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Population Studies of the Sandeel, *Ammodytes personatus* (Girard), in Sendai Bay and Its Neighborhood

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Summary

Two subpopulations of sandeel, *Ammodytes personatus* (Girard), cohabiting in Sendai Bay and its neighborhood, were examined from several aspects, *i.e.*, morphology, ecology and genetics to clarify their features of life history and the adaptive significance of their cohabitation.

Group N, a subpopulation with notch type otolith, has modes of vertebral and gill raker counts at 63 and 23, respectively. However, Group A, a subpopulation with arrowhead type otolith, has modes at 65 and 28, respectively.

Group N is found in Sendai Bay, having Bertalanffy's k and L_∞ values of 0.842 and 16.28 cm, respectively and a five-year life span.

Group A inhabits the area off northern Miyagi Prefecture and is often found mixed with Group N, having k and L_∞ values of 1.012 and 19.71 cm, respectively. It has a life span of six years.

Some yearling fish of Group N participate in spawning (about 30 per cent in 1978), whereas few yearlings of Group A spawn in their second year. At the same time fish of Group N are more fecund than those of Group A of identical size. Further, the maximum GSI is 30 per cent for Group N, while it is 23 per cent for Group A. However, the fish of Group A produce more eggs during their lifetime than those of Group N due to their larger size.

It becomes evident from electrophoretic analysis of the polymorphism of α-GPDH that the frequency of α-$Gpdh^F$ is about zero in Group N and about 0.3 in Group A. This demonstrates that Group N is more homogeneous and stable genetically when compared with Group A.

From the above, it seems that Group N uses more resources for reproduction, while Group A puts energy into growth as well as maintenance.

In Sendai Bay and its neighborhood, Group N presumably plays the role of stabilizing the population of sandeel, whereas Group A's role is to increase the recruitments rapidly. The adaptive significance of cohabitation of two subpopulations in Sendai Bay and its neighborhood is attributable to sharing different roles between them.

Total landings of the sandeel in Miyagi Pref. and those at Onagawa Fish Market are shown in Fig. 1. This shows the large fluctuation as evident from the coefficients of variation, implying that its population size also makes a large scale

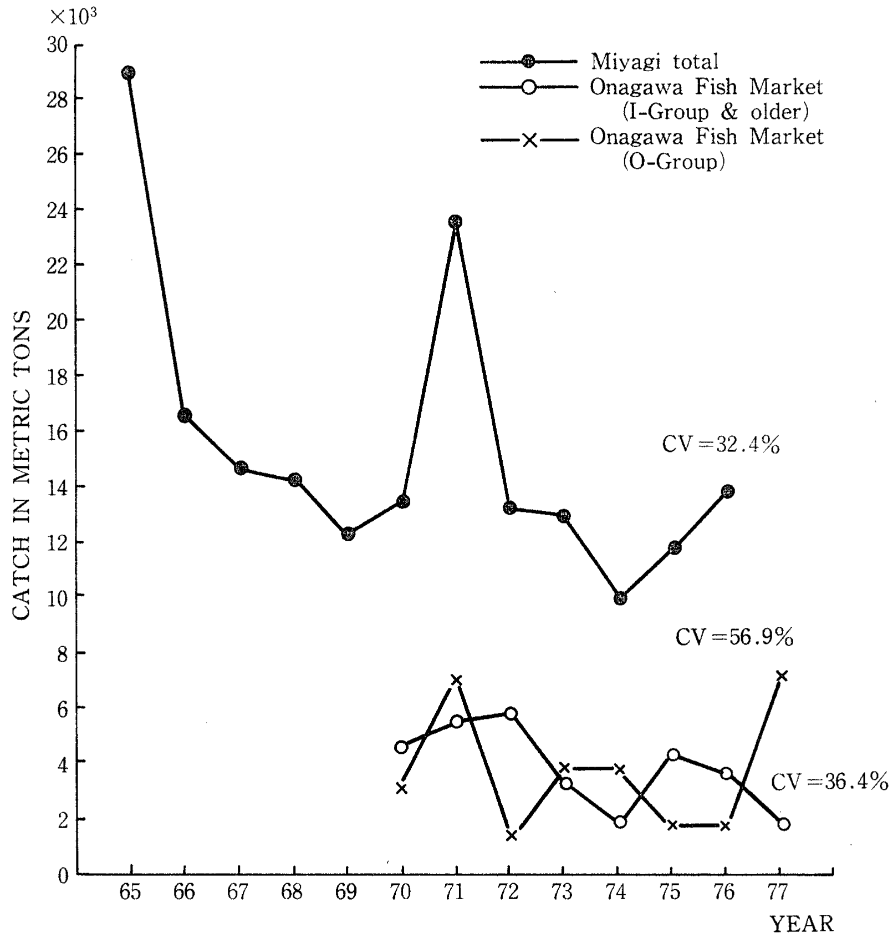

Fig. 1. Total landings of sandeel in Miyagi Pref. and those at Onagawa Fish Market. CV: coefficient of variation in landings.

fluctuation. In the works carried out by Hatanaka and Okamoto (1) and Ishigaki and Kaga (2) it becomes evident that, along the Pacific coast of Japan there are two subpopulations of sandeel that have modes of vertebral count at 63 and 65 (urostyls are inclusive), respectively and different growth patterns. The major range of the 65-vertebra group is around Hokkaido and that of 63-vertebra group is along the southern coast of Japan. These two groups cohabit in the seas off Aomori and Miyagi Prefs (3).

Thus, the purpose of the present work is to clarify the population structures of the sandeel in Sendai Bay and neighborhood and to examine the life historical features: distribution, growth, life span and reproduction of the two subpopulations by the method of comparative ecology.

Materials and Methods

Adult fish were commercially caught after spawning in December and January. This was followed by catch of newly born larvae and juveniles after March, and the fishery lasted until mid-July, when both adult and young began estivation in the sandy bottom with warming of the sea.

The samples of sandeel examined were obtained from April 1977 to October 1978. During the fishing season the samples were obtained from landings in Onagawa and Watanoha Fish Markets, Miyagi Pref. For the samples in the estivating period, some fish were obtained from Mr. Kodama, Miyagi Prefectural Fisheries Experimental Station, and the fish, which were to be discarded at sea because they were thin and economically valueless, were kindly brought back by fishermen of the small trawlers based on Haragama Port, Fukushima Pref. The rest were available at the above-mentioned ports from net-entangled fish.

As a rule, collected specimens were preserved in sea water with ten per cent formalin. Some specimens were carried to the laboratory in cold storage, where most fish were preserved in ten per cent formalin solution. Also, a portion of them were kept in a freezer at -20°C.

In this experiment, formalin-preserved fish were washed with water, while frozen ones were defrosted in running water.

Population Structure

Materials and Methods

The samples examined are shown in Table 1. Body length, from snout to anterior margin of lower caudal fin, and body weight were measured. The otolith structure and gill raker of the left 1st arch were observed and counted. The sex of some fish was determined, and their vertebral number was counted from atlas to urostyle.

Electrophoresis was carried out to examine the polymorphism of α-glycerophosphate dehydorogenase (α-GPDH, EC 1.1.1.8) in the skeletal muscle of sandeel. After defrosting, about 1 g of fish muscle was homogenized with an equivalent amount of distilled water in a glass homogenizer and centrifuged for

TABLE 1. *Date, Locality, Number and Length Range of the Samples*

Date	Locality	Number	Length range in cm
Apr. 27 1977	Ishinomaki Bay	31	14.4-20.5
Dec. 2	Off Haranomachi in Fukushima Pref.	69	14.4-20.6
Dec. 23	Sendai Bay	50	7.0-18.3
Jan. 13 1978	Snedai Bay	34	8.2-16.3
Mar. 28	South of Tashiro Is.	36	11.7-15.6
Apr. 28	Kinkasan Straits	15	5.3- 6.9
May 8	East coast of Kinkasan	26	8.9-20.6
May 9	East coast of Kinkasan	73	13.1-21.6
July 7	South coast of Kinkasan	68	6.8-12.8
Oct. 27	Sendai Bay	47	7.7-20.2
	Total	449	

ten minutes at 3,000 rpm. The resultant clear supernatant was used for electrophoresis. Alternately, body fluid was taken directly from the muscle for this purpose. A small piece of filter paper dipped into the liquid was put into eleven per cent starch gel. Then, horizontal starch gel electrophoresis was performed for sixteen hours with a constant current of 0.2 mA/cm^2 at a temperature lower than 10°C in an icebox to detect the phenotypes of α-GPDH isozymes. According to the Shaw and Prasad's (4) method, 0.155 mole tris–0.043 mole citric acid was prepared as electrode buffer, and after electrophoresis, sliced gels were incubated at 37°C in a reaction dye mixture containing α-glycerophosphate substrate disodium salt.

Results

1) *Otolith*

As will be described below, the otolith structure can be separated into two types on the basis of differences in gill raker and number of vertebra. In the case of the first type, the anterior face of the otolith is notched, whereas the second is slender-shaped (Plate 1). Thus the former is called the Notch Type (Type N), and the latter is called the Arrowhead Type (Type A).

Arrowhead type Notch type

PLATE 1. Otolith types of sandeel.

2) *Gill Raker Number*

The range of gill raker number observed was from 16 to 31. The frequency distributions of gill raker number are shown in Fig. 2 by sex and by each otolith type. In both otolith types, gill raker numbers reached the specific fixed number at about 7 cm in body length. Length range of the fish in Fig. 2 is 7.6 to 20.9 cm.

