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Seasonal genetic changes of natural *Porphyra* patches (Bangiales, Rhodophyta)*

Cambios genéticos estacionales en las manchas de *Porphyra* (Bangiales, Rhodophyta)

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ABSTRACT

To analyze seasonal genetic changes of natural *Porphyra* patches in the same location, isozymic analysis was carried out by starch gel electrophoresis. Eleven isozyme loci: *Aat, Cat, Dia, Gpi, G6pdh, Gdh, Mdh, Mpi, Pgm, 6Pgdh* and *Sod* were scored in *Porphyra* gametophytic thalli collected between November 1987 and April 1988 from one location, which was divided into 3 sampling sites, from the seashore to the offshore, at Fukushima Prefecture-Japan. A visible change due to time was observed in the allele frequencies. The allelic combination of the 11 loci for the 3 sampling sites varied from 1 to 14. The predominant combination changed due to time. The new alleles found at *Gpi* and *Sod*, indicate the clone of *Porphyra pseudolinearis* Ueda. Combination with the new alleles were only observed from November up to the middle of January. The first change (from November to December) of the predominant allelic combination revealed, that the clone of *P. pseudolinearis* tends to disappear, increasing at that time the population of *Porphyra yezoensis* Ueda, and that the second change (from March to April) revealed the predominance of another clone of *P. yezoensis*. The seasonal change of the predominant allelic combination leads to the conclusion that the clonal propagation of these gametophytes is the responsible for the formation of patches.

Key words: *Porphyra*, isozymes, allelic combinations, patches, clonal propagation.

RESUMEN

Para estudiar los cambios genéticos estacionales en las manchas que forman las especies de *Porphyra*, análisis isoenzimáticos fueron llevados a cabo usando la técnica de electroforesis de almidón. Once loci isoenzimáticos: *Aat, Cat, Dia, Gpi, G6pdh, Gdh, Mdh, Mpi, Pgm, 6Pgdh* y *Sod*, fueron examinados en talos gametofíticos de *Porphyra* recolectados entre los meses de noviembre de 1987 y abril de 1988, en 3 sitios de muestreo de la localidad de Soumashinko. Un cambio visible en las frecuencias alélicas fue observado en el tiempo. Las combinaciones alélicas de los 11 loci en los 3 sitios de muestreo varían de 1 a 14. La combinación predominante cambió en el tiempo. Los nuevos alelos encontrados en *Gpi* y *Sod* indican el clon de *Porphyra pseudolinearis* Ueda. Las combinaciones alélicas con los nuevos alelos fueron solamente observadas desde noviembre hasta la primera quincena de enero. El primer cambio (noviembre a diciembre) de la combinación alélica predominante muestra que el clon de *P. pseudolinearis* tiende a desaparecer, aumentando al mismo tiempo la población de *Porphyra yezoensis* Ueda; y el segundo cambio (marzo a abril) muestra la predominancia de otro clon de *P. yezoensis*. El cambio estacional de la combinación alélica predominante lleva a la conclusión de que la propagación clonal de esta especie es la responsable de la formación de manchas.

Palabras claves: *Porphyra*, isoenzimas, combinaciones alélicas, manchas, propagación clonal.

INTRODUCTION

A series of studies using electrophoretic data to analyze genetically the population structure of the edible seaweed *P. yezoensis* have been previously reported (Fujio *et al.* 1985, Fujio *et al.* 1987, Gil-Kodata *et al.* 1988). Fujio *et al.* (1987) examined a natural population of *P. yezoensis* in one location and demonstrated that the population structure had a remarkable tendency to be composed by a number of patches and that the observed number of allelic combinations at one linkage group at *Aat-Cat-Dia-Gpi-Mpi-6Pgd-G6pd* loci was significantly lesser than the expected number. The results suggest that the population structure of *P. yezoensis* shows a tendency to consist of several patches by clonal propagation of this haploid plant.

