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A Correlation of Heterozygosity with Growth Rate in the Pacific Oyster, *Crassostrea gigas*

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Summary

Twenty wild populations of the Pacific oyster, *Crassostrea gigas*, were assayed by starch gel electrophoresis for the genetic variations of five enzyme loci (*Idh-1*, *Pgm*, *Aat-2*, *Gpi-1b*, and *Lap-1b*). Homozygote excess at the five loci was observed in some wild populations and an inbreeding structure was suggested. The inbreeding coefficient(F) was estimated from the observed and expected heterozygosities and the estimate for the oyster population was 0.152 in average, the range being 0 to 0.415. It suggests that the population of the wild Pacific oyster as a whole has a tendency to form an inbreeding structure.

It was further observed that the populations having a higher inbreeding coefficient tended to have a lower body weight, and that individual heterozygosity was positively correlated with body weight. It was concluded that heterozygosity and growth rate are positively correlated but this correlation is not necessarily a causal one.

The electrophoretical surveys on protein polymorphisms have revealed that almost all populations are characterized by a large amount of genetic variation. Several studies on enzyme polymorphisms in marine molluscs have revealed that the frequencies of homozygotes were often higher than the expected values under Hardy-Weinberg's equilibrium (1–8). The homozygote excess at the *Idh-1* locus in the Pacific oyster population was reported previously and an inbreeding structure was suggested (8).

Inbreeding causes an increase in the frequencies of homozygous genotypes and a decrease of heterozygous genotypes. Therefore, the influence of a change of population on inbreeding must be connected with a difference of genotypic value between homozygotes and heterozygotes. The most observed consequence of inbreeding is the reduction of the fitness. Imai and Sakai (9) described that the inbreeding of Pacific oyster for three generations caused no decrease in the rate of fertilization at mating but as the generations proceeded and progeny of the 4th generation failed to produce vigorous larvae. Longwell and Stiles (10) reported that marked fertilization failures occurred on sib-inbreeding of American oyster (*Crassostrea virginica*) and that the larvae showed a low survival and growth rate.

In oysters, there can be a great amount of variation in shell size among individuals of the same age growing under uniform conditions. We observed this to be true in a cultured population of the Pacific oyster (8). This observation induced us to study the relation of genetic factors and the differences of heterozygosity to growth rates. Assuming that individual electrophoretic homozygosity will be positively correlated with the degree of homozygosity by descent, the present study was designed to elucidate a possible association of heterozygosity with growth rate.

Materials and Methods

The Pacific oyster, *Crassostrea gigas* was collected from wild populations on the Pacific coasts of Miyagi, Fukushima, Hyogo, and Hiroshima. The oysters were collected from January to May before the onset of reproduction and the meat weight was measured. Prior to weighing, the oysters were removed from their shells and then were placed on filter papers to release most of the free water. Lists on gene frequencies at the five enzymic loci were given in the previous paper (11). An additional four populations were examined for the five loci and the gene frequency was calculated. The observed heterozygosity was counted from phenotypic frequencies for each locus and the expected heterozygosity was calculated from the gene frequencies.

Results

Twenty wild populations were assayed for the genetic variations of five enzymic loci (*Idh-1*, *Pgm*, *Aat-2*, *Gpi-1b*, and *Lap-1b*). Table 1 summarized the observed and expected heterozygosities at each locus and at the five loci for the 20 different wild populations. The observed heterozygosity (Ho) is the ratio of the number of observed heterozygotes to the total number of oysters examined. The observed heterozygosity is to be compared with the expected heterozygosity (He) obtained from $He=1-\Sigma p_i^2$, where p_i^2 is the gene frequency. We can divide the 20 different populations into two groups as follows. The first group includes the population in which the observed heterozygosity fits the expected value under Hardy-Weinberg's equilibrium. The second group includes the population in which the observed heterozygosity is smaller than the expected heterozygosity. The deviation of observed heterozygosity from the expected value was statistically significant at more than one locus. The deficiency of heterozygosity reflected a homozygote excess.