In the case of Type N the mode of gill raker of both sexes is 24, while in Type A it is 28. In both otolith types, there is no significant difference between the means of gill raker numbers for both sexes.

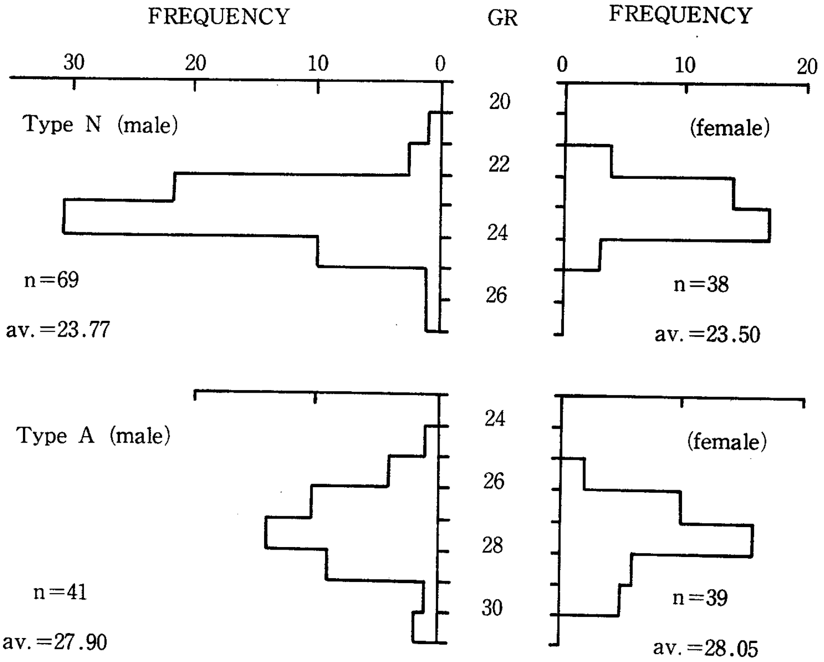

Fig. 2. Frequency distributions of the gill raker number (GR) by sex and otolth type.

Type N: F-test for variance,
F=1.461 (0.75<P<0.90),
T-test for mean,
t=1.482 (P<0.95).

Type A: F-test for variance,
F=1.422 (0.75<P),
T-test for mean,
t=0.577 (P<0.95).

3) *Vertebral Number*

Since the vertebral number reaches the fixed figure presumably in the very early stage, fish over 7.0 cm were examined. Frequency distributions of the vertebral number are noted in Fig. 3, showing that the mode is situated at 63 for each sex of Type N, while it is situated at 65 for Type A. No statistical differences are found between the means of either sex.

Type N: F-test for variance,
F=1.339 (P<0.95),
T-test for mean,
t=0.814 (0.4<P<0.5),

Type A: F-test for variance,
F=1.714 (P<0.95),
T-test for mean,
t=0.121 (P<0.9).

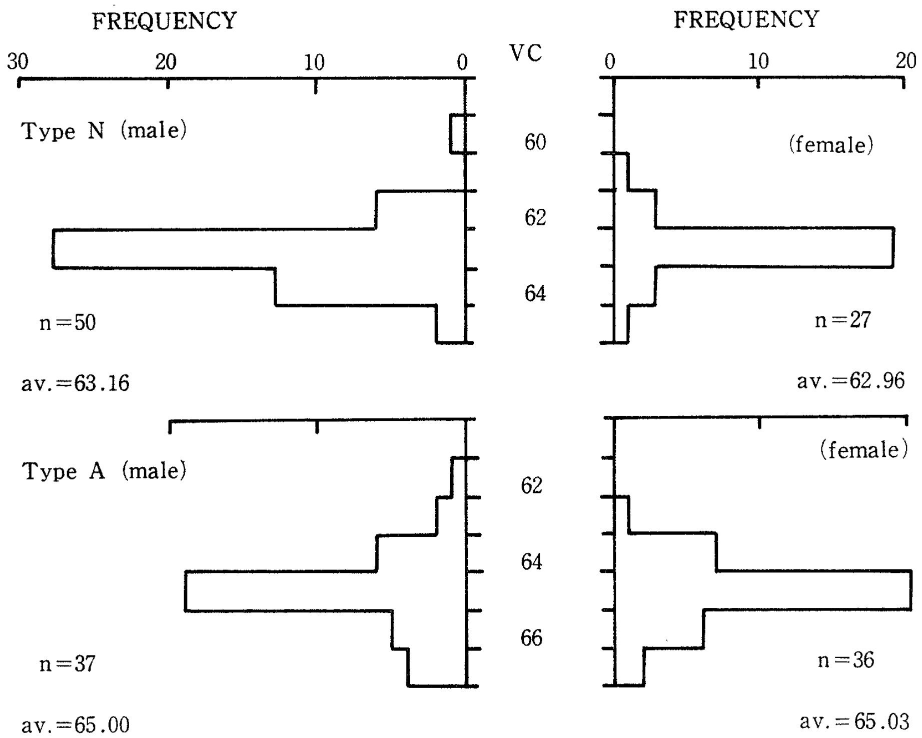

Fig. 3. Frequency distributions of the vertebral count (VC) by sex and otolith type.

4) *Relationship between Otolith Type and Meristic Characters*

Correlations are shown between gill raker number and vertebral number by otolith type in Table 2, revealing the intimate relationship between them. Using the gill raker number is more appropriate than the vertebral number to distinguish between the two subpopulations, since the overlapping between the frequency distributions of the subpopulations is considerably smaller in the case of the former than the latter.

Table 2. ***Correlation between Gill Raker Number (GR) and Vertebral Count (VC) by Otolith Type***

Type N (n=163)

GR \ VC	60	61	62	63	64	65
21				1	1	
22			6	6	1	1
23	1	1	6	30	15	2
24		2	10	34	20	5
25			1	13	4	
26			1			
27					1	
28					1	

Type A (n=84)

GR \ VC	62	63	64	65	66	67	68
24			1				
25			1				
26			2	3	1		
27			3	11	5	2	1
28		1	4	19	8	2	
29	1	1	4	6	1	1	
30				4		1	
31						1	

5) *α-GPDH Isozymes in Skeletal Muscle*

α-GPDH, the enzyme taking part in glycolysis and pentose phosphate pathways, was examined for the samples ranging in size from 4 to 20 cm.

An example of electrophoretic patterns is shown in Plate 2. The patterns are divided into three types, F,S, and FS, according to number and mobility of α-GPDH isozymes. It is suggested that the α-GPDH isozymes are dimers controlled by the two alleles, α-$Gpdh^F$ and α-$Gpdh^S$, at a single locus. This demonstrates that the genotypes are *F/F*, *F/S* and *S/S*. The results of electrophoretic experiments on three samples taken in Ishinomaki Bay, off Haranomachi and south of Tashiro Is. (Table 1) are shown in Table 3-a. All fish of the three samples were adults. In the case of the sample collected in Ishinomkai Bay the difference between the observed value and the expected one is small. In the sample collected off Tashiro Is. only Type S is observed, showing that these samples are composed of homogeneous genetic groups. In the case of the sample off Haranomachi the difference between observed and expected values is large, showing heterogeneity. Therefore this sample was separated into subsamples according to otolith type, as shown in Table 3-b. It can be shown in this table that fish of Type N are found to be from a single breed, while those of Type A are not. The difference between the observed and expected values of the frequencies of phenotype is smaller than in the original sample.

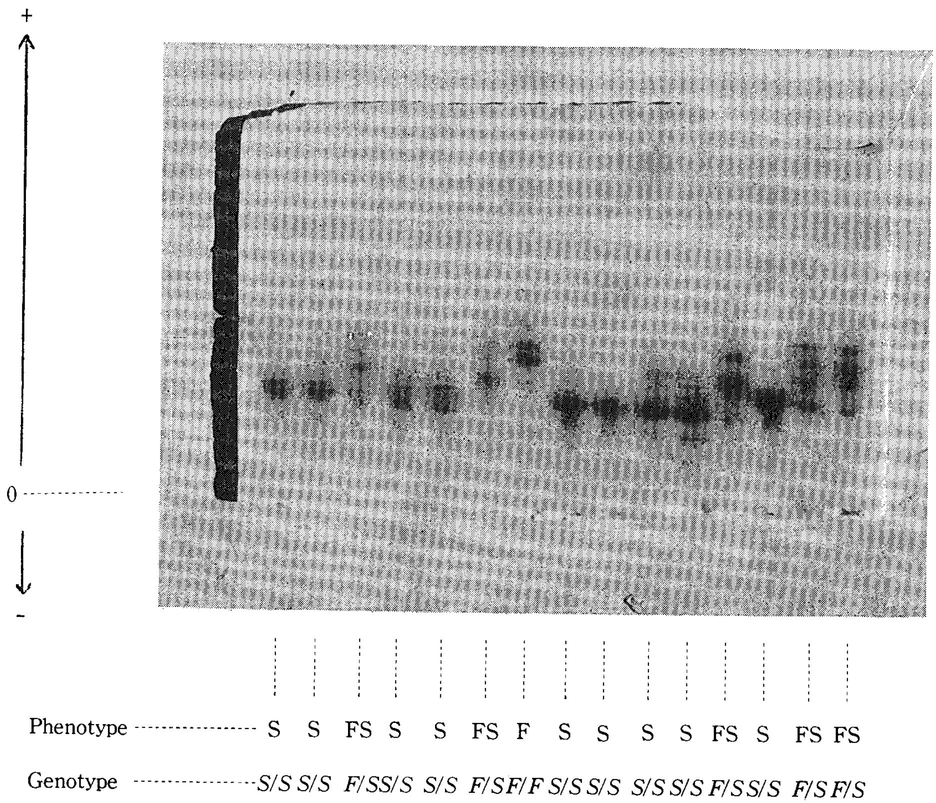

PLATE 2. Starch gel electrophoretic patterns of α-GPDH in skeletal muscle extracts of sandeel.