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However, it has not been determined whether a certain clone has always grown and propagated in a location during propagational seasonal or not, though the haploid thalli has propagated itself. It would be important to estimate the population structure of this species. Gil-Kodata *et al.* (1988) examined both natural and cultured populations, and demonstrated that only one allelic combination at a linkage group of the seven loci was predominant in cultured populations and this allelic combination was one of the combinations observed in natural populations.

The purpose of this study is to examine seasonal genetic changes of natural *Porphyra* patches in the same location.

MATERIALS AND METHODS

Natural thalli of *Porphyra* species were collected from one locality (Soumashinko, 38°N - 141°E) at Fukushima Prefecture, Japan. This collection was divided into 3 sampling sites with distances of 50 m between them, from nearshore to offshore. Samples were collected 3 to 6 times between November 1987 to April 1988.

Thalli were blotted dry between filter paper, and then wrapped and stored at −80°C until electrophoretic analysis. Each thallus was weighted and ground with a small amount of quartz sand and two volumes of 0.5 M saccharose (1 volume = weight of thallus) in a glass homogenizer. The homogenates were frozen overnight, and then thawed and centrifuged at 3,000 rpm for 25 minutes. The supernatants were subjected to horizontal starch gel electrophoresis for 4 hours, and the gel was stained for 11 enzymes. The enzymes were aspartate aminotransferase (AAT E.C. 2.6.1.1), catalase (CAT E.C. 1.11.1.6), diaphorase (DIA E.C. 1.6.4.3), glucose-phosphate isomerase (GPI E.C. 5.3.1.9), glucose-6-phosphate dehydrogenase (G6PDH E.C. 1.1.1.49), glutamate dehydrogenase (GDH E.C. 1.4.1.3), malate dehydrogenase (MDH E.C. 1.1.1.37), mannose-phosphate isomerase (MPI E.C. 5.3.1.8), phosphoglucomutase (PGM E.C. 2.7.5.1), 6-phosphogluconate dehydrogenase (6PGDH E.C. 1.1.1.44) and superoxide dismutase (SOD E.C. 2.7.5.1).

The procedure used to detect genetic variation in the eleven enzymes and the nomenclature of the alleles followed the Tomarihama Collection (Gil-Kodaka *et al.* 1988). The nomenclature of enzymes follows the Enzyme Committee (E.C.) (Nomenclature committee of IUB, 1979) using a standardized abbreviation in capital letters for the enzyme and italized letters for the corresponding loci.

RESULTS

1. *Fluctuation of Allelic Variation*

The eleven isozyme loci coding 11 enzymes showed activities as a single band in the anodal region. The observed electrophoretic variants are illustrated in Fig. 1. New alleles were found at *Gpi* and *Sod* loci. The *A*, *B* and *C* alleles at the *Gpi* were identical to the alleles observed in *P. yezoensis* collected in Tomarihama (Gil Kodaka *et al.* 1988), and the faster new one was designated as *A'* allele. The *A* allele at *Sod* was identical to Tomarihama Collection, and the slower new allele was designated as *B* allele. The alleles at the remaining 9 loci were identical to the Tomarihama Collection. Two alleles were observed at *Cat, G6pd, Gdh, Mdh, Pgm, 6Pgd* and *Sod,* 3 alleles at *Aat* and *Dia,* and 4 alleles at *Gpi* and *Mpi.*

Allele frequencies at the 11 isozyme loci for the 3 sampling sites are given in Tables 1 to 3. The first sampling site is the nearset to the seashore and represents 6 samplings at different times (Table 1). The proportion of polymorphic loci (P), in which the frequency of the most common allele was no greater than 0.950 (95% criterion), varied from 0 to 0.636 with a mean of 0.212; and the proportion of variant alleles (P*), in which the frequency of the most common allele was greater than 0.950, varied from 0 to 0.545 with a mean of 0.182. The average heterozygosity (H), which is the value of the expected heterozygosity obtained when 2 haploid gametes pair at random, was calculated