A homozygote excess could be due to an inbreeding structure of the population. If this is the case, a difference between the first and second groups could be led by inbreeding coefficient(F). The inbreeding coefficient(F) was estimated from $F=1-Ho/He$, where Ho stands for observed and He for expected heterozygosity at the five loci. The estimated F was given in Table 1. The first group was smaller than

TABLE 1. *Heterozygosity and Inbreeding*

Group	Population	No. of oysters	*Idh-1*	*Pgm*
I	Akoh, Hyogo	60	0.466 (0.460)	0.516 (0.579)
	Ishinomaki, Miyagi	50	0.360 (0.393)	0.340 (0.367)
	Onagawa-1, Miyagi	60	0.366 (0.428)	0.483 (0.507)
	Matsushima-3, Miyagi	50	0.300 (0.352)	0.560 (0.585)
	Watari, Miyagi	225	0.394 (0.431)	0.538 (0.588)
	Onagawa-2, Miyagi	50	0.320 (0.355)	0.540 (0.594)
	Yasuura, Hiroshima	105	0.361 (0.421)	0.571 (0.623)
	Mangokuura-1, Miyagi	50	0.300 (0.324)	0.560 (0.610)
	Mangokuura-5, Miyagi	53	0.340 (0.370)	0.528 (0.599)
	Matsushima-2, Miyagi	65	0.338 (0.376)	0.461 (0.481)
II	Mangokuura-3, Miyagi	75	0.360 (0.406)	0.346 (0.518)
	Mangokuura-4, Miyagi	120	0.258 (0.262)	0.416 (0.527)
	Ondo-2, Hiroshima	75	0.373 (0.504)	0.386 (0.487)
	Matsushima-1, Miyagi	50	0.240 (0.350)	0.440 (0.580)
	Haragama, Fukushima	60	0.250 (0.357)	0.450 (0.587)
	Watanoha, Miyagi	120	0.333 (0.424)	0.466 (0.600)
	Ojika, Miyagi	50	0.260 (0.400)	0.480 (0.665)
	Mangokuura-2, Miyagi	50	0.180 (0.333)	0.280 (0.416)
	Ondo-1, Hiroshima	60	0.333 (0.467)	0.450 (0.684)
	Kesennuma, Miyagi	54	0.184 (0.311)	0.240 (0.333)

Number in parentheses presents the expected

0.100 in the F value and the second group was greater. The average for the populations examined as whole was 0.152 in the F value, the range being 0 to 0.415. It suggests that the population of the wild Pacific oyster as a whole has a tendency to form an inbreeding structure.

Furthermore, Table 2 gives the mean meat weight for each population. Although there were a few exceptional populations, it was observed that the populations of higher inbreeding coefficient tended to have lower weight. A comparison of the mean weight in the first and second groups revealed that the two groups showed a significant difference in average of mean weight. However, a clear correlation of the mean weight with the inbreeding coefficient was not observed in the 20 different populations ($r=0.253$). The difference of the weight distribution among wild populations was attributed to the age composition in a population and to the environmental conditions under which the wild popultion grew. The test was done in 12 populations (Ishinomaki, Matsushima, Watari, Mangokuura, Watanoha, and Ojika) in Sendai Bay in which growing condition was considered to be uniform. The result indicated a clear correlation of the mean weight with the inbreeding coefficient ($r=0.568$) as shown in Fig. 1. Regression of the mean weight on the inbreeding coefficient was calculated as $Y=-11.9X+6.2$. The regression coefficient for the equation means that high inbreeding causes a higher reduction of growth rate.

