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Title	POPULATION IDENTIFICATION OF WALLEYE POLLOCK, THERAGRA CHALCOGRAMMA (PALLAS), IN THE VICINITY OF JAPAN
Author(s)	IWATA, Munehico
Citation	MEMOIRS OF THE FACULTY OF FISHERIES HOKKAIDO UNIVERSITY, 22(2), 193-258
Issue Date	1975-03
Doc URL	https://hdl.handle.net/2115/21859
Type	departmental bulletin paper
File Information	22(2)_P193-258.pdf

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POPULATION IDENTIFICATION OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA* (PALLAS), IN THE VICINITY OF JAPAN

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I. Introduction

The Yearbook of Fishery Statistics of FAO described the nominal catch of marine fishes as 16.17 million metric tons in the northeast and northwest regions of the Pacific for the year 1971. Out of this catch walleye pollock (*Theragra*

* This work was submitted as a partial fulfillment of the requirements for a Doctor's degree in Fisheries Science at Hokkaido University in 1974.

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chalcogramma, PALLAS) was estimated as 3.64 million metric tons (21.8%). Total landing was rapidly increasing during six years from 1965 to 1971.[1)]

Development of the walleye pollock fishery of Japan was mainly due to the invention of the methods for "Surimi" production,[2)] and that of "frozen storage of Surimi for long term".[3)] Nowadays, the surimi is one of the most important protein sources for a number of food products.

However, if the studies on this species are reviewed from the viewpoints of population biology or the management of stocks, it can be said without much hesitation that these studies did not have enough scientific knowledge to successfully manage the stocks.

Taking this fact into account, the author assumed that more reliable population identification might be the first useful step towards a better understanding of the harmony which may exist in the maintenance of stocks of this species and fisheries. Therefore the population identification of walleye pollock, whose landing is biggest in the Japanese fishery, was attempted through the use of more refined techniques. The biological concepts of population identification were also considered.

In this study, the term "population" is used as an all-inclusive term by the author, and directly when other studies are quoted. The English word "pollock" is rather common, (Suketodara in Japanese and Mintai in Russian are also incontestable common names), but both the scientific and the English common names have been inconsistent; so the author has followed "A list of Common and Scientific Names of Fishes"[4)] by the committee on names of fishes of the United States of America.

II. History of the Biological Studies on Walleye Pollock

Most of the reports dealing with this species inhabiting the northern Pacific were presented by Japan and Soviet Russia, whereas it drew little attention from the United States of America. The studies can be cited with the reports published by Lindberg,[5)] Moiseev,[6)] Kasahara,[7)] and Kibesaki.[8)] The Russian viewpoint on walleye pollock fishery had been expressed by Serobaba[9)] as the Soviet interest in the expanded Japanese fishery activities in the eastern Bering Sea and the area of the Kamchatka Peninsula, clearly emphasizing the importance of this fishery. In the United States and Canada, the interest about this species has confined to classification,[10)] and biological surveyes by trawlers.[11),12)] Kasahara[7)] introduced the Japanese fisheries of this species in the Bering Sea or the Northeast Pacific. Kodiak Marine Fisheries Laboratory of the U.S. Department of Commerce, National Marine Fisheries Service, had a limited program of research on pollock (personal information from Dr. Jay C. Quast, 1973).

The biological information obtained so far will be outlined under specific headings, as in the following.

Special distribution

Walleye pollock which were caught by salmon gill-net in the basin of the Okhotsk Sea or the Bering Sea region inhabit the more shallow waters. The surface water temperature was from 4° to 5°C during June in the middle region of the Bering Sea, and 6° to 7°C during July, in the western waters of the south Kamchatka Peninsula.[13] Otter trawlers catch pollock at 100–150 meters on the continental shelf of the eastern Bering Sea during spring and summer. At the southern boundary of their range in the Pacific off Japan, pollock are caught at depths of 300 meters or more, during the same months. These results may be suggestive of the fact that this species is adapted to inhabit a water of suitable temperature rangs.