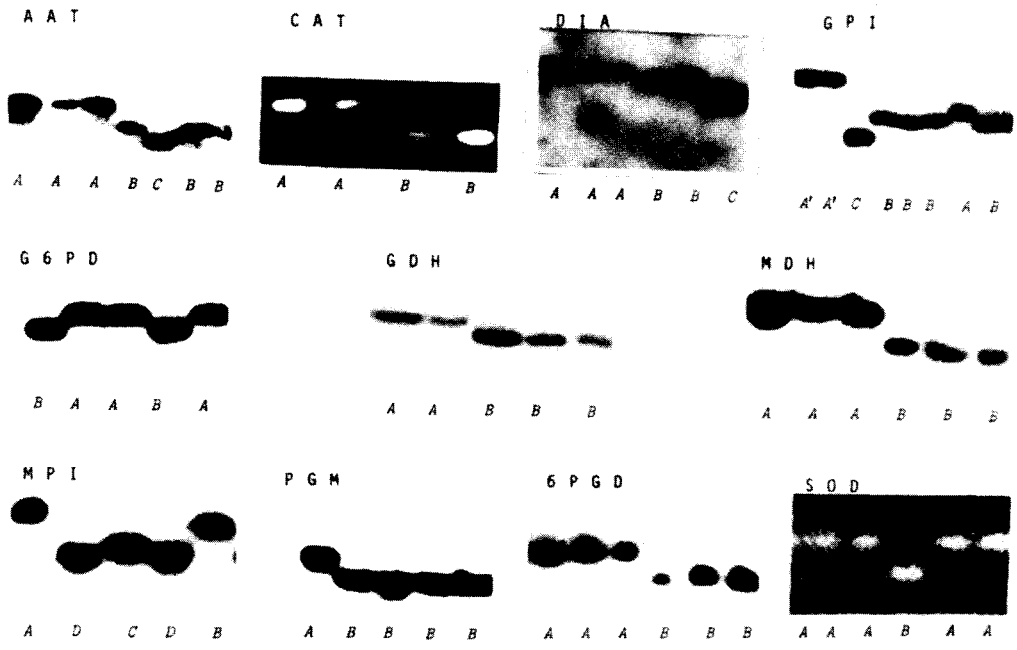

Fig. 1: Electrophoretic pattern of enzyme variation in *Porphyra* gametophytic thalli.
Patrón electroforético de las variaciones genéticas en los talos gametofíticos de *Porphyra.*

from the allele frequencies at all loci and it varied from 0 to 0.181 with a mean of 0.077. The second sampling site, located between the nearest and the farthest sites, refers to samples collected at 3 different times (Table 2). The proportion of polymorphic loci was 0, while the proportion of variant loci varied from 0 to 0.454 with a mean of 0.151. The average heterozygosity ranged from 0 to 0.028 with a mean of 0.009. At last, the third sampling site, which is the farthest, consists of samples collected at six different times (Table 3). The proportion of polymorphic loci varied from 0 to 0.727 with a mean of 0.491 and the proportion of variant loci ranged from 0 to 0.273 with a mean of 0.136. The heterozygosity varied from 0 to 0.268 with a mean of 0.132. These results show that the genetic variability fluctuates broadly in the nearest site while it decreases at the middle and farthes sites.

A visible change was observed in the allele frequencies of some isozyme loci. For example, a monomorphic locus changed to a polymorphic locus and vice versa. In the first sampling site, the predominant allele was kept in samplings collected between December and March, but changed at *Aat, Dia, Gpi, Gdh* and *6Pgd* loci in April. However, at *Mpi* locus, this change was observed in March. In the second sampling site, the most common allele changed at *Aat, Dia, Gpi, G6pd, Mpi, Pgm* and *6Pgd* loci from November to December. In the third sampling site, the frequency of the most common allele was kept between December and March, but the replacements of the alleles were observed at *Aat, Cat, Dia, Gpi, Gdh* and *Mpi* loci in April. These changes could be caused by the formation of other clones.

2. *Distribution of Allelic Combinations*

Allelic combinations of the 11 isozyme loci were counted. The type of allelic combination with frequencies higher than 0.100 are given in Table 4. The allelic combination with frequencies lesser than 0.100 are pooled as "others".