The observation that the lower mean weight is more pronounced in the first

Coefficient(F) in Wild Populations of Oyster

Aat-2	*Gpi-1b*	*Lap-1b*	Five loci	F
0.533 (0.491)	0.133 (0.157)	0.300 (0.269)	0.390 (0.390)	0.000
0.520 (0.487)	0.340 (0.326)	0.380 (0.395)	0.388 (0.393)	0.013
0.466 (0.467)	0.233 (0.212)	0.350 (0.319)	0.380 (0.386)	0.016
0.520 (0.536)	0.360 (0.354)	0.300 (0.282)	0.408 (0.421)	0.031
0.530 (0.518)	0.214 (0.205)	0.277 (0.292)	0.391 (0.401)	0.031
0.340 (0.361)	0.280 (0.268)	0.300 (0.291)	0.356 (0.373)	0.046
0.409 (0.395)	0.228 (0.242)	0.276 (0.289)	0.367 (0.393)	0.067
0.440 (0.437)	0.200 (0.217)	0.340 (0.397)	0.368 (0.396)	0.071
0.415 (0.440)	0.170 (0.225)	0.321 (0.318)	0.355 (0.390)	0.091
0.461 (0.481)	0.184 (0.186)	0.200 (0.239)	0.329 (0.365)	0.099
0.360 (0.486)	0.173 (0.207)	0.186 (0.227)	0.325 (0.368)	0.117
0.391 (0.431)	0.158 (0.172)	0.308 (0.362)	0.306 (0.350)	0.126
0.240 (0.262)	0.373 (0.417)	0.253 (0.327)	0.325 (0.398)	0.184
0.080 (0.096)	0.340 (0.395)	0.200 (0.229)	0.260 (0.329)	0.210
0.400 (0.514)	0.167 (0.187)	0.333 (0.437)	0.320 (0.415)	0.229
0.366 (0.455)	0.183 (0.233)	0.166 (0.283)	0.303 (0.398)	0.239
0.260 (0.367)	0.300 (0.391)	0.160 (0.269)	0.292 (0.417)	0.300
0.320 (0.453)	0.140 (0.233)	0.200 (0.328)	0.224 (0.352)	0.364
0.283 (0.444)	0.233 (0.459)	0.200 (0.373)	0.300 (0.484)	0.381
0.333 (0.502)	0.092 (0.155)	0.092 (0.251)	0.181 (0.309)	0.415

value under Hardy-Weinberg's equilibrium.

TABLE 2. *Inbreeding Coefficient and Mean Weight*

Group	Population	No. of oysters	F	Mean weight (g)
I	Akoh, Hyogo	60	0.000	3.10±0.19
	Ishinomaki, Miyagi	50	0.013	5.80±0.34
	Onagawa-1, Miyagi	60	0.016	6.36±0.37
	Matsushima-3, Miyagi	50	0.031	7.85±0.57
	Watari, Miyagi	225	0.031	6.71±0.39
	Onagawa-2, Miyagi	50	0.046	7.49±0.50
	Yasuura, Hiroshima	105	0.067	2.50±0.07
	Mangokuura-1, Miyagi	50	0.071	6.89±0.45
	Mangokuura-5, Miyagi	53	0.091	2.98±0.39
	Matsushima-2, Miyagi	65	0.099	7.67±0.36
	Average		0.047	5.70±0.64
II	Mangokuura-3, Miyagi	75	0.117	1.92±0.08
	Mangokuura-4, Miyagi	120	0.126	2.27±0.11
	Ondo-2, Hiroshima	75	0.184	2.51±0.15
	Matsushima-1, Miyagi	50	0.210	3.64±0.26
	Haragama, Fukushima	60	0.229	5.10±0.39
	Watanoha, Miyagi	120	0.239	1.39±0.05
	Ojika, Miyagi	50	0.300	4.72±0.25
	Mangokuura-2, Miyagi	50	0.364	2.56±0.13
	Ondo-2, Hiroshima	60	0.381	1.63±0.09
	Kesennuma, Miyagi	54	0.415	8.41±0.81
	Average		0.257	3.41±0.68