TABLE 3-a. *Results of Electrophoretic Experiment for α-GPDH Isozymes in the Skeletal Muscle Extracts of Sandeel*

Date Locality		Frequency of phenotype F	FS	S	Total
Apr. 27 1977	O	2	11	18	31
Ishinomaki Bay	E	1.82	11.37	17.81	31.00
Dec. 2 1977	O	7	11	51	69
off Haranomachi	E	2.26	20.46	46.28	69.00
Mar. 28 1978	O	0	0	36	36
south of Tashiro Is.	E	0	0	36.00	36.00

. O: Observed, E: Expected

TABLE 3-b. *Results of Separation by Otolith Type of the Specimens off Haranomachi on Dec. 2, 1977*

Otolith Type		Frequency of phenotype F	FS	S	Total
Type N	O	0	2	31	33
	E	0.03	1.92	30.05	33.00
Type A	O	7	9	20	36
	E	3.66	15.64	16.70	36.00

O: Observed, E: Expected

Arranging of the above results, α-$Gpdh^F$ allele frequencies, gill raker number and the vertebral count distributions of four groups are presented in Table 4. This shows that the mode of 24 for gill raker number and that of 63 for vertebra number corresponds to the very low α-$Gpdh^F$ allele frequency, whereas when they are 28 and

TABLE 4. *α-$Gpdh^F$ Allele Frequency, Gill Raker Number (GR) and Vertebral Count (VC) in Four Samples*

Sample	α-$Gpdh^F$ allelle freq. & SE*	GR 22	23	24	25	26	27	28	29	30	31	VC 61	62	63	64	65	66	67
Apr. 27 1977 Ishinomaki Bay	0.242±0.054						5	7	2	1				2	8	11	7	3
Dec. 2 1977 (Type N) off Haranomachi	0.030±0.021		11	13	7	1	1						3	16	13	1		
Dec. 2 1977 (Type A) off Haranomachi	0.319±0.055				1	4	4	12	8	5	3			2	8	18	5	3
Mar. 28 1978 South of Tashiro Is.	0.00	3	7	22	3			1				1	9	15	9	1		1

*SE: standard error

65, respectively, the gene frequency is high. These facts prove the existence of the two genetically isolated breeds.

Developmental Stage and Yearly Cycle of Life

The criteria dividing the life history of sandeel into developmental stages were due to Watanabe and Hattori's work (5).

1) *Developmental Stage*

1. Egg stage

The egg stage is defined as the period from spawning to hatching. A fertilized egg is transparent and yellow having some oil globules. In sea water the eggs sink to the bottom. The diameter of ripe ova is 0.70–0.75 mm, and when fertilized it becomes 0.85–0.95 mm (Chida, (6)).

2. Yolk sac stage (4.0–4.5 mm long)

The yolk sac stage is defined as the period after hatching until completion of yolk absorption. Newly hatched larva was noted to be 4.0 mm long as a result of the experiments of artifiical hatching in Seto Inland Sea (Inoue, (7)), and off Hokkaido (Kitaguchi, (8)), while it is 4.3 mm in nature (Chida, (6)). After a few days from yolk absorption the fish become larvae.

3. Larval stage (4.5–30.0 mm long)

The larval stage is difined as the period from the beginning of feeding after yolk absorption until the begining of swimming and schooling. When the yolk has been absorbed at 4.5 mm long, the pectoral fin is observed, the snout becomes sharp, and lower jaw protrudes beyond the upper jaw, but not as far as that of adult (Inoue, (7)). These facts are related to the acquisition of the swimming and feeding abilities. According to the observation by Miyagi Prefectural Fisheries Experimental Station, sandeel larvae over 30 mm long have not been collected by surfacial net hauling showing that swimming and hence schooling ability of fish under 30 mm is weak.

4. Juvenile stage (30–50 mm long)

In the juvenile stage the body is white-colored all over its surface like white-bait and black spots begin to be observed on head, snout, upper jaw and the base of fins. The pectoral fin is fan-like, having 13–14 rays, like those of the adult. The fork of the caudal fin is already formed. Plicae laterales are observed on the ventral surface. The lateral line is observed at 36.5 mm long. The soft ray number of each fin reaches the specific fixed number, whereas black spots on the body surface are not as fully distributed as they are in the adult. From 42 to 45 mm in length pigment spots increase around the eyes and the dorsal surface.

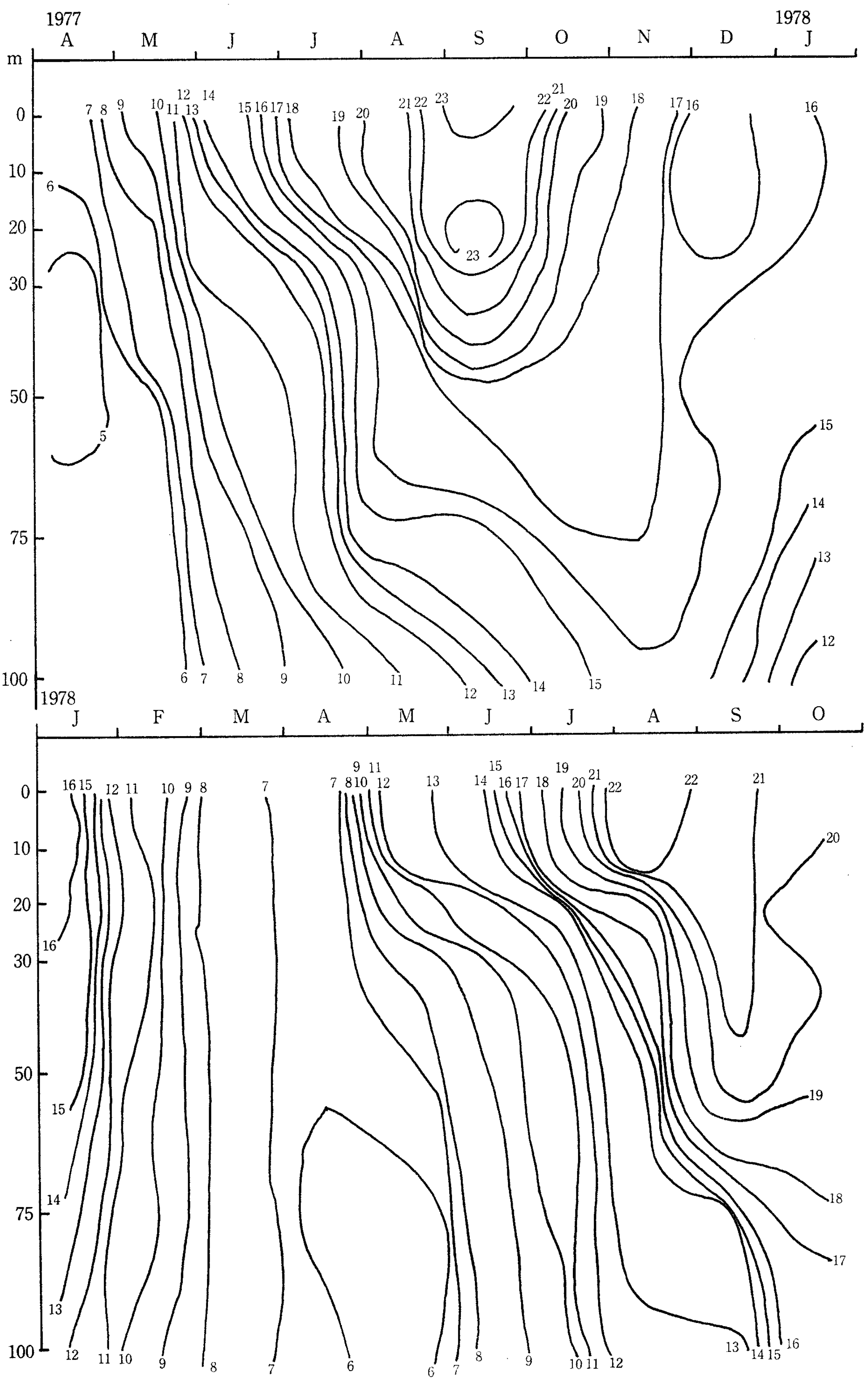

Fig. 4. Water temperature isopleth at 37°50′N, 141°25′E.
Data from the observations by Fukushima Prefectural Fisheries Experimental Station.

5. Young stage (50–70 mm long)

In this stage fish are easily identified as such. At 70 mm long the gill rakers reach their fixed figure.

6. Preadult stage (body length for Group N: 70–100 mm, body length for Group A: 70–140 mm)

The body organization is nearly identical with that of the adult.

7. Adult stage

In the spawning season, the fish of Group N reach 130 mm in length, while those of Group A reach a 160 mm.