TABLE 1

Allele frequencies at eleven isozyme loci in natural populations of *Porphyra* collected 6 times from Soumashinko (Near)

Frecuencias alélicas en 11 loci isoenzimáticos en poblaciones naturales de *Porphyra* recolectadas 6 veces de Soumashinko (Cerca)

Locus	Allele	1987.12.16	1988.1.13	1988.1.28	1988.2.25	1988.3.11	1988.4.9
Aat	N	45	105	75	90	45	105
	A	1.000	0.828	0.973	1.000	0.578	0
	B	0	0.162	0.027	0	0.356	0.343
	C	0	0.010	0	0	0.066	0.657
Cat	N	45	105	75	90	45	105
	A	1.000	0.905	1.000	1.000	1.000	0.724
	B	0	0.095	0	0	0	0.276
Dia	N	45	105	75	90	45	105
	A	1.000	0.895	0.973	1.000	1.000	0
	B	0	0.105	0.027	0	0	1.000
Gpi	N	45	105	75	90	45	105
	A'	0	0	0.040	0	0	0
	A	1.000	0.848	0.960	1.000	0.380	0
	B	0	0.010	0	0	0.340	0.676
	C	0	0.142	0	0	0.280	0.324
G6pdh	N	45	105	75	90	50	105
	A	0	0	0.013	0	0	0
	B	1.000	1.000	0.987	1.000	1.000	1.000
Gdh	N	45	105	75	90	50	105
	A	0	0.181	0	0	0.200	1.000
	B	1.000	0.819	1.000	1.000	0.800	0
Mdh	N	45	40	75	90	45	105
	B	1.000	1.000	1.000	1.000	1.000	1.000
Mpi	N	45	105	75	90	50	105
	A	1.000	0.857	0.987	1.000	0.380	0
	B	0	0	0.013	0	0	0
	C	0	0.143	0	0	0.620	1.000
Pgm	N	45	105	75	90	45	105
	B	1.000	1.000	1.000	1.000	1.000	1.000
6Pgdh	N	45	45	75	90	45	105
	A	0	0.122	0	0	0	1.000
	B	1.000	0.878	1.000	1.000	1.000	0
Sod	N	65	105	75	90	45	105
	A	1.000	1.000	0.973	1.000	1.000	1.000
	B	0	0	0.027	0	0	0
P		0	0.636	0	0	0.364	0.273
P*		0	0	0.545	0	0	0
H		0	0.136	0.026	0	0.181	0.117

N: Number of thalli tested; P: Proportion of polymorphic loci; P*: Proportion of variant loci; H: Average of expected heterozygosity.

In the nearest site, the number of the observed allelic combinations varied from 1 to 12. The combination (1) Aat^{A}-Cat^{A}-Dia^{A}-Gpi^{A}-Mpi^{A}-$6Pgd^{B}$-Sod^{A}-Pgm^{B}-Mdh^{B}-Gdh^{B} was predominant in the 5 samplings collected from December to March, while the combination (3) Aat^{C}-Cat^{A}-Dia^{B}-Gpi^{B}-Mpi^{A}-$6Pgd^{B}$-$G6pd^{B}$-Sod^{A} Pgm^{B}-Mdh^{B}-Gdh^{A} predominated in the samples collected in April. The middle site showed 1 or 2 allelic combinations. The combination (1) observed in the nearest site, was predominant in the 2 samplings collected in December and March, while the combination (5) Aat^{A}-Cat^{A}-Dia^{B}-$Gpi^{A'}$-Mpi^{B}-$6Pgd^{A}$-$G6pd^{A}$-Sod^{A}-Pgm^{A}-Mdh^{B}-Gdh^{B} predominated in the November sampling. The farthest site varied from 1 to 14 allelic combinations. The combination (1) predominated in the 2 samplings collected in February and March, the combination (2) was predominant in the 2 samplings collected in December and the first half of January; the combina-