Geographic distribution

Walleye pollock were caught in the summer seasons of 1969 and 1970 in the Gulf of Anadyr.[14] One kilogram catch of pollock had also been reported from the Bering Strait (64°–30′N, 167°–58′W), whose water temperature was 0.5°C.[12),15] Maeda *et al.*[16] described the difficulties involved in the fishery in typically cold northern waters. The distributions on the southwestern limit in the western Pacific Ocean had been reported by Abe[17] based on two instances where a number of pollock were caught by a bottom long line in Tokyo Bay, and by a bottom trap net in Sagami Bay. In the Sea of Japan, the spawning groups migrate to East Korea Bay, and the southern limit is set by the warm current coming through the Korean Strait.[18] This species was also captured from waters shallower than 300 meters along the Pacific coast of Nroth America, from the Gulf of Alaska to Oregon State.[12]

Tagging experiments

Hokkaido Fisheries Experimental Station conducted a tagging experiment in the area off Rishiri Island in the Sea of Japan in 1931.[19] Two fish, tagged with a celluloid plate, were caught, respectively, at the western coast of Sakhalin after 48 days, and after 665 days in the East Korea Bay. Tagging experiments on a large scale have been carried out by the Fisheries Experiment Station of the Government-General of Chosen (Korea) since 1932 in the East Korea Bay. They reported that spawners migrated from Peter the Great Bay to the East Korea Bay along the 50–200 m, depth zone.[20] Results of these two early experiments were described by Ogata.[21]

Recent experiments were concentrated in three regions: around Hokkaido; eastern Kamchatka Peninsula; and eastern Bering Sea. In the northern Sea of Japan, coloured rubber bands used to attach bait to the hook were carried by a lot of walleye pollock. They were collected from some fish meal factories. This

special experiment suggested that spawners in the northern Sea of Japan migrated northward through the winter season along the coast of Hokkaido. Furthermore, another experiment, using a plate tag, in Ishikari Bay suggested that the spawners migrated to the west coast of Sakhalin Island, and one fish migrated to Uchiura Bay in the Pacific region.[22),23)]

A remarkable number of tagged fish are showing their migration behaviour in the Okhotsk Sea.[24)] The tagged fish in the northeastern coast off Hokkaido were recaptured from various areas of the northern Sea of Japan, Telpenia Bay, the western and eastern coasts of the south Kamchatka Peninsula, in the channel of Nemuro, and the south coast of Iturup Island.

Off the east coast of the Kamchatka Peninsula, eleven fish were recaptured in the area along the northern Kuril Island and off the southeastern Kamchatka Peninsula. One tagged fish migrated from off Cape Olyutorskiy to off Cape Navarin.[25)] Similar experiments were carried out at the edge of the continental shelf off St. Mathew Island in the eastern Bering Sea. Tagged fish were recaptured from the northern to the southern portions of this area.[14)]

Spawning, Development, and Early Stages of Life

A number of studies have described the spawning behaviour, the development of eggs or larvae, and their distribution. They will be summarized below, in the same order.

The spawning period extends from three to four months in certain areas. In higher latitudes, spawning generally begins later than in lower latitudes. For instance, the adult fish, mainly 4–5 years old, enter shallower waters after mid-September. The floating eggs collected by a larvae net in mid-December were numbered 100–200 thousand per 10 minutes of towing. The highest density of eggs, observed in the last ten days of December, was 300 thousand eggs.[26)] However, this period lasted from late March to June off the western coast of the Kamchatka Peninsula.[27)] About 80% of the adults have completed by the latter half of May. After this period, floating eggs became scant, and larvae of 8 to 11 mm size increased in abundance.[28)].

Echo sounder records indicate that the spawning fish are distributed vertically in two or three strata. The females dominated the upper stratum, and the juveniles or males concentrated in the lower one.[29),30)]

Ovary fecundity (number of eggs) had been correlated to the body size in certain areas. For example, in Kumaishi, on the southwest coast of Hokkaido, the specimens of sizes 36–40, 41–45, 46–50 cm had, 168,500, 217,500, 324,400 mean ova, respectively. The egg diameter was known to grow from 0.8 to 1.0 mm, as the ova gradually become transparent. The maximum diameter was 1.5 mm.[31)] Kamiya[32)] reported that the transparent eggs measured 1.35–1.45 mm in diameter,

and had no oil-glouble. In contrast, Yamamoto and Hamashima[33] and Yusa[34] observed five to six oil-globules in the eggs. The colour or pigmentation of ova was reported as carotene orange.[35] Body form and mortality in the embryonic and early larval stages were compared among different incubations of water temperature.[36]