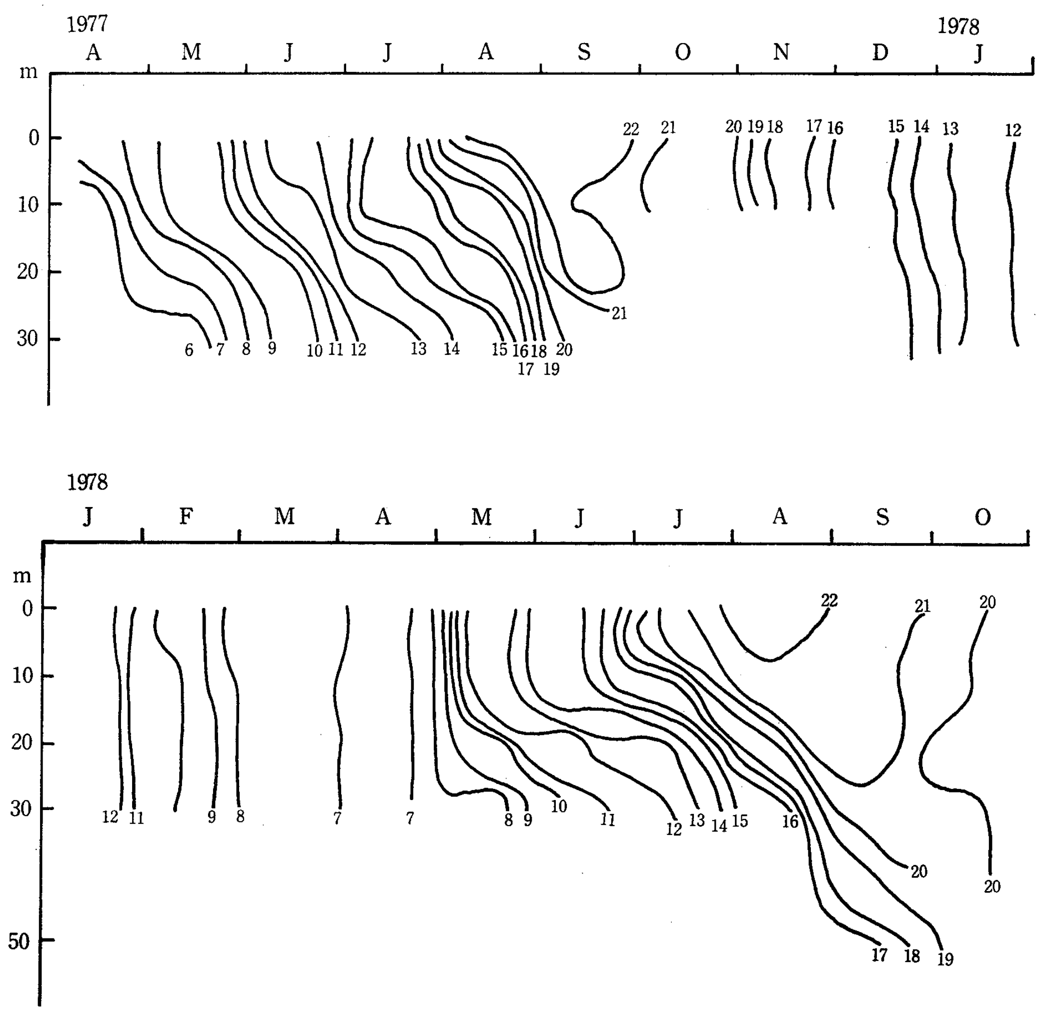

Fig. 5. Water temperature isopleth at 37°49.5′N, 141°11.8′E. See the explanation of Fig. 4. for data.

2) *Yearly Cycle of Life*

1. Feeding season: February-July

As will be described below, after spawning in central Sendai Bay the sandeel begin to feed on *Eupha usia pacifica.* From February to March they migrate to the circumference of the Oshika Peninsula and the coast of the northern Joban District, where they stay and grow until early July.

2. Estivating season: July-November

As the surface temperature rises beyond about 15°C (in mid-July in the case of 1977, Fig. 4), the sandeel move to central Sendai Bay and estivate unfed in the sandy bottom.

3. Spawning season: December-January

In December, as bottom temperature falls below 15°C (in December in the case of 1977, Fig. 5), the sandeel recover from estivation and an increase in maturity occurs, at this time they scarcely take food. They carry out spawning during a very short time in early January, which is then followed by the onset of feeding above the bottom of the estivating area until late January.

The Feature of Life History of the Sandeel

The life historical features of the sandeel, *i.e.*, distribution and migration, growth and life span, and reproduction are examined below.

To study the distribution and migration of the sandeel, information was gathered from fishermen and from "The Prompt Report" published by Fukushima Prefectural Fisheries Experimental Station. "The Prompt Report" was available from April 1977 to December 1978. Subpopulations were identified by counting vertebra and by electrophretic examination.

Using length measurements early growth was examined and growth parameters were calculated. For age determination, the ring number of otolith was observed according to Kitakata's (9) method.

The gonads were weighed and the gonad index (GI: $10^4 \times$[gonad weight(g)]/[body length(cm)]^3) and gonosomatic index (GSI: $10^2 \times$[gonad weight(g)]/[body weight(g)] were calculated. Since distributions of oocyte diameter from an ovary of sandeel are unimodal (Fig. 6) and there are no differences among the modes due to the locality of the ovary, fecundity was examined using the gravimetric method by weighing exactly a piece from the central portion of an ovary.

1) *Distribution and Migration*

Diagrammatic representation of the geographical distribution of sandeel is shown in Fig. 7. Moreover, the number of vertebra and the frequency of α-*Gpdh*^{F} allele of some samples are shown in Table 5 to identify subpopulations. In the

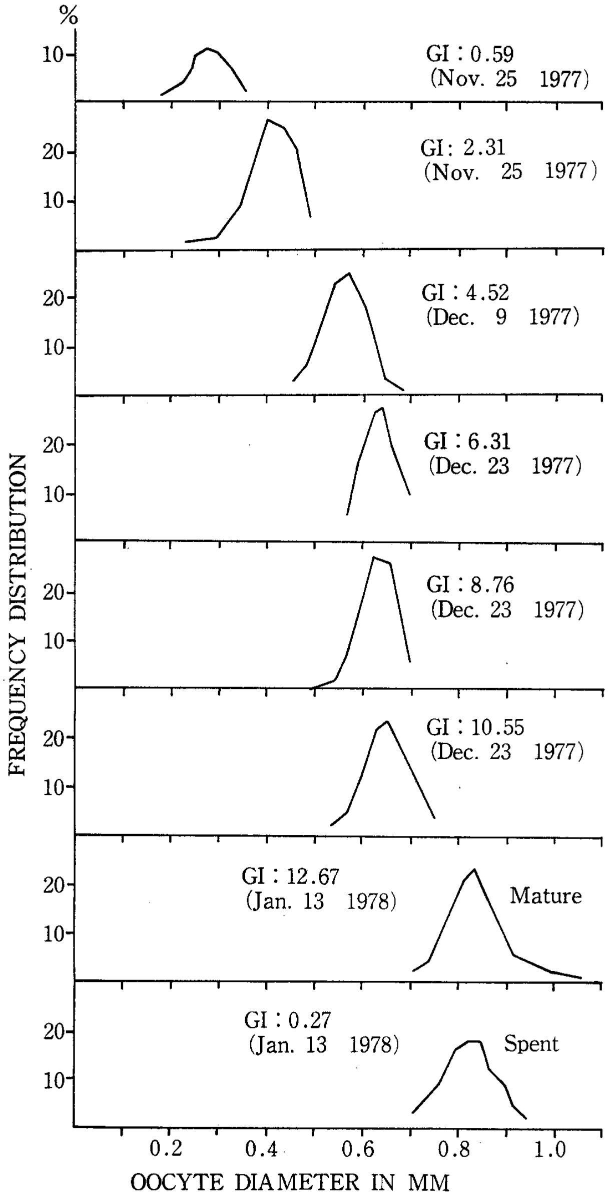

Fig. 6. Progressive development of oocyte diameter of two-year-old sandeel of Group N, 14.2–15.5 cm long. GI denotes gonad index.

case of 63 vertebrae the mode of α-*Gpdh*^{F} allele frequency is low, while in the case of 65 vertebrae the frequency is high, thus showing close correlations.

Larva, juvenile, young and preadult specimens are contained in the age-0 group.

Seemingly, Group N larvae hatch in central Sendai Bay from December to Jnauary (for spawning ground, see '*Reproduction*' below), and they are transported to north and distributed along the southern coast of the Oshika Peninsula.