TABLE 2

Allele frequencies at eleven isozyme loci in natural populations of *Porphyra* collected 3 times from Soumashinko (Middle)

Frecuencias alélicas en once loci isoenzimáticos en poblaciones naturales de *Porphyra* recolectadas 3 veces de Soumashinko (Centro)

Locus	Allele	1987.11.27	1987.12.16	1988.3.11
Aat	N	70	85	75
	A	0.014	1.000	1.000
	B	0.986	0	0
Cat	N	70	78	75
	A	1.000	1.000	1.000
Dia	N	70	95	75
	A	0.014	1.000	1.000
	B	0.986	0	0
Gpi	N	70	95	75
	A'	0.986	0	0
	A	0.014	1.000	1.000
G6pdh	N	70	95	75
	A	0.986	0	0
	B	0.014	1.000	1.000
Gdh	N	70	95	75
	B	1.000	1.000	1.000
Mdh	N	70	95	75
	B	1.000	1.000	1.000
Mpi	N	70	95	75
	A	0.014	1.000	1.000
	B	0.986	0	0
Pgm	N	70	95	75
	A	1.000	0	0
	B	0	1.000	1.000
6Pgdh	N	70	95	75
	A	1.000	0	0
	B	0	1.000	1.000
Sod	N	70	95	75
	A	1.000	1.000	1.000
P		0	0	0
P*		0.454	0	0
H		0.028	0	0

N: Number of thalli tested.
P: Proportion of polymorphic loci.
P*: Proportion of variant loci.
H: Average of the expected heterozygosity.

tion (6) Aat^{B}-Cat^{B}-Dia^{B}-Gpi^{C}-Mpi^{C}-$6Pgd^{B}$ $G6pd^{B}$-Sod^{A}-Pgm^{B}-Mdh^{B}-Gdh^{B} predominated in the samples collected in the second half of January, while the combination (8) Aat^{A}-Cat^{A}-Dia^{A}-Gpi^{A}-Mpi^{A}-$6Pgd^{A}$-$G6pd^{B}$-Sod^{A}-Pgm^{B}-Mdh^{B}-Gdh^{B} was predominant in the April sampling.

Only the combination (1) was observed in the 3 sampling sites, that is, in 5 out of the six samplings in the nearest site, in 2 out of the three samplings in the middle site and in 2 out of the six samplings in the farthest site. The combination (2) was observed in 2 out of the six samplings in the nearest site and in 3 out of the six samplings in the farthest site. The combination (3) was observed in 1 out of the six samplings in the nearest and farthest sites respectively. The allelic combinations (5), (9), (10) and (11) with the new alleles, *A'* at the *Gpi* and/or *B* at the *Sod*, were only observed from November up to the middle of January in the middle and farthest sites.

DISCUSSION

Comparing with the data on *P. yezoensis* from Tomarihama (Gil Kodaka *et al.*

TABLE 3

Allele frequencies at eleven isozyme loci in natural populations of *Porphyra* collected 6 times from Soumashinko (Far)

Frecuencias alélicas en 11 loci isoenzimáticos en poblaciones naturales de *Porphyra* recolectados 6 veces de Soumashinko (Lejos)