TABLE 3(1). *Mean Weight of Genotypes in Wild Populations of Oyster*

Population	*Idh*-1		*Pgm*		*Aat*-1	
	Heterozygote	Homozygote	Heterozygote	Homozygote	Heterozygote	Homozygote
	g	g	g	g	g	g
Akoh, Hyogo	3.33±0.33(28)*	2.89±0.23(32)	2.99±0.30(31)	3.21±0.25(29)	3.25±0.30(32)*	2.91±0.24(28)
Ishinomaki, Miyagi	6.39±0.53(18)**	5.46±0.45(32)	7.17±0.61(17)**	5.09±0.37(33)	5.75±0.48(26)	5.85±0.52(24)
Onagawa-1, Miyagi	6.31±0.49(22)	6.39±0.51(38)	6.62±0.56(29)*	6.12±0.50(31)	6.06±0.55(28)	6.62±0.50(32)
Matsushima-3, Miyagi	8.09±1.05(15)*	7.75±0.69(35)	9.03±0.84(28)**	6.35±0.62(22)	8.36±0.87(26)*	7.30±0.73(24)
Watari, Miyagi	6.84±0.63(87)*	6.63±0.51(138)	6.94±0.55(122)*	6.44±0.57(103)	7.15±0.59(120)*	6.21±0.51(105)
Onagawa-2, Miyagi	7.60±0.99(16)*	7.43±0.58(34)	8.51±0.72(27)**	6.28±0.61(23)	9.28±1.09(17)**	6.56±0.44(33)
Yasuura, Hiroshima	2.88±0.11(38)**	2.29±0.09(67)	2.67±0.10(60)**	2.28±0.11(45)	2.77±0.12(43)**	2.32±0.09(62)
Mangokuura-1, Miyagi	7.87±0.96(15)**	6.47±0.49(35)	7.06±0.61(28)*	6.67±0.69(22)	8.11±0.78(22)**	5.93±0.47(28)
Mangokuura-5, Miyagi	3.38±0.52(18)*	2.77±0.46(35)	2.94±0.54(28)	3.02±0.57(25)	3.18±0.70(22)*	2.83±0.45(31)
Matsushima-2, Miyagi	8.14±0.67(22)*	7.43±0.44(43)	7.87±0.58(30)*	7.49±0.47(35)	7.47±0.58(30)	7.84±0.47(35)
Mangokuura-3, Miyagi	2.00±0.12(27)*	1.87±0.10(48)	1.95±0.14(26)*	1.90±0.09(49)	2.14±0.10(27)**	1.79±0.10(48)
Mangokuura-4, Miyagi	2.38±0.23(31)*	2.23±0.13(89)	2.82±0.20(50)**	1.88±0.10(70)	2.37±0.18(47)*	2.21±0.14(73)
Ondo-2, Hiroshima	3.15±0.30(28)**	2.12±0.14(47)	3.44±0.29(29)**	1.92±0.10(46)	3.18±0.36(18)**	2.30±0.16(57)
Matsushima-1, Miyagi	4.50±0.45(12)**	3.36±0.30(38)	4.05±0.38(22)**	3.31±0.36(28)	5.25±1.06(4)**	3.50±0.26(46)
Haragama, Fukushima	6.33±0.69(15)**	4.69±0.45(45)	5.13±0.58(27)*	5.08±0.53(33)	6.43±0.66(24)**	4.22±0.42(36)
Watanoha, Miyagi	1.57±0.09(40)**	1.31±0.06(80)	1.50±0.07(56)*	1.29±0.07(64)	1.48±0.08(44)**	1.33±0.07(76)
Ojika, Miyagi	5.31±0.54(13)**	4.51±0.29(37)	5.04±0.43(24)*	4.41±0.29(26)	4.91±0.30(13)*	4.65±0.33(37)
Mangokuura-2, Miyagi	3.31±0.41(9)**	2.40±0.13(41)	3.32±0.19(14)**	2.27±0.15(36)	3.13±0.26(16)**	2.30±0.14(34)
Ondo-1, Hiroshima	1.73±0.20(20)*	1.58±0.09(40)	1.71±0.11(27)*	1.57±0.14(33)	1.72±0.14(17)*	1.59±0.11(43)
Kesennuma, Miyagi	8.42±1.34(8)*	8.41±0.93(46)	9.54±1.54(13)*	8.06±0.95(41)	11.03±1.77(18)**	7.10±0.77(36)

Number in parentheses presents number of oysters of the corresponding genotype. Two stars indicate significant difference between heterozygote and homozygote.