From April to mid-July they develop into the preadult stage. In June 1977, fish of age-0 sandeel were widely distributed close to Enoshima Is., Eutamata Is., Yoriiso and Matsukawaura Inlet. They then disappeared from those waters

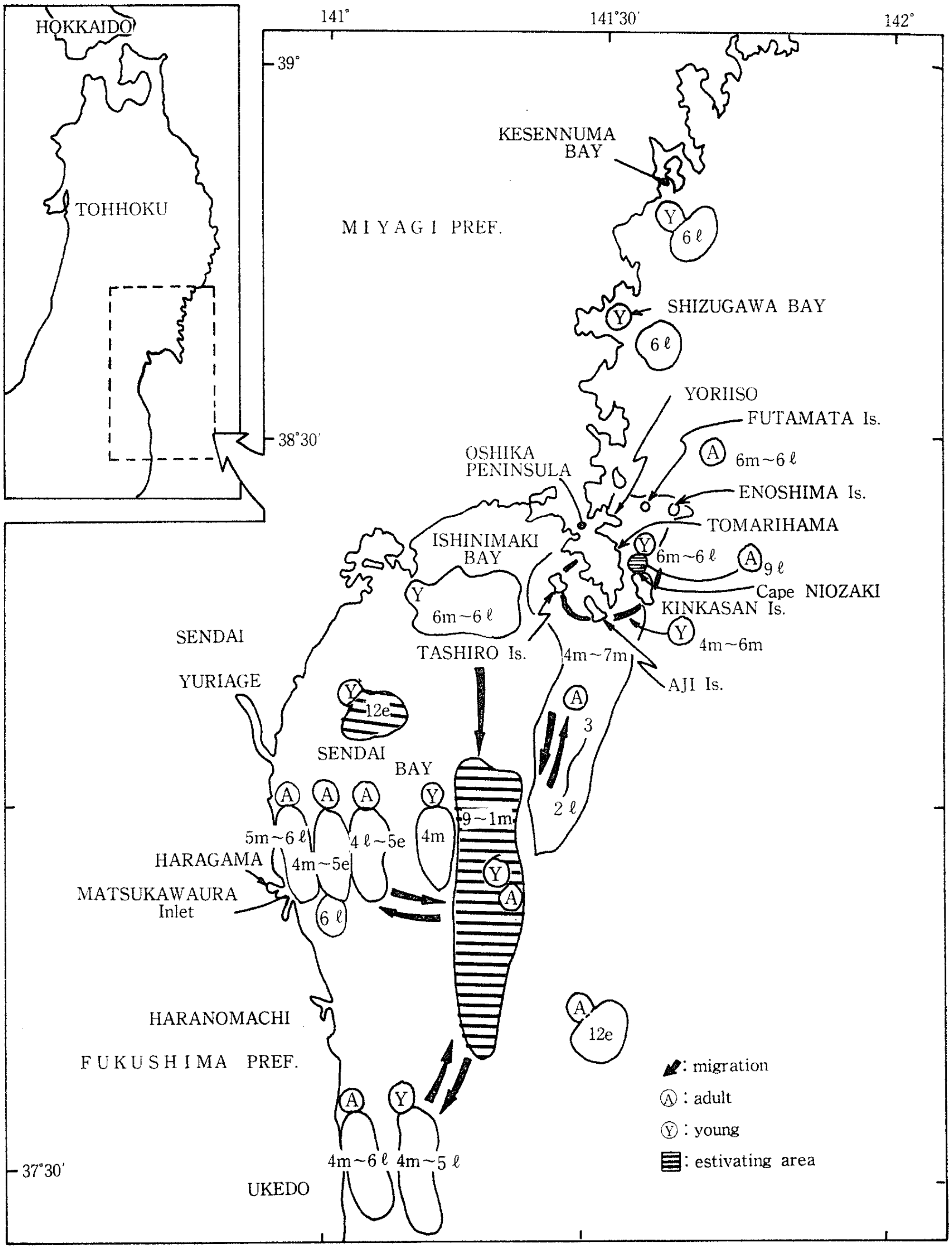

Fig. 7. **Diagrammatic representation of the distribution and migration of the sandeel. For example, 6_e,6_m and 6_l denote early June, mid-June and late June, respectively.**

and moved to the estivating areas. During February and March spent adults of Group N were observed feeding in the waters south of Tashiro and Aji Islands. Their range became to spread out over the southern coast of Oshika Peninsula in April like age-0 fish and they were also found off Matsukawaura Inlet.

In September the estivating young and adult were found to be buried in the medium-sized sand of 0.2 to 2.0 mm across (10) in central Sendai Bay, partially off

Cape Niozaki of Kinkasn Is. and off Yuriage. Estivation lasted until early December.

Age-0 fish of Group A were distributed in Kesennuma Bay, and off Tomarihama Beach on the east coast of the Oshika Peninsula. Their schools were composed exclusively of larvae, suggesting that spawning was carried out most intensively in these areas.

Group N in the feeding season was distributed near the Oshika Peninsula and Kinkasan Is. and along the central and southern coast of Sendai Bay. Usually

TABLE 5. *Frequency Distributions of Vertebral Count (VC) and α-$Gpdh^F$ Allele Frequencies of Sandeel*

No.	Locality	Date	VC											α-$Gpdh^F$ allele freq.				
			59	60	61	62	63	64	65	66	67	68	Total	0.0	0.1	0.2	0.3	Total
Adult																		
1	Kinkasan Off Cape Niozaki	Apr. 28, '77	1	1	2	3	14	12	4	4			41		-•-			30
2	Off Cape Niozaki	Sep. 6			1	5	10	7	7	3			33		-•-			30
3	Off Cape Higashinozaki	June 7, '78				6	11	8	4				29					
4	Off Cape Higashinozaki	July 7			1	6	19	4	1				31	-•-				31
5	Off Cape Higashinozaki	13		1	3	15	17	14	4	1			55					
6	south coast	May 26, '77				3	14	8	8	1	1		35		-•-			35
7	south coast	June 24			1	6	10	8	3	2			30		-•-			30
8	east coast	May 9					2	6	22	14	5		49					
9	Ishinomaki Bay	APR. 27, '77					2	8	11	7	3		31			-•-		31
10	South of Aji Is.	Feb. 24 '78			3	4	21	12	3				43					
11	South of Aji Is.	Mar. 28			2	16	36	21	9	2			86	-•-				32
12	South of Tashiro Is.	Mar. 28			1	9	15	9	1		1		36	•				36
13	Off Sendai	Jan. 13 '78						4	13	12	1	1	31			-•-		31
14	Sendai Bay	Sep. 30, '77			2	7	22	4	2	1	1		39	-•-				30
15	Sendai Bay	Nov. 11				2	2			1			5					
16	Sendai Bay	25		1	1	10	20	13	3	3	2		53					
17	Sendai Bay	Dec. 9		1		7	18	5	3	2			36					
18	Sendai Bay	16			1	5	17	7	4				34					
19	Sendai Bay	23			2	7	16	9	2	1			37					
20	Sendai Bay	Oct. 27, '78		1	1	7	26	5	7				47					
21	Off Haranomachi	Dec. 2, '77				8	27	27	30	9	4		105					
21′														-•-				33
21″																	-•-	36
22	Off Ukedo	May 6, '77			1	1	3	3	10	8	3	1	30			-•-		31

TABLE 5. (*Continued*)

No.	Locality	Date	VC 59	60	61	62	63	64	65	66	67	68	Total	α-*Gpdh*^{F} allele freq. 0.0	0.1	0.2	0.3	Total
Young																		
23	Kesnnuma Bay	June 7, '78		1	1		5	4	13	4	1		29			•		30
24	Enoshima Is.	June 17, '77			1	6	12	5					24	•				30
25	Futamata Is.	June 24			2	5	20	3					30	•				30
26	Yoriiso	June 8			1	7	18	3	1				30	•				30
27	Tomarihama Beach	June 24				1	5	8	9	5	2		30			•		22
28	Kinkasan Straits	2				3	9	12	6				30	•				30
29	Kinkasan Straits	7			1	1	6	3	3	5		1	20					
30	Kinkasan Straits	Apr. 28, '78			1	3	7	4					15					
31	Off Cape Higashinozaki	July 7				4	11	5	3				23		•			23
32	Off Cape Higashinozaki	July 7					1	1	7	4			13			•		14
33	Kinkasan east coast	May 8				2	12	7	1				22					
34	Tashiro Is.	9											—	•				36
35	Off Haramaga	June 28 '77											—	•				34

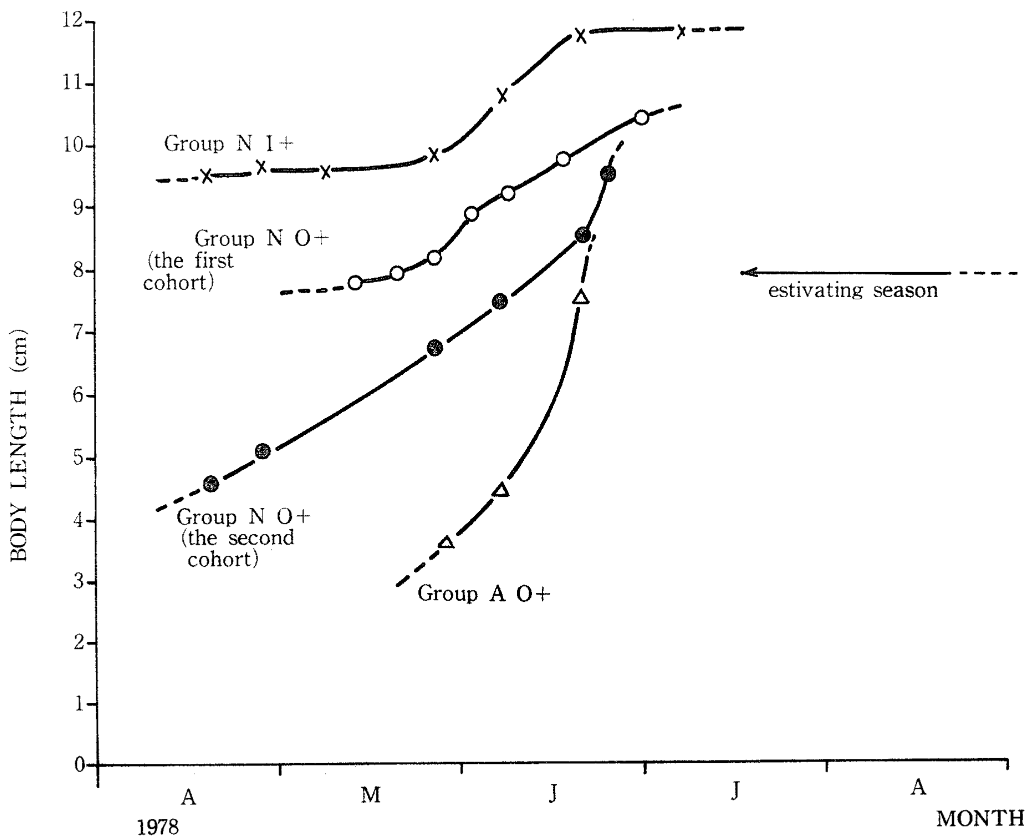

FIG. 8. Growth in mean length of 0 and I Groups.

adults of Group A formed a school by themselves (No. 8, 9, 13 and 22 in Table 5.), but sometimes they were intermingled with Group N in a school. Age-0 fish were distributed off the northern coast of Oshika the Peninsula as exclusive patch (No. 23, 27 and 32 in Table 5).