Locus	Allele	1987.12.16	1988.1.13	1988.1.28	1988.2.25	1988.3.11	1988.4.9
Aat	N	105	74	80	95	95	40
	A	0.286	0.432	0.063	0.042	0.053	1.000
	B	0.714	0.554	0.937	0.716	0.947	0
	C	0	0.014	0	0.242	0	0
Cat	N	81	59	75	91	95	40
	A	0.333	0.271	0	0.341	0.053	1.000
	B	0.667	0.729	1.000	0.659	0.947	0
Dia	N	105	69	75	95	95	40
	A	0.219	0.362	0.013	0.011	0	1.000
	B	0.781	0.638	0.974	0.989	1.000	0
	C	0	0	0.013	0	0	0
Gpi	N	105	75	78	100	95	40
	A'	0	0.400	0.115	0	0.011	0
	A	0.286	0.093	0	0.029	0.021	1.000
	B	0.076	0.027	0	0.371	0.063	0
	C	0.638	0.480	0.885	0.600	0.905	0
G6pdg	N	89	64	75	95	95	40
	A	0.337	0.469	0.093	0	0	0
	B	0.663	0.531	0.907	1.000	1.000	1.000
Gdh	N	105	65	75	96	95	40
	A	1.000	0.970	1.000	0.979	1.000	0
	B	0	0.030	0	0.021	0	1.000
Mdh	N	101	69	75	95	95	40
	A	0.168	0	0.013	0	0	0
	B	0.832	1.000	0.987	1.000	1.000	1.000
Mpi	N	101	69	75	95	95	40
	A	0.287	0.014	0.107	0.021	0.011	1.000
	B	0.079	0.493	0	0.126	0.021	0
	C	0.634	0.493	0.880	0.853	0.968	0
	D	0	0	0.013	0	0	0
Pgm	N	105	75	77	95	95	40
	A	0	0	0.026	0	0	0
	B	1.000	1.000	0.974	1.000	1.000	1.000
6Pgdh	N	104	70	75	95	95	40
	A	0.971	1.000	1.000	0.968	1.000	1.000
	B	0.029	0	0	0.032	0	0
Sod	N	101	75	75	105	95	40
	A	0.733	0.653	0.933	1.000	1.000	1.000
	B	0.267	0.347	0.067	0	0	0
P		0.727	0.636	0.455	0.364	0.273	0
P*		0.091	0.091	0.273	0.273	0.091	0
H		0.260	0.268	0.093	0.135	0.034	0

N: Number of thalli tested; P: Proportion of polymorphic loci; P*: Proportion of variant loci; H: Average of the expected heterozygosity.

1988), the present data shows the decrease of 1 or 2 alleles in some of the isozyme loci, such as the *C* allele at *Cat, Dia, G6pd* and *Mdh, E* allele at *Mpi* and *D, E* alleles at *Gpi.* This decrease is considered to be dependent on the differences of collection localities. On the other hand, 2 new alleles named as *A'* at the *Gpi* and *B* at the *Sod* were found from November up to January. These new alleles have not been found in *P. yezoensis.* According to Miura *et al.* (1978), these alleles were identical to the alleles observed in *P. pseudolinearis* ("uppurui-nori" in japanese) collected from Kesennuma - Miyagi Prefecture. Ogawa in Tokuda *et al.* (1987) points out that the period of growing of *P. pseudolinearis* is from the

TABLE 4

Distribution of allelic combinations in natural populations of *Porphyra* at the three sampling sites in Soumashinko

Distribución de las combinaciones alélicas en las poblaciones naturales de *Porphyra* en los 3 sitios de muestreo de Soumashinko