Hatching began 7 days after artificial fertilization at 9°–11°C water temperature.[32] The newly hatched larvae were over 3.00 mm in length. Yamamoto and Hamashima[33] reported that hatching started on the tenth day, after fertilization in 7°–10°C water temperature and the larvae measured about 3.6 mm. While the ova are floating freely at the surface, the protoplasmic germ disc or embryo lies at the lower pole, and the yolk at the upper. An irregular network-like pattern is visible on the surface of the chorion until hatching occurs. The larvae hatched twelve days after fertilization in 6°–7°C water temperature. Observations are available only for larvae up to 25 days old.[34]

Eggs were generally more abundant in the coastal zone than offshore from late May to late June. The body length of the larvae caught at 55°N, off the western Kamchatka Peninsula, on June 8, 1956, was about 10 mm. Larvae length-frequencies were bimodal, and the larger group was represented by the body length of 36–40 mm. This fact suggests that the spawning season was prolonged, and at least some groups hatched at different times survivied.[36] The body length distibution ranged from 6 to 35 mm during July in the Okhotsk Sea. During the same period in the Bering Sea, the range was from 22 to 41 mm.[37] Hattori[38] had described characteristics and forms of larvae of 5.7–23.4 mm size which were collected at eastern area from C. Erimo.

Juveniles, which were able to swim first, appeared in May off southern Hokkaido. They were collected from mid-May to mid-July by the stationary nets in Kami-iso Bay and Uchiura Bay during 1969–1973. Their body length varied from 2.8 cm to 8.5 cm. Since a sample did not always show a monomodal distribution, therefore, it is suggested that surviving juveniles came out at various times during the long spawning season (Iwata, unpublished data). After the juveniles had attained 7 or 8 cm, they began to migrate to deeper waters. After one year, they were collected mainly on the continental slope in canyons along the Pacific coast of Hokkaido, and had increased to 10–13 cm in body length.[39),40] However, after one year in the East Korea Bay, their size was reported to be between 18 and 20 cm.[26]

Age and Growth

Various methods for age determination have been successully applied. Structures used were the vertebral centrum, otolith and scale. Uno was the first to try to estimate the age of walleye pollock from the Sea of Japan, under

the hypothesis that transparent rings actually denote the age.[41),42)] Mosher determined the age in six species of the virgin stock from the Bering Sea.[43)] Only 26% of the counted rings on the otolith sections, were found consistent when repeatedly analysed, and that reason was explained as a discrepancy on the basis of complexity in otolith edges.

The relationship between the otolith ring and age was also studied by Ishida[44)] for juveniles during different seasons. He reported that the transparent ring appeared during winter; that almost all individuals formed one, and that the ring turned opaque by the next spring. The ring counts of centra coincided to an average of 60% with the otolith for a given group of specimens. The ring formation of vertebra began about 1.5 months later than that of the otolith.[45)] Although both scales and otoliths have been used for age determination in a number of individuals, the variations between the counts of either material, increased in the specimens of over 4 years of age.[21)]

Recently, Zver'kova[46)] calculated the growth equation after the results of age determination, and discussed a decrease in growth rate after sexual maturity. Yamaguchi and Takahashi[47)] presented the same formula using scales for the specimens from the eastern Bering Sea. They suggested that the growth rate increased during the years 1965–1968.

However, the age determination group of Japanese Fisheries Agency's Special Scientific Program produced an interim report with the conclusion that exact age determination with otoliths might be considerably difficult for specimens over four years old.

Population identification

Several Japanese scientists studied the morphometric, meristic, and other characteristics of walleye pollock in order to identify the populations around Hokkaido. First in this series, was the report of Ishida[44)] who made a survey based on body length, otoliths, and scales. He analyzed the relation of body length to otolith length or width, the frequency distribution of body length, and the age character of otoliths. Some differences among the fishes from a few regions were recognized with the studies on otolith shapes and growth curves, but he pointed out that more advanced analyses were needed to identify various populations. He, however, pointed out in the report for the explanation of Hokkaido fisheries that, there were at least two populations comprised in a larger-size group and a middle-size group, in the western Erimo region. He also recognized the detectable differences of growth and otolith character, which may exist between the fishes inhabiting the Sea of Japan and the Okhotsk Sea.[48)] Subsequently, the Tohoku Regional Fisheries Laboratory[49)] investigated the differences of those two groups in the western Erimo region by studying the body

