and perceptive capabilities. This is best illustrated by the different shell shapes between locations and the consistency of shell shape of M. balthica at each specific location.

Depending on scale, habitats can be defined by a few broad parameters or a seemingly infinite number of specific ones. The essential habitat parameters that are percieved by an organism and that might have an effect on an organism are difficult to determine, as mentioned previously the relationship of M. balthica to a number of habitat parameters has been investigated. Gilman (1979) conducted transplant experiments with M. balthica in the western North Atlantic and concluded that temperature was an essential habitat parameter, with respect to growth and survival, other factors were not considered. Temperature, as an essential habitat parameter might be manifest as different shell shapes along a north-south gradient, perhaps evidenced within the studied populations along the western North Atlantic. The

maximum surface water temperature gradually decreases

form $30^{\circ}C$ at the Sarah's Creek(1) population to $15^{\circ}C$ at

the Pottery Creek population(6). The maximum surface

water temperature at the Hudson Bay(7) and Disko Fjord(8)

populations is $5.0^{\circ}C$. However; because the New

Hampshire(5) and the Disko Fjord(8) populations do not

agree with this trend, and because they are very similar

to one another, it is likely that habitat factors other

than temperature may also be percieved by and have an

effect on life history aspects of M. balthica. The mean

surface water temperature of Greenland coastal water is

approximately $0.83^{\circ}C$, the range is approximately -1.6 to

$5.0^{\circ}C$. The mean surface water temperature at the New

Hampshire site is $11.0^{\circ}C$, the range is -2.0 to $27^{\circ}C$.

Macoma balthica shell shape appears to be closely

aligned and sensitive to habitat parameters. For

example, the habitat parameters might define a frame or

mold, the mold defines an optimum shape for a bivalve for

that particular habitat. This of course is not limited

to bivalve shell shapes but may apply to any direct

organism-habitat interaction, provided the organism does

not have the ability to alter the habitat mold. As an

organism enters a particular habitat its survival is

related to its ability to conform to the mold of that

habitat. It is suggested that M. balthica, especially

those of the western North Atlantic, conform highly to so called "habitat molds", allowing them to become fine tuned to a particular habitat.

This does not imply that shell shape cannot be used to distinguish genetically distinct populations, but that it can be difficult when comparing similar organisms in like habitats. Two geographically discrete populations, within like habitats, of similar shell shapes, may not be genetically alike and equally capable of obtaining the most advantageous shell shape for that particular habitat. Because western North Atlantic M. balthica are capable of a wide variety of shell shapes it is not unlikely that similarities between some eastern and western North Atlantic M. balthica occur. They are closely related bivalves, at the very least members of the same genus, occupying similar habitats along comparable geographic ranges. The similarity of shell shapes between some eastern and western North Atlantic M. balthica populations may be more an indicator of comparable habitats then of genetic identity.

Perhaps a better indication of discrete populations between eastern and western North Atlantic M. balthica might be the range of available shell shapes. A bivalve capable of producing many shell shapes probably contains a different genetic composition then one restricted with

respect to shell shape, certianly it is easy to realize the advantage of the former. It is difficult to determine if eastern North Atlantic M. balthica are genetically restricted or restricted by habitat characteristics. Specimens were obtained from a number of habitats (eelgrass beds, intertidal and shallow water subtidal fine sand/mud, and deep water mud) encompassing much of its' eastern North Atlantic range. Yet, the variety of shapes of specimens from the eastern North Atlantic was slight compared to western North Atlantic populations. The ability of the western North Atlantic M. balthica to produce a variety of shell shapes is a distinctive characteristic of western North Atlantic populations.