TABLE 3(2). *Mean Weight of Genotypes in Wild Populations of Oyster*

Population	*Gpi-1b*		*Lap-1b*	
	Heterozygote	Homozygote	Heterozygote	Homozygote
	g	g	g	g
Akoh, Hyogo	3.43±0.57(8)*	3.04±0.21(52)	3.15±0.29(18)*	3.07±0.25(42)
Ishinomaki, Miyagi	6.48±0.74(17)*	5.44±0.36(33)	5.58±0.66(19)	5.92±0.39(31)
Onagawa-1, Miyagi	6.96±0.96(14)*	6.18±0.39(46)	6.47±0.63(21)*	6.30±0.46(39)
Matsushima-3, Miyagi	8.60±1.02(18)*	7.43±0.69(32)	9.52±1.29(15)**	7.14±0.58(35)
Watari, Miyagi	6.77±0.83(49)*	6.69±0.45(176)	7.32±0.74(65)*	6.47±0.47(160)
Onagawa-2, Miyagi	9.18±0.94(14)**	6.83±0.56(36)	8.41±0.97(15)*	7.09±0.57(35)
Yasuura, Hiroshima	2.84±0.12(24)**	2.40±0.09(81)	2.95±0.13(29)**	2.33±0.08(76)
Mangokuura-1, Miyagi	8.23±1.23(10)*	6.55±0.47(40)	8.15±0.72(17)**	6.23±0.55(33)
Mangokuura-5, Miyagi	4.86±1.22(9)**	2.59±0.38(44)	3.69±0.86(17)*	2.64±0.40(36)
Matsushima-2, Miyagi	7.95±0.85(12)*	7.60±0.41(53)	8.07±0.82(13)*	7.57±0.41(52)
Mangokuura-3, Miyagi	2.18±0.18(13)**	1.86±0.08(62)	2.22±0.17(14)**	1.85±0.08(61)
Mangokuura-4, Miyagi	2.52±0.31(19)*	2.23±0.12(101)	2.27±0.22(37)	2.27±0.13(83)
Ondo-2, Hiroshima	2.84±0.22(28)**	2.31±0.20(47)	2.68±0.30(19)*	2.45±0.18(56)
Matsushima-1, Miyagi	4.71±0.37(17)**	3.08±0.31(33)	4.13±0.72(10)**	3.52±0.28(40)
Haragama, Miyagi	5.56±0.60(10)*	5.01±0.45(50)	5.42±0.55(20)*	4.95±0.51(40)
Watanoha, Miyagi	1.80±0.13(22)**	1.29±0.05(98)	1.52±0.14(20)*	1.36±0.05(100)
Ojika, Miyagi	4.55±0.54(15)	4.79±0.29(35)	4.52±0.58(8)	4.75±0.29(42)
Mangokuura-2, Miyagi	3.80±0.48(7)**	2.36±0.11(43)	2.99±0.25(10)**	2.46±0.15(40)
Ondo-1, Hiroshima	1.77±0.18(14)*	1.59±0.11(46)	2.00±0.14(12)**	1.54±0.10(48)
Kesennuma, Miyagi	16.18±1.00(5)**	7.62±0.80(49)	11.96±2.80(5)**	8.05±0.84(49)