form, the ratios of head length/depth of the caudal peduncle, caudal fin length/fork length, and body proper length/body depth. Though not any clear conclusion on population distribution could be drawn, more detail studies separated the population into three types morphometrically, that is, A-middle, A-large, and B type.[50),51)] Population identification in the western Erimo region was carried out with the help of the relationship between otolith rings and their radius[52)]; and the relationships between body length and otolith weight or orbit[53)] as well. The transition from A type to B type in this region was revealed by their studies. In the eastern Hokkaido region, the existence of three groups was suggested separately in the areas off Hiroo, Kushiro, and Iturup Island.[54)]

Populations in the Sea of Japan were separated into four based on a statistical analysis of vertebral counts.[55)] Only one population was reported in the northern Sea of Japan, as a result of the distribution range of body length and vertebral counts, without statistical consideration.[23)]

There have not been enough surveys in the Okhotsk Sea, so far. Abashiri Fisheries Experimental Station (mimeograph) has separated the Terpenia Bay group from the eastern Hokkaido fish group by the differences in vertebral number.

Recent studies made in the eastern Bering Sea have been rather conflicting. Maeda,[16)] who analyzed statistically the relationship of body length or body weight with otolith width or otolith weight, found a discontinuity of fishing grounds. He estimated the presence of two populations, east and west of Pribilof Islands, respectively. But, Takahashi and Yamaguchi[14)] who carried out tagging experiments in this region, found that there was some interchange between the two populations reported by Maeda.[56)] The term "populations" in all of these studies was used without definition.

On Subspecies

No population studies of walleye pollock have been conducted along the North American coast, south of the Bering Sea. Discussions have been concentrated upon the reasonability of subspecies, *Theragra chalcogramma fucensis* (Jordan and Gilbert, 1894). According to the studies of Schults and Welander,[57)] "*Theragra chalcogramma* (Pallas, 1811) has been considered as divisible into two subspecies, *T. c. chalcogramma* of northeastern Asia and Alaska, and *T. c. fucensis*, Jordan and Gilbert[58)] described the latter from Puget Sound, Washington. This subspecific separation was originally based on only four specimens from Puget Sound and three from Alaska, and an inadequate number. --- The differences indicated above appear to represent the usual trend among most fishes, namely an increase in the number of segmental units in waters of lower temperatures. Since the difference in the number of fin rays is not so great between Puget Sound and Alaska, --- We do not venture to synonymize them on the available evidence."

Scientific names have come from the Greek roots *ther* (beast) and *agra* (food of fur seals); and *chalcos* (brass) and *gramma* (mark).[59,10]

III. Morphometric Analysis

Shimizu[60] explained the animal form as growth and its variation in time and space. The body form reflects the history of species and specimens whose form they owe to ontogenesis and growth. In a species, the differences of environments through the process of ontogenesis and growth also lead to local variations. These phenomena were proved by incubation experiments of walleye pollock eggs under various controlled temperatures.[36] Furthermore, Martin[61] studied the body forms of *Salvelinus fontinalis* in three hatchery stocks in which the fish were characterized by different growth rates.

Two factors for discussing the form as emphasized by Shimizu, are not independent of each other. They should be considered in a certain growth stage when the spatial forms, namely local variations are analyzed. It is well known that all adults do not grow in similar figures from larvae. Quetelet clarified, for example, that there was a change of direction, or "point of inflection", in the curve of weight at the age of one or two years, and there were certain other features in our human curves which the scale of the diagram did not make clear; and all these differences are due to the fact that a child is changing shape as he grows, --- Boy and man are not similar figures (quoted from Thompson)[62]. However it may be hard to analyze the variation of form of walleye pollock throughout their growth, due to the unreliability of age determination methods. Therefore, the concept and method of relative growth which were proposed independently by Nomura,[63-65] Huxley, and Teissier[66] are used in this study, since the time dimension can be a latent factor in growth process.