Enzymes

The slight variations in allele frequencies that occurred within the studied populations from either the eastern or western North Atlantic were not unexpected. Other invertebrates whose genetic population structure have been determined includes Aurelia aurita (Zubkoff and Lin, 1975), Limulus polyphemus (Selander et al., 1970), Cyathura spp. (Parker et al., 1979), Arbacia puntulata (Marcus, 1980), Metridium spp. (Walsh and Somero, 1981; Buchlin and Hedgecock, 1982), Goniobasis sp. (Chambers,

1980), _Ctenodiscus_ _crespatus_ (Schick et al., 1981),
Busycon _spp._ (Edwards and Humphrey, 1981), _Hydrobia_ _spp._
(Lassen, 1979), _Corbicula_ _SPP._ (Hillis and Patton, 1982),
Littorina _spp._ (Berger, 1973, 1977; Snyder and Gooch,
1973), _Crassostrea_ _spp._ and _Saccostrea_ _spp._ (Buroker et
al., 1975, 1979a, 1979b; Singh and Zouros, 1978; Koehn
and Shumway, 1982), _Macoma_ _spp._ (Reid and Dunnil, 1969;
Levinton, 1973; Green et al., 1983), _Mytilus_ _edulis_
(Milkman and Beatty, 1970; Koehn et al., 1976; Singh and
Zouros, 1978; Murdock et al., 1975; Skibinski et
al.,1980; Beaumont and Beveridge, 1983; Beaumont et al.,
1983; Gartner-Kepkay et al., 1980, 1983) and others
(Gooch, 1975; Burton, 1983). _Mytilus_ _edulis_ and
Crassostrea _spp._ have probably been the most thoroughly
investigated of all marine bivalves. Variations in
allele frequencies along microgeographic and
macrogeographic ranges are common in marine bivalves and
are often associated with environmental and habitat
differences (Koehn and Mitton, 1972; Koehn et al., 1973;
Levinton, 1973; Mitton et al., 1973; Singh and Zouros,
1978; Theisen, 1978; Koehn, 1983). Because there is such
a large geographic distance between studied populations
of _Macoma_ _balthica_ it is difficult to identify any clinal
variations on a microgeographic or macrogeographic scale.
Green (1983) found that the genetic heterozygosity of two
intertidal populations of _M._ _balthica_ increased slightly
with increased distance above mean low water. It is

likely that the variations in allele frequencies of the studied populations of M. balthica on each side of the North Atlantic are caused by environmental and habitat differences. Unique alleles that occur among either 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 gone undetected in other populations.

Though studied populations on each side of the North Atlantic are very similar with respect to the loci investigated the eastern and western North Atlantic populations are quite different from one another. There are no reports of unique alleles fixed at a locus occurring between populations of a single species. The presence of the MDH-1 locus only on the western North Atlantic represents considerable genetic differentiation between eastern and western North Atlantic populations. Varvio-Aho and Vainola (1983) have been trying to resolve the MDH system of M. balthica in the Baltic Sea. Though they have had difficulties, they could identify only one locus for this system. Fujio et al. (1984) found a variable number of MDH loci among 25 different species of molluscs; Corbicula japonica has one MDH locus while Crassostrea and Ostrea species each have 5 loci. The presence of this unique locus on the western North Atlantic, as well as many unshared alleles between

eastern and western North Atlantic populations, strongly indicates that the eastern and western North Atlantic populations of M. balthica are genetically distinct from one another. As a general descriptor, genetic similarity values indicate that eastern and 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, Mytilus galloprovincialis and Modiolus modiolus. Genetic similarity between the Mytilus species was less than 0.9, and between the genera Mytilus and Modiolus less than 0.25. Buroker et al. (1979a, 1979b) found that the genetic similarity among five species of Crassostrea was less than 0.8, and 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, M. 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, its habitat. As an adult it has only a limited ability for

survival out of the sediment. Newly settled spat reside approximately 1 mm below the sediment surface and adults reside as much as 30 cm below the sediment surface (Gilbert, 1973; Schaffner, 1983). While buried, the pressure from surrounding sediment assists the adductor muscles in maintaining a correct valve position. When out of the sediment, the adductor muscles, working as antagonists to the elastic shell ligament, become fatigued, causing the shell to gape and the organism to die. Because of this long range migration by mature M. balthica is impossible.