Type of allelic combinations												Collection date						
	Aat	*Cat*	*Dia*	*Gpi*	*Mpi*	*6Pgdh*	*G6pdh*	*Sod*	*Pgm*	*Mdh*	*Gdh*	1987 11.27	1987 12.16	1988 1.13	1988 1.28	1988 2.25	1988 3.11	1988 4.9
Near													45*	105*	75*	90*	45*	105*
(1)	*A*	*A*	*A*	*A*	*A*	*B*	*B*	*A*	*B*	*B*	*B*	–	1.000	0.780	0.961	1.000	0.379	0
(2)	*B*	*B*	*B*	*C*	*C*	*A*	*B*	*A*	*B*	*B*	*A*	–	0	0.057	0	0	0	0.219
(3)	*C*	*A*	*B*	*B*	*A*	*B*	*B*	*A*	*B*	*B*	*A*	–	0	0	0	0	0	0.562
(4)	*B*	*A*	*A*	*B*	*C*	*B*	*B*	*A*	*B*	*B*	*B*	–	0	0	0	0	0.133	0
	Others												0	0.163	0.039	0	0.488	0.219
Number of allelic combinations													1	11	4	1	12	6
Middle												68*	78*				75*	
(1)	*A*	*A*	*A*	*A*	*A*	*B*	*B*	*A*	*B*	*B*	*B*	0	1.000	–	–	–	1.000	–
(5)	*A*	*A*	*B*	*A'*	*B*	*A*	*A*	*A*	*A*	*B*	*B*	0.986	0	–	–	–	0	–
	Others											0.014	0				0	
Number of allelic combinations												2	1				1	
Far													68*	38*	75*	86*	95*	40*
(1)	*A*	*A*	*A*	*A*	*A*	*B*	*B*	*A*	*B*	*B*	*B*	–	0	0	0	0.407	0.864	0
(2)	*B*	*B*	*B*	*C*	*C*	*A*	*B*	*A*	*B*	*B*	*A*	–	0.559	0.369	0.013	0	0	0
(3)	*C*	*A*	*B*	*B*	*A*	*B*	*B*	*A*	*B*	*B*	*A*	–	0	0	0	0.186	0	0
(6)	*B*	*B*	*B*	*C*	*C*	*B*	*B*	*A*	*B*	*B*	*B*	–	0	0	0.828	0	0	0
(7)	*B*	*B*	*B*	*C*	*B*	*A*	*B*	*A*	*B*	*B*	*B*	–	0	0	0	0.116	0	0
(8)	*A*	*A*	*A*	*A*	*A*	*A*	*B*	*A*	*B*	*B*	*B*	–	0	0	0	0	0	1.000
(9)	*A*	*A*	*B*	*A*	*A*	*A*	*A*	*B*	*B*	*A*	*A*	–	0.102	0	0	0	0	0
(10)	*A*	*A*	*A*	*A'*	*B*	*A*	*A*	*B*	*B*	*B*	*A*	–	0	0.132	0	0	0	0
(11)	*B*	*B*	*A*	*A'*	*B*	*A*	*A*	*B*	*B*	*B*	*A*	–	0	0.132	0	0	0	0
	Others												0.339	0.367	0.159	0.291	0.136	0
Number of allelic combinations													13	14	10	9	10	1

– : No collection.

* : Number of thalli tested.

beginning of autumn up to the winter and in *P. yezoensis* is from autum up to the late spring. These facts could lead to the conclusion that there are 2 different species of *Porphyra*, that is, *P. yezoensis* and *P. pseudolinearis*.

In the middle site, the change of the predominant allelic combination (5) in November to the combination (1) in December revealed that the clone of *P. pseudolinearis* tends to disappear, increasing at that time the population of *P. yezoensis*. In the nearest and farthest sites, these changes revealed the predominance of other clones of *P. yezoensis* later in the season. These changes could be explained by the clonal propagation of this plant in which a particular allele at a locus could be fixed in more than one generation. That is, the life history of *Porphyra* has 2 phases, conchocelis phase, which is diploid, and adult phase, which is haploid. At the adult

phase, there is an asexual propagation that produces minospores in which the *whole set of* genes from one individual is transmitted to its offspring.

A previous report (Gil Kodaka *et al.* 1988) showed that only one allelic combination Aa^{B}-Cat^{B}-Dia^{B}-Gpi^{C}-Mpi^{C}-$6Pgd^{A}$-$G6pd^{B}$ at a linkage group of 7 loci was predominant in cultured *P. yezoensis* collected from Shichigahama and Matsushima (Miyagi Prefecture) and this allelic combination was one of the observed combination in natural *P. yezoensis* from Tomarihama (Miyagi Prefecture). With regard to a linkage group at 7 loci, the above combination was observed in the nearest and farthest sites in this study [see combination (2)]. The allelic combination Aat^{A}-Cat^{A}-Dia^{A}-Gpi^{A}-Mpi^{A}-$6Pgd^{B}$-$G6pd^{B}$ observed in the 3 sampling sites has not been observed in Tomarihama, suggesting a local differentiation.

This study leads to the conclusion that the seasonal change of the predominant allelic combination is due to clonal propagation of this plant and it is the responsible for the formation of patches.

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