Martin[60] explained the relative growth mechanics as follows. The relative growth method consists essentially in plotting the logarithm of some dimension of a body component against the logarithm of a dimension of the whole body over a series of sizes of the organism concerned. Such logarithmic plots almost invariably show a linear relationship over extensive ranges of body size.[66] This linear relation between the logarithms indicates that although the body form is rarely constant over the greater part of growth, these continuous changes in form can be described by determining the value of the slope, k, in the relative growth equation, $Y=bX^k$ or $\log Y=\log b+k\log X$. If the body dimensions in equation are of the same order, for example, as partial length against body length, the slope k will be approximately one. If the area is plotted against length, k value that approximate two is expected against length, and if the volume or weight is plotted against length, k approximates three. In practice, measurements are generally not taken throughout the growth of an individual, but rather a series of specimens

of different sizes is measured and the resultant data are plotted, so that each point represents the end of one particular ontogenetic line of growth. The best line through these end points has been considered representative of the relative growth of an average individual for the body part considered.

Then the recognition of the differences between samples was directed to detect the geographical variations depending upon the statistical allometry equations of samples.

Although the statistical calculations in the analysis of relative growth of all combinative cases of multiple factors, involving large samples, required extensive time, if done manually, the FORTRAN programs used with the computer FACOM 230–60 at the Hokkaido University, completed these computations quickly.

1. *Materials and Methods*

These samples were mostly collected by fishing boats in the Sea of Japan, the Okhotsk Sea, and the Pacific region where these boats catch walleye pollock by Danish seine or otter trawl. Some samples from the eastern Pacific or Bering Sea, included here, were sampled by the T/S Oshoro Maru, Faculty of Fisheries, Hokkaido University. The number of sample lots analysed here is 30, and the total number of specimens, 1828 (Table 1, Fig. 1).

The procedures before measurement varied in the course of studies as follows.

CASE 1:	(a)	received soon after catch
(in field)	(b)	kept on ice for some days
	(c)	frozen
CASE 2:	(a)	measured soon after receiving
(in laboratory)	(b)	kept frozen for some days, and then measured

It was found out that the measured part of fish changed during storage. Fresh specimens have natural elasticity. Therefore the snout length or the distance between both eyes, was over or underestimated. The shape of the eye, in this case the conjunctiva or the nictitating membrane, swelled up, so the diameter of the eye was overestimated. Consequently it was impossible to measure all specimens with the same precision. The three values, snout length, eye diameter, interorbital width, might be underrated as compared with other measurements.

The following 12 measurements and their means were evaluated (Fig. 2).

BL: body length
HL: head length
SNL: snout length
EYD: eye diameter
DEY: interorbital width
BW: body weight
OLM: mean of otolith lengths

Table 1. *Sample number and area, date of collection, number of specimens for each experiment, and fishing gears.*

	Sample number and area*	Date of collection	Number of specimens			fishing** gears
			form[1]	verteb.[2]	T.O.[3]	
1	Kumaishi	7 III '72			94	LL
2	Kumaishi	5 II '70	47	47		LL
3	Kudo	23 I '70	49	49	145	LL
4	Ofuyu	24 II '73				DS
5	Mashike	29 III '69		49		DS
6	Teuri Yagishiri Is.	29–30 XII '69		25		DS
7	Rishiri Rebun Is.	25 XII '69	64			DS
8	North Wakkanai	17 I '69		65	60	DS
9	North Wakkanai	10 II '73				DS
10	Moneron Is.	7 XII '69		30		DS
11	Moneron Is.	29 III '69		30		DS
12	Kholmsk	25 XII '69	83			DS
13	Kholmsk	26–27 II '69		30		DS
14	Il'inskiy	27–29 III '69		30		DS
15	Il'inskiy	23–25 V '69	40	40	60	DS
16	West Sakhalin	7 II '73				DS
17	Staritsa	24–29 III '69	50	28		DS
18	Belkina	4 XII '69	85	73		DS
19	Belkina	18 XII '69	119	100		DS
20	Belkina	10 II '73			72	DS
21	Rausu	8 IV '69	50	48		GN
22	Rausu	21 IV '70	96	96		GN
23	Rausu	11 II '73			108	GN
24	Abashiri	10–11 IV '69	98	66		DS
25	East from Soya C.	21 X '69		29		DS
26	Aniva Bay	23 X '69	50	48		DS
27	Aniva Bay	19 XII '69	50	63		DS
28	Aniva Bay	24 V '69	50	50		DS
29	Aniva Bay	20 VII '69	40	39		DS
30	Terpeniya	24 V '69	26	26		DS
31	Northern Sakhalin	30 VIII '70		26		GN
32	Northern Sakhalin	2I X '70		31		GN
33	Northern Sakhalin	3I X '70		37		GN
34	Magadan	21–30 XI '68	68			OT
35	Magadan	9I X '70		30		OT
36	Magadan	21 XI–2 XII '70		18		OT
37	Western Kamchatka	2I I '70	87	87		OT
38	Western Kamchatka	13 I '70		69	96	OT
39	Hachinohe	21 I '73			59	DS
40	Usujiri	8 XII '72	54			GN
41	Uchiura Bay	18 I '69	46	26		GN
42	Uchiura Bay	18 I '69		25		GN
43	Uchiura Bay	30 I '70		83	60	GN
44	Uchiura Bay	11 I '73				GN
45	Kushiro	8 IV '69	80	24		DS
46	Kushiro	18 I '69			48	DS
47	Kushiro	18 IV '70		60	49	DS
48	Itrup Is.	10 II '73				DS
49	Northern Kuril Is.	10–17 X '69		40		OT