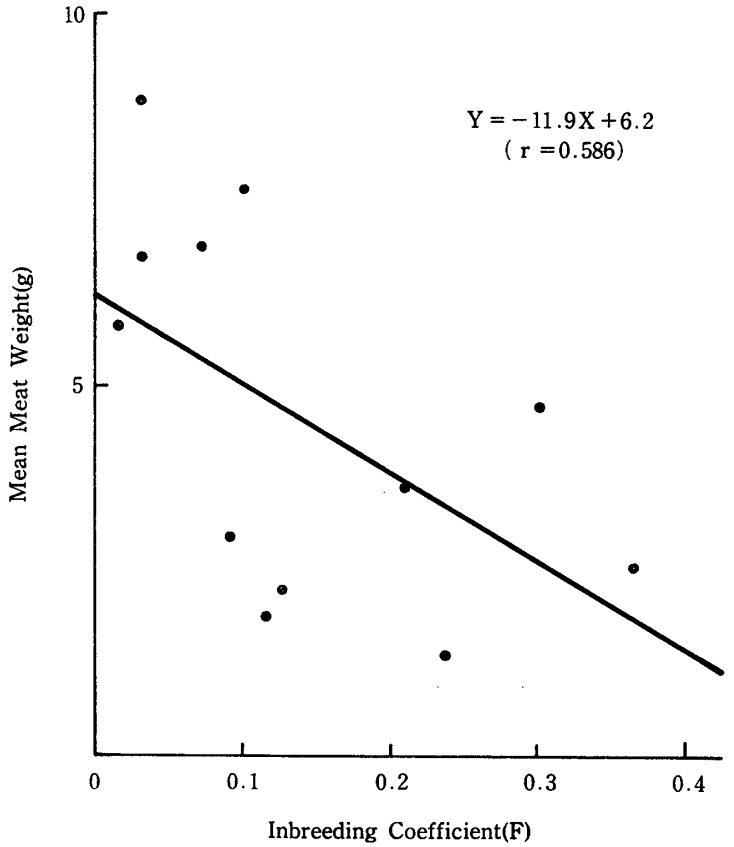

FIG. 1. Correlation between the mean weight and the inbreeding coefficient (F)

TABLE 4. *A Correlation between Mean Weight and Number of Heterozygous Loci*

	Number of loci at which an oyster is heterozygous				
	0	1	2	3	4+5
	g	g	g	g	g
Akoh, Hyogo	1.80±0.50(3)	3.37±0.31(18)	2.66±0.25(23)	3.92±0.67(11)	3.12±0.66(5)
Ishinomaki, Miyagi	1.90(1)	5.02±0.48(13)	5.85±0.44(26)	6.18±1.05(8)	10.70±1.30(2)
Onagawa-1, Miyagi	6.10±0.30(2)	6.55±0.67(19)	6.25±0.68(25)	5.88±0.48(12)	9.25±2.55(2)
Matsushima-3, Miyagi	2.30±0.40(2)	7.49±0.71(15)	6.51±0.77(16)	9.47±1.25(14)	13.03±3.26(3)
Watari, Miyagi	6.64±1.74(10)	6.29±0.72(35)	6.40±0.60(68)	6.58±0.83(80)	10.62±1.97(31)
Onagawa-2, Miyagi	4.76±0.66(5)	6.54±0.58(17)	6.09±0.56(14)	11.23±1.21(12)	9.80±1.70(2)
Yasuura, Hiroshima	1.41±0.12(10)	2.15±0.09(32)	2.64±0.13(35)	3.06±0.14(21)	3.40±0.25(7)
Mangokuura-1, Miyagi	4.56±1.09(5)	6.64±0.67(19)	6.18±0.69(13)	7.67±1.60(7)	10.27±1.23(6)
Mangokuura-5, Miyagi	1.35±0.83(6)	2.96±0.57(14)	3.26±0.64(22)	2.58±0.93(9)	6.65±4.45(2)
Matsushima-2, Miyagi	8.31±0.96(11)	6.72±0.54(18)	7.64±0.63(22)	8.21±0.99(11)	9.33±2.63(3)
Mangokuura-3, Miyagi	1.36±0.12(12)	1.95±0.13(34)	2.12±0.17(17)	1.87±0.30(9)	2.53±0.27(3)
Mangokuura-4, Miyagi	1.46±0.20(14)	2.23±0.15(49)	2.31±0.20(39)	2.87±0.49(15)	3.30±0.06(3)
Ondo-2, Hiroshima	1.53±0.10(16)	2.05±0.25(19)	2.51±0.20(20)	3.66±0.37(17)	4.20±1.10(3)
Matsushima-1, Miyagi	2.47±0.29(15)	3.83±0.55(16)	3.99±0.58(10)	4.45±0.47(7)	6.40±0.00(2)
Haragama, Fukushima	1.70±0.47(4)	4.31±0.54(28)	6.54±0.72(18)	6.06±0.92(8)	6.30±0.00(2)
Watanoha, Miyagi	0.98±0.10(20)	1.40±0.09(45)	1.38±0.09(34)	1.66±0.13(16)	2.10±0.22(5)
Ojika, Miyagi	4.19±0.54(9)	4.58±0.41(15)	5.00±0.51(20)	4.95±0.44(6)	
Mangokuura-2, Miyagi	1.91±0.12(19)	2.46±0.17(16)	3.26±0.34(7)	3.71±0.41(7)	4.00(1)
Ondo-1, Hiroshima	1.24±0.32(8)	1.52±0.14(25)	1.83±0.17(16)	1.90±0.21(11)	
Kesennuma, Miyagi	5.72±0.83(22)	9.81±1.64(19)	9.16±1.70(9)	14.98±2.46(4)	
Average	3.08±0.49	4.44±0.52	4.58±0.50	5.54±0.77	6.76±0.84