In the estivating and spawning seasons, two subpopulations are distributed mixed in central Sendai Bay, showing the ratio (abundance of Group N to that of A) of 9:1.

2) *Growth*

Growth of age-0 and -1 sandeel in 1978 is shown in Fig. 8. This shows that Group N has two cohorts. Larval fish of both subpopulations reach about 10 cm in length at the end of June before estivation. Differential growth between the two cohorts of Group N is observed until the end of June.

Age-0 fish of Group A grows up quickly and approaches the size of Group N, whereas the former are produced later. The sandeel in Sendai Bay grows most quickly in the early summer.

Growth curves for the successive yearly mean length and year-to-year change in growth rate of the two groups are depicted in Fig. 9. This shows quick growth in their first year, espesially in Group A, and subsequent low and steady growth for both groups.

L_∞ and k, growth parameters for Groups N and A, are 16.28 cm and 0.842,

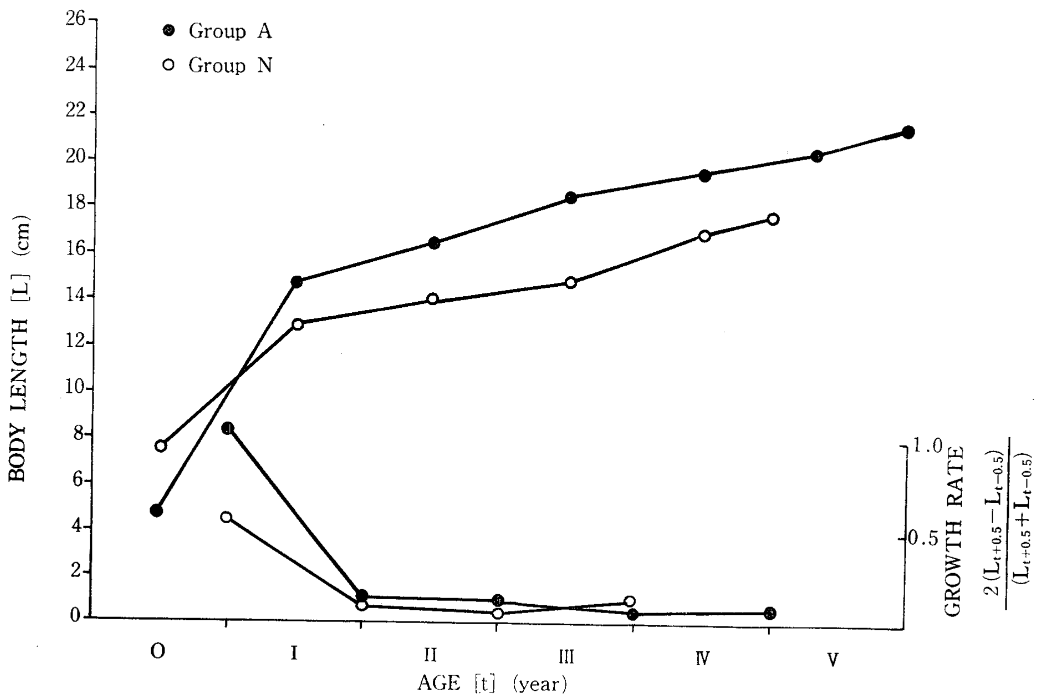

FIG. 9. Growth curves for the successive mean length (top) and year-to-year change in growth rate of the two groups of sandeel (botlom).

and 19.71 cm and 1.012, respectively. On the other hand, the life span is estimated to be 5 and 6 years for Groups N and A, respectively. The observed maximum length is 17.5 cm and 23.1 cm, resulting in the following ($k \times T$) values.

$$k \times T = 4.21 \text{ for Group N},$$

$$k \times T = 6.07 \text{ for Group A}.$$

Since k has the dimension of 1/time, growth pattern can be compared in the use of $k \times T$ (Kawasaki, (11)), showing the faster growth for Group A.

3) *Reproduction*

The spawning season of sandeel was from late November 1977 to mid-January, 1978. The mean GI of the fish of age-1 and older are shown in Fig. 10. Intensive spawning in Sendai Bay was carried out presumably from late December to early January, when a great number of mature and spent fish were caught. Water tem-

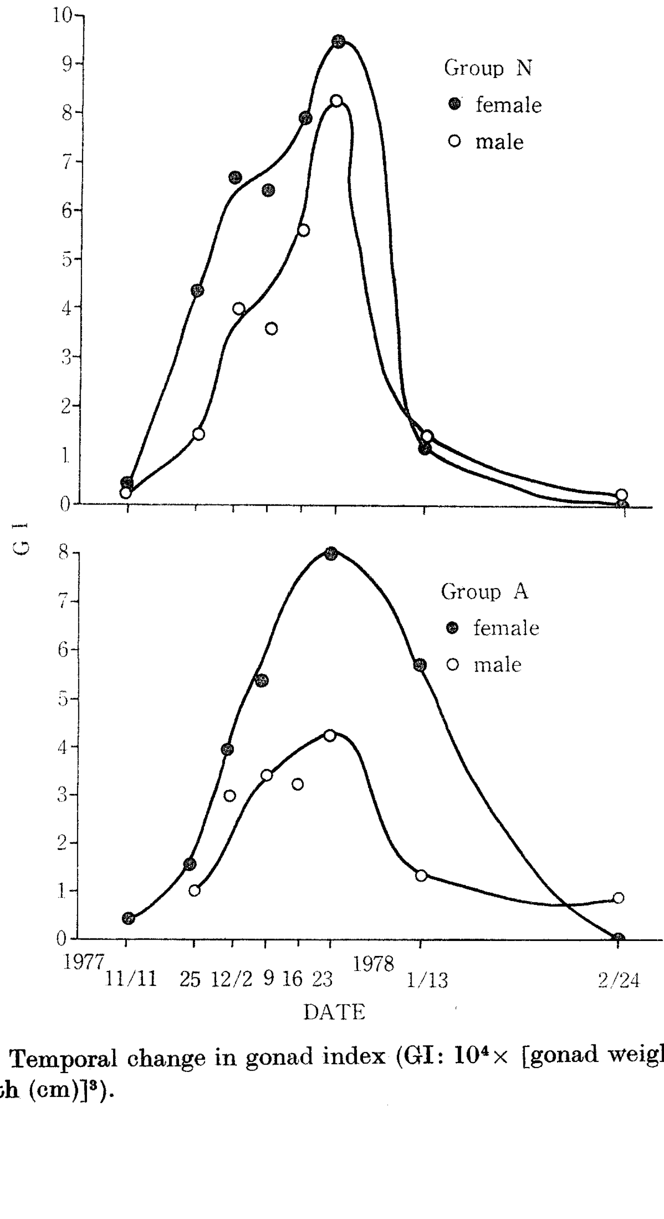

Fig. 10. Temporal change in gonad index (GI: $10^4 \times$ [gonad weight (g)]/[body length (cm)]^3).

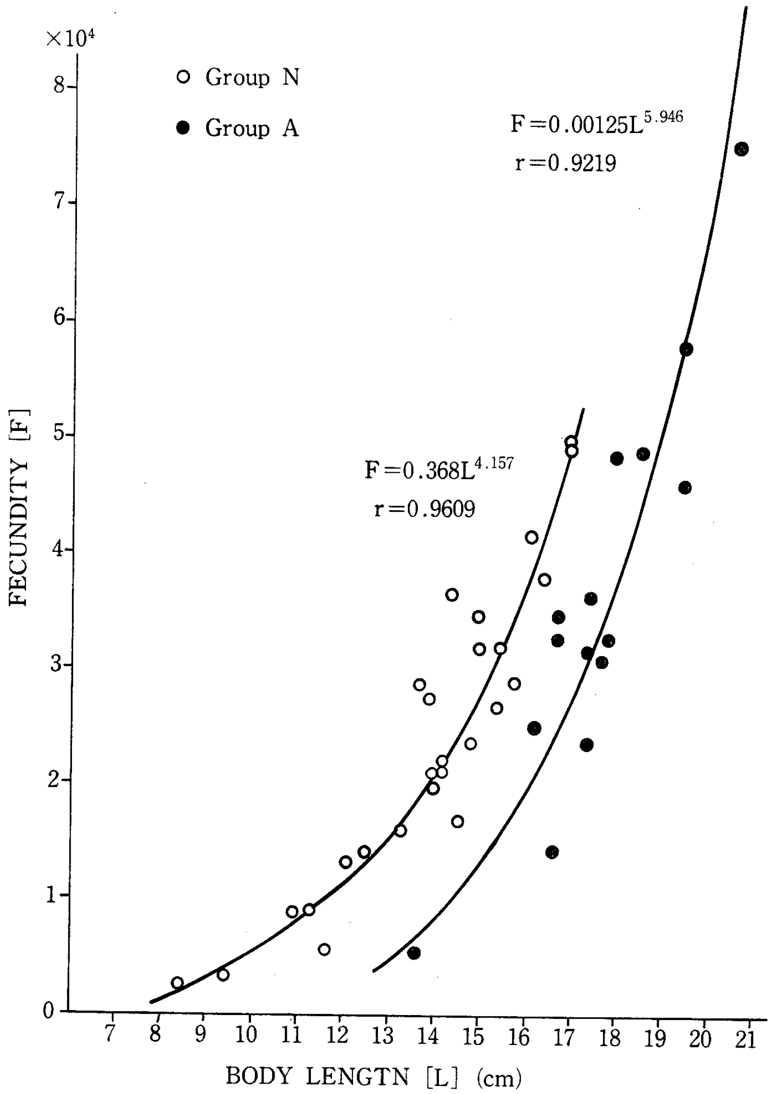

FIG. 11. Regression of fecundity on body length.

perature in December was 12 to 15°C as seen in Fig. 5. Fish of Group A had spawned for a longer period of time than Group N as shown in Fig. 10.