Because M. balthica is apparently incapable of a sustained migration as an adult, it must depend on a passive mode of dispersal of its planktonic larvae to maintain range continuity. The planktonic larval period of M. balthica is approximately two months long (Lammens, 1967; Ankar, 1979; Gilbert, 1979). It is generally possible for molluscs to postpone metamorphosis from a planktonic to a benthic state (Bayne, 1965; Seed, 1976). There is no indication that M. balthica is an exception to this phenomenon. Though delayed metamorphosis provides more time for encountering an adequate habitat, it is not without costs; both viability and survivorship decrease (Thorson, 1950, 1961; Bayne, 1965). As absolute larval longevity values are unknown, it will be assumed that M. balthica can delay metamorphosis for as long as

one month, providing a planktonic larval duration of 90
days maximum. Laboratory experiments with _Mytilus_ _edulis_
(Bayne, 1965) indicate that metamorphosis can be delayed
up to 40 days at $10^{\circ}C$ and 2 days at $20^{\circ}C$.

There are four primary factors for successful
transoceanic transport of teleplanic larvae: the
direction and speed of available ocean currents, the
distance between populations, the maximum duration of
larval development and larval behavior (Scheltema, 1972,
1972a, 1978; Colebrook, 1982; Burton and Feldman, 1982;
). The currents that would operate as vectors for
transoceanic larval transport for _M._ _balthica_ are
illustrated in Figure 14. Using estimates of velocity
for travel along these currents (Scheltema, 1966) the
time required for passive travel from the western to
eastern Nothern Atlantic can be determined (Table 13).
When these estimates are compared with the estimated
maximum planktonic duration of _M._ _balthica_ larvae,
presented above, 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 between opposite sides of the North

Figure 14.   Major ocean currents in the North Atlantic,
             stipled areas indicate distribution of <u>Macoma</u>
             <u>balthica</u>.

Table 13. The days required for transAtlantic drift
           between the locations indicated. Calculated
           using drift velocity estimates determined by
           Scheltema, 1966.

	Stornway, Scotland	Galway, Ireland	Bay of Biscay, France
Hebron, Labrador	230		
St. Johns, New Foundland		155	
Norfolk, Virginia			300

Atlantic. This scheme has been proposed by Kraeuter (1974) for the colonization of the North American coast by Littorina littorea. Kraeuter determined that direct larval drift from northern-central Europe is highly unlikely, requiring approximately 200 days. Therefore, he suggested that Greenland and Iceland operated in the past as stepping stones for L. littorea and that these locations have since become unsuitable for L. littorea because of climatic changes and glacial advances. Berger (1973, 1977), genetically compared eastern and western North Atlantic populations and presented a similar hypothesis to explain the present day distribution of Littorina littorea. Whether or not M. balthica utilized a similar mechanism for colonization of North America is not certain. It is unlikely that Greenland and Iceland operate as stepping stones today, M. balthica occurs only on western Greenland (Madsen, 1983) 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 manner in which M. balthica could have become established in its North Atlantic range.

A few sporadic fossil records of M. balthica exist for as far back as 60 million years (Moore, 1969). The Atlantic ocean is approximately 130 million years old (Dietz and Holden, 1970; Sclater and McKenzie, 1979).

Perhaps M. balthica established its pan-Atlantic distribution during post-genesis of the Atlantic basin and as the Atlantic broadened by continental drift (Hallam, 1983; Kennett, 1982) transoceanic exchange of larvae was continually reduced. With this hypothesis, also used to describe the distribution of a number of other species (Sterrer, 1973; Vermiej, 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). Although M. balthica may have once existed as contiguous populations throughout the North Atlantic, possibly as a result of the phenomenon of plate tectonics, it now exists as two allopatric populations which are slowly diverging according to the potential of each.

Conclusion

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

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