group of homozygote excess suggests that there might be difference between homozygotes and heterozygotes at each locus. A comparison of the mean weight in homozygotes and heterozygotes revealed that heterozygotes have a tendency to show a greater weight than homozygotes at each of the five loci (Table 3). The difference between homozygotes and heterozygotes was statistically significant in 9 of 20 populations examined at the *Idh-1*, in 8 at the *Pgm*, 10 at the *Aat-2*, 9 at the *Gpi-1b*, and 8 at the *Lap-1b*. Although the opposite pattern was observed in a few populations, the difference between homozygotes and heterozygotes was not statistically significant.

The greater weight of heterozygotes suggested that there might be a correlation between the weight and the number of loci for which an individual is heterozygous. In Table 4, we give the mean weight of oysters that were heterozygotes for 0, 1, 2, 3, or more than 4 loci. It could be seen that there might be a correlation between the degree of heterozygosity and the meat weight of individuals in all

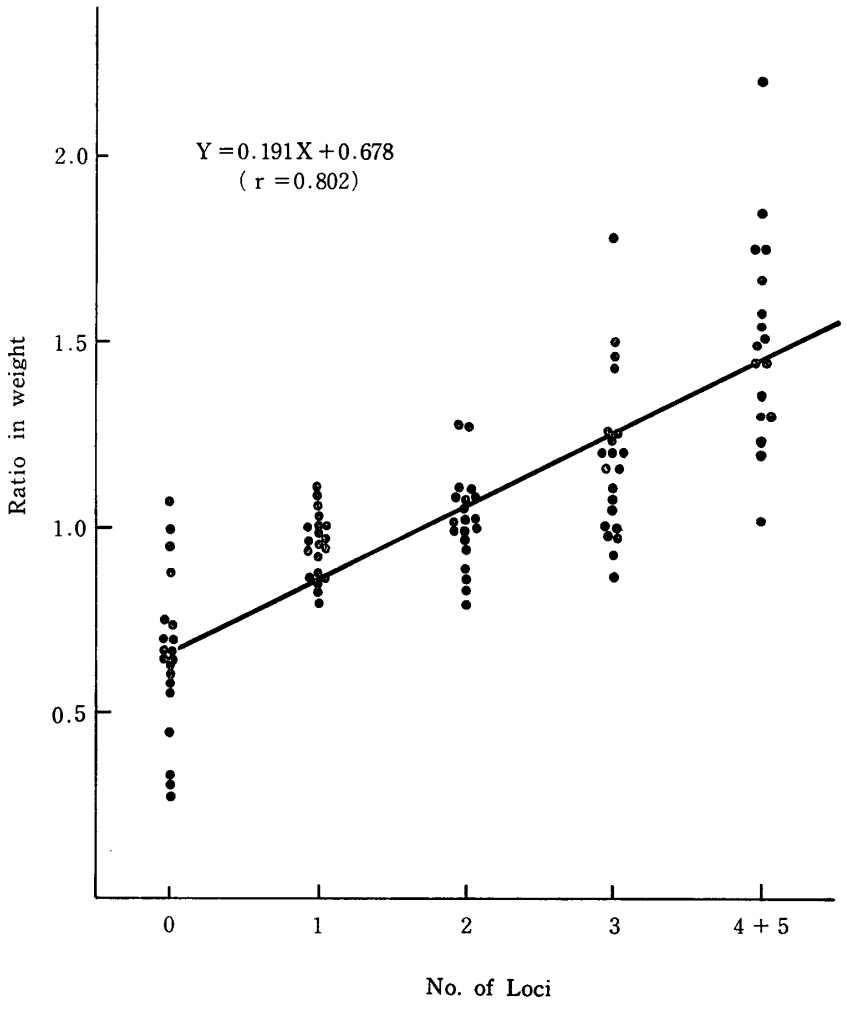

FIG. 2. Correlation between the mean weight and heterozygosity

populations, as a whole. Heterozygotes for 3 or more than 4 loci are heavier than heterozygotes for 1 or 2 loci on the average, whereas homozygotes for five loci (the table gives 0 in the number of loci) are lighter than heterozygotes for 1 or 2 loci.

To elucidate a further correlation between the weight and the number of loci for which an individual is heterozygous, the ratios of the weight of heterozygotes to the weight of total oysters were plotted in Fig. 2. The result indicated a clear correlation between the degree of heterozygosity and the individual weights ($r=0.802$). Regression of the mean weight on the number of loci was calculated as $Y=0.191X+0.687$. Coefficient of regression means that the higher degree of heterozygosity causes a higher growth rate. In other words, higher inbreeding produce higher reduction of growth rate.

Discussion

The present results can be summarized that a general excess of homozygosity is observed and that this excess is negatively correlated with growth rate. The observation of an excess of homozygosity is in complete agreement with observations made in other marine molluscs. Singh and Zouros (7) surveyed five loci in American oyster and reported homozygote excess in four of them. In the present study, all five loci showed such a excess. As an explanation for the homozygote excess, the "Wahlund effect" has been proposed by Tracey *et al.