The relationship between body length and fecundity is shown in Fig. 11. Since diameter of ovarian eggs is unimodally distributed from yolk formation to spawning (Fig. 6), most eggs may be laid simultaneously. The smallest mature female is 8.4 cm long for Group N and 13.6 cm for Group A, showing that some sandeel spawn in their first year.

As shown in Fig. 11, fish of Group N are more fecund than those of Group A of the identical size. However, fecundity per female is greater in Group A, because of the larger size of spawners.

Maximum-GSI-on-length curves are shown in Fig. 12. Maximum GSI is thirty per cent for Group N, when the age of fish is two or three years old, and it is twenty-three for Group A of three years.

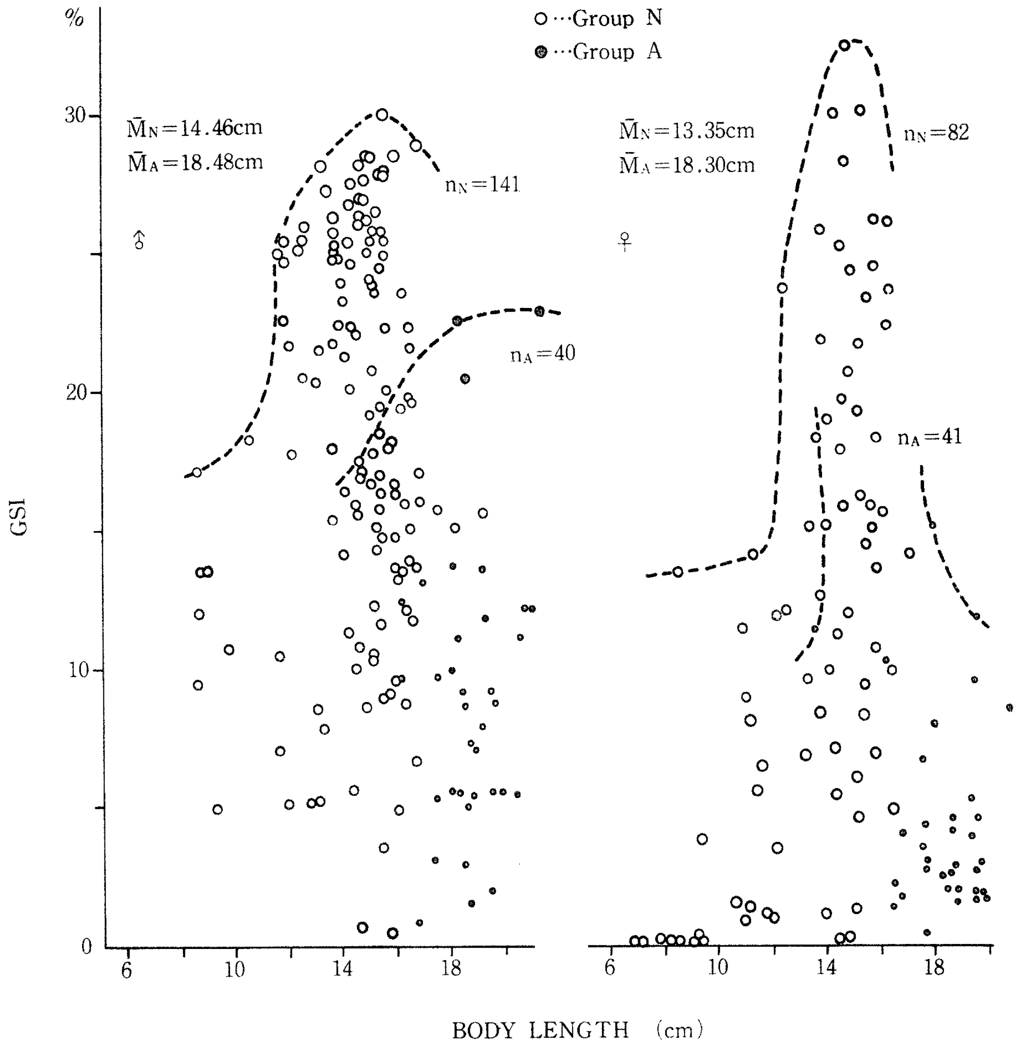

Fig. 12. Relation of gonosomatic index (GSI: $10^2 \times$[gonad weight (g)]/[body weight (g)] to body length in the spawning season (1977–1978).

Conclusion and Discussion

Since the earlier times, two subpopulations of the Japanese sandeel have been distinguished from each other, depending on their modes of vertebral number at 63 and 65 (Hatanaka and Okamoto (1), Ishigaki and Kaga (2)). They are believed to be in contact with one another off Miyagi Pref. (Matsubara and Ochiai, (3)). Moreover, it has been clarified that each run of sandeel off various parts of Japan has peculiar ecological features concerning growth, longevity, etc. (Kitakata, (9)). However, the adaptive significance of these differences in life history has so far never been discussed. An interesting problem for investigation is the mechanism of formation of these two subpopulations and the adaptive significance of their cohabitation in the waters near Miyagi Pref. The investigation was carried out by the method of comparative ecology. In Table 6, the correlates of the features of the two subpopulations are shown. Some of these features will be given in more detail below.

TABLE 6. *Correlates of the Features of Two subpopulations*

subpopulation		Group N	Group A
Morphology	Otolith type Gill raker number mode Vertebral number mode	notch type 24 63	arrowhead type 28 65
Ecology	Range	near the Oshika Peninsula & Kinkasan, central Sendai Bay (often cohabitating)	Kesennuma Bay, Tomarihama, Ishinomaki Bay & off Ukedo (often cohabitating)
	L_∞	16.28 cm	19.71 cm
	k	0.842	1.012
	L_{max} (Life span)	17.5 cm (5 years old)	23.1 cm (6 years old)
	Proportion in estivating area	90%	10%
	Fluctuation in catch	short-spaced	large scale
	Spawning season	late Dec. to Jan.	late Dec. to Feb.
	Regression of fecundity on length (cm)	$F=0.368L^{4.157}$	$F=0.00125L^{5.946}$
Genetics	*α-Gpdh*^{F} allele frequency	low (O or nearly O)	high (about 0.3)

Distribution and Migration

Two subpopulations were distributed in a mixed state off Miyagi Pref. but the occurrence of Group A as a single shoal was conspicuous. In general, Group A tended to be distributed off the northern part of Miyagi Pref. and Group N tended to be distributed in Sendai Bay.

Growth and Life Span

Fish of both groups grew fast in early summer especially in June, and reached about 10 cm by the end of June (Fig. 8). Early growth was higher in Group A than in Group N (Fig. 8). A fish of Group A, 13.6 cm long sampled on Jan. 13, 1978 after estivation, turned out to be born in 1977, showing that the fish of Group A exceed those of Group N in growth within a year after birth.

Bertalanffy's growth parameters were 0.842 for k, relative speed to approach asymptotic length, 16.28 cm for L_∞, asymptotic length, and the life span was five years in the case of Group N. Whereas the values were 1.012, 19.71 cm respectively and the life span was six years for Group A. The maximum observed length was 17.5 cm and 23.1 cm for Groups N and A, respectively. As Kawasaki (11) stated, the index to express comparative growth speed is ($k\times T$), where T is the generation time and tentatively expressed as the life span or the mean reproductive age. $(k \times T)$ was 4.21 for Group N and 6.07 for Group A. From these facts it is understood that the fish of Group A grew faster, lived longer and reached a larger size than those of Group N.

Reproduction

Some fish of Group N participated in spawning early in their first year. The spawning lasted from late December to January. Few fish of Group A spawned in their first year and the spawning season was a little longer, which was from late December to February. A difference between subpopulations was also found in fecundity and the fish of Group N were more fecund than those of Group A of identical size (Fig. 10).

In comparing the fecundity of the two subpopulations (Fig. 11), the fish of Group N were more fecund than those of Group A of identical size, and the fecundity per female was more in Group A, especially in larger fish. That the fish of Group A have more eggs in comparison with those of Group N became clear also when observing the maximum-GSI-on-length curves in Fig. 11. Namely, while the maximum GSI is 30 per cent for Group N, it is 23 per cent for Group A. This means that growth is slower and more resources are put into reproduction in Group N, whereas fish of Group A grow faster and the utilization of matter and energy for reproduction is small. However, eggs per female are more abundant in Group A due to the large absolute quantity of reproductive substance per fish.