* (5). The "Wahlund effect" is simply that if the sample is composed of the progeny of subpopulations which do not exchange gamates, then the homozygotes will be more than expected from Hardy-Weinberg's equilibrium. Tracey *et al.* (5) observed that the homozygosity excess among juveniles of *Mytilus californianus* was much higher than in adults and proposed the "Wahlund effect" as the explanation of homozygote excess. Koehn *et al.* (4) surveyed six loci in *Mytilus edulis* but reported homozygote excess in only two of them. They suggested that the "Wahlund effect" could explain the homozygote excess only in part, and that the selection on a microgeographical scale could not be excluded because a negative correlation between shell size and homozygote excess was observed.

The simplest explanation for a homozygote excess so widely spread over the genome is that it results from the inbreeding structure of the population. Such circumstances are considered responsible for the genetic differentiations among the wild population (11). This result suggests that the population structure of the wild oyster as a whole has a tendency to split into a number of local subpopulations in which the effect of random genetic drift prevails. In this connection, Singh and Zouros (7) found a general excess of homozygosity in American oysters and suggested that there might be substantial inbreeding in the population. If this is the case, the proportion of the genome becoming homozygous by descent will vary greatly among individuals, and so will the number of homozygous deleterious genes. In the present study, a great amount of variation in meat weight among

individuals was observed. Similar variation in shell size of a cultured population was observed previously (8). Although the difference of the weight distribution among wild populations was attributed to the age composition and/or environmental conditions, the growth rate would influence overall fitness to a great extent. Therefore, it is expected that the number of homozygous deleterious genes will be negatively correlated with the growth rate and that the individual electrophoretic homozygosity will be positively correlated with the degree of homozygosity by descent. As a result, there will be a correlation between the electrophoretic heterozygosity and growth rate. The present study provided evidence for a positive correlation between the enzyme heterozygosity and growth rate.

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