The adaptive significance of high fecundity in Group A can be seen in the high average age of spawners. The intrinsic rate of natural increase r as a measure of the biotic potential is formulated as below:

$$r \fallingdotseq \ln(\Sigma\, l_X m_X)/T$$

where l_X is the probability at age 0 of surviving to age X, m_X is the number of female eggs laid by the average female in the age interval $(X-0.5)$ to $(X+0.5)$ and T is cohort generation time, mean age of mothers in cohort at birth of female offspring. Since the effective l_X is small and T is large in Group A, resulting in small r, m_X become large to prevent too small r.

Kawasaki (11), one of the authors, distinguished between Type I with high variability in biomass and Type II with low one as two extremes in the pattern of fluctuation in number of the marine teleosts. Moreover, Type I was subdivided into two subtypes, Subtype IA which makes the short-spaced and irregular variation and Subtype IB which makes large scale and periodical variation. These three types show the adaptive modes of fluctuation in number, based on the life histories selected in the respective environment through the process of evolution. Type I has adapted to the variable environment, horizontally temperate and subarctic seas, and vertically surface layer. Type II has been selected in a stable environment, horizontally tropical and subtropical areas, and vertically subsurface and bottom layers. Futher, Subtype IA has corresponded to the environmental component of short-interval variation and IB to that of large-scale fluctuation.

The crucial difference in the life history between Types I and II is whether more resources are used for the preservation of brood or for the preservation of the individual. In this sense the fundamental form of Type I is Subtype IA, which is short-lived, early reproductive and more fecund in contrast with Type II of long life, late reproduction and low fecundity. In order to increase the population rapidly to cope with the large-scale environmental betterment, however, life must be long in contradiction to putting more energy into the preservation of brood. Subtype IB is the result of the third life history in which the relative growth speed, *i.e.* ($k \times T$), becomes higher to resolve this contradiction.

The above mentioned relations are expressed as a triangle (Kawasaki, (11)). As seen in Fig. 13, the basic axes of this triangle are longevity, relative speed of growth and fecundity. Any species or subpopulation is situated somewhere inside this triangle.

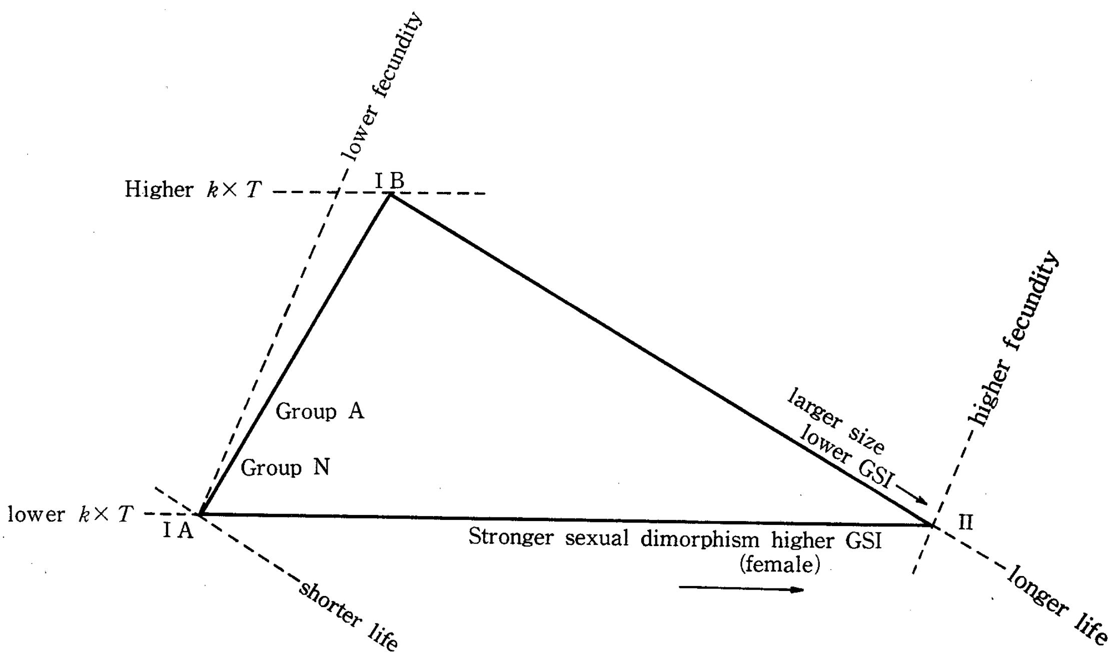

Fig. 13. Triangle showing the relation between the three selected extremes of the life historical patterns in marine teleosts (From Kawasaki (11)) and the supposed loci of Groups N and A.

The sandeel as a species occupies the locus close to Vertex IA in the triangle. On the subpopulation level Group N is typical and Group A is located somewhat near Vertex IB (Fig. 13), judging from their life histories.

With the purpose of scrutinizing the problem of recruitment, year-to-year change in landings in Miyagi Pref. was examined by areas (Fig. 14). Land-

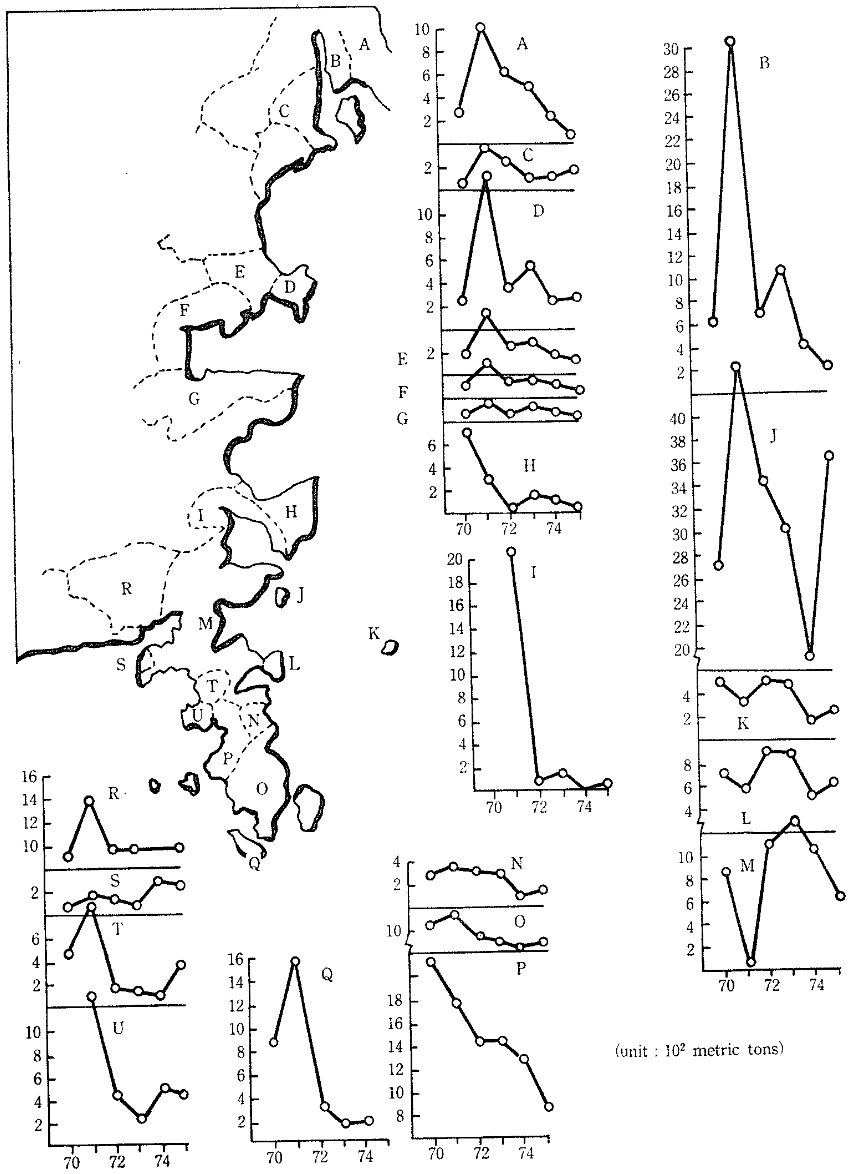

FIG. 14. Year-to-year change in landing in the respective designated area.

ings in all areas north of Oshika Peninsula showed extraodinary peaks in 1971, exhibiting a large cohort born in this year (Fig. 14). The coastal seas north of Oshika Peninsula are the major range of Group A. The variation in recruitment of Group A is thought to be wide judging from six year change and they presumably spread around the areas north of Oshika Peninsula when the year class was strong. These facts show that Group A is situated nearer the Vertex IB than Group N.

The result of the study on polymorphism of α-GPDH reveals that whereas the frequency of α-*Gpdh*^{F} is about zero in Group N, it is about 0.3 in the case of Group A. This shows that the former population is stable and the latter is plastic genetically.

In the coastal region along Miyagi Pref. Group N is relatively abundant, numbering 90 per cent of the estivating fish, and presumably plays the role in stabilizing the species population. On the other hand, it is presumed that the role of Group A is to increase the recruitment rapidly when the environment becomes improved, resulting in wider range and prosperity of species. The adaptive significance of this cohabitation of two subpopulations off Miyagi Pref. is attributable to sharing different roles between them.

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