Table. 1 (Continued)

	Sample number and area*	Date of collection	Number of specimens			fishing** gears
			form[1]	verteb.[2]	T.O.[3]	
50	Northern Kuril Is.	16–23 XI '68		29		OT
51	Northern Kuril Is.	23–27 XI '68		28		OT
52	Northern Kuril Is.	19–21 VII '69	30	29		OT
53	Northern Kuril Is.	21–28 XI '69				OT
54	Northern Kuril Is.	11–13 XII '69	50	87		OT
55	Inkanyush Cape	14 IV 1970	69			OT
56	Western St. Matthew	4 VII 1973		29	30	OT
57	Western Plibilof I	10 V 1973			30	OT
58	Northern Unimak Is.	20 VII 1970			50	OT
59	Northern Unimak Is.	24 X 1972			31	OT
60	Eastern Kodiak Is.	24 VII 1970	45			OT
61	Dry Bay, Alaska	20 VII 1970	53			OT

* See the numbered localities in Fig. 1.

** LL....long-line, DS....Danish seine, GN....gill-net, OT....Otter trawl.

1), 2) and 3) for the analyses of morphometry, vertebral counts and tetrazolium oxidase respectively.

OLR: length of right otolith
OLL: length of left otolith
OWM: mean of otolith widths
OWR: width of right otolith
OWL: width of left otolith
OGM: mean of otolith weights
OGR: weight of right otolith
OGL: weight of left otolith
PFL: pelvic fin length

The following analyses were performed by the FORTRAN program, but males and females were combined together after preliminary examinations:

1. Each value was translated into common logarithms, and allometry equations of $\log Y = k \log X + \log b$ were calculated by the method of least squares. These regression lines were determined after rejection of inappropriate data by 5% significance level of rejection curves. Confidence intervals of 5% level of correlation coefficients (r) and regression coefficients (k) were computed:

$$b - t_{(0.05)}\, s_b \leq \beta \leq b + t_{(0.05)}\, s_b$$

where b is regression coefficient; $t_{(0.05)}$ the probability of t value at the 5% significance level, and s_b the standard deviation of the regression coefficients:

$$s_b = s_{y \cdot x} / \sqrt{\sum x^2}$$

where $s_{y \cdot x}$ is the sample standard deviation from regression. The null hypothesis at 5% significance level was tested in the cases where the population regression coefficient was zero or one after the following equation:

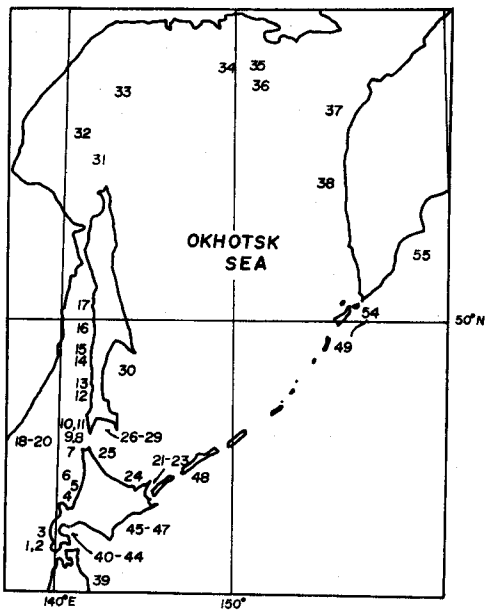


Fig. 1–a

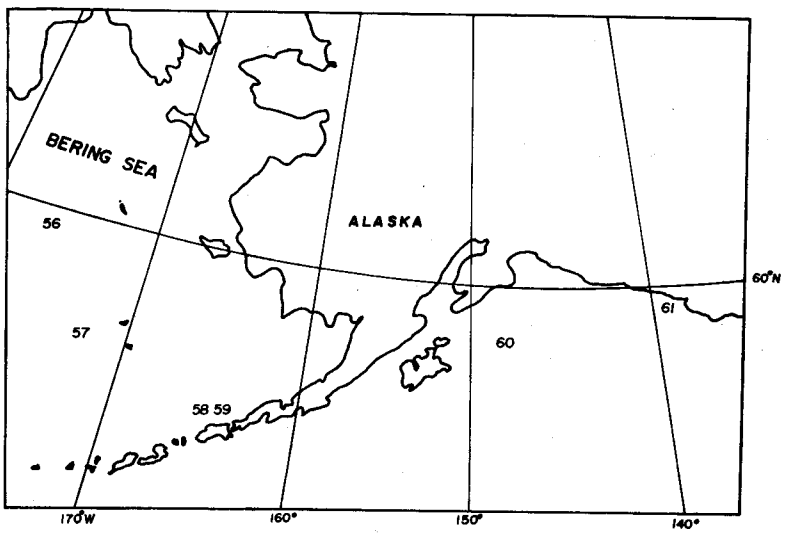


Fig. 1. Maps showing sampling locations for the morphological, vertebral counts, and genetic analyses in walleye pollock in the vicinity of Japan and the northeastern Pacific region.

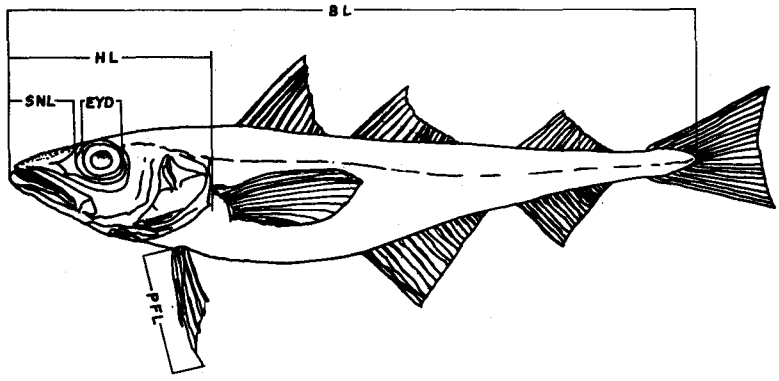


Fig. 2. Measurements of external characters of walleye pollock, *Theragra chalcogramma* (PALLAS).

$$t = \frac{b-\beta}{s_b}$$

Coefficients which were significant at the 5% level are marked by asterisks in Table 2.

2. Allometry equations were determined in 105 relative growth combinations, so that each factor was matched with the other fourteen factors. The test of significant differences of regression coefficients or adjusted means were calculated by the method of covariance analysis by Snedecor and Cochran.[67]

2. *Primary Investigations*

Application of allometry equations

This equation can be presented as

$$y = \log b + kx$$

where $\log Y = y$, $\log X = x$. This equation is a simple equation, where X is a standard measurement of body part and Y means a comparable part. Samples from Rishiri-Rebun Island (Sp 7) were investigated by the X-Y PLOTTER SYSTEM in order to judge, whether or not, the forms of walleye pollock fit into this equation.

Fourteen figures of the combinations comparing body length and the other 14 measurements have also been described (Fig. 3). Rejection curves were lined up after rejection by 5% significance level. The rejection curves of the combination of *BL-HL, BL-BW* showed much narrowness. The second group represented nine combinations concerning otoliths. The combinations of *BL-SNL, BL-EYD,* and *BL-DEY* were characterized by wider scattering of data.

Though walleye pollock matures at a size of 35–40 cm in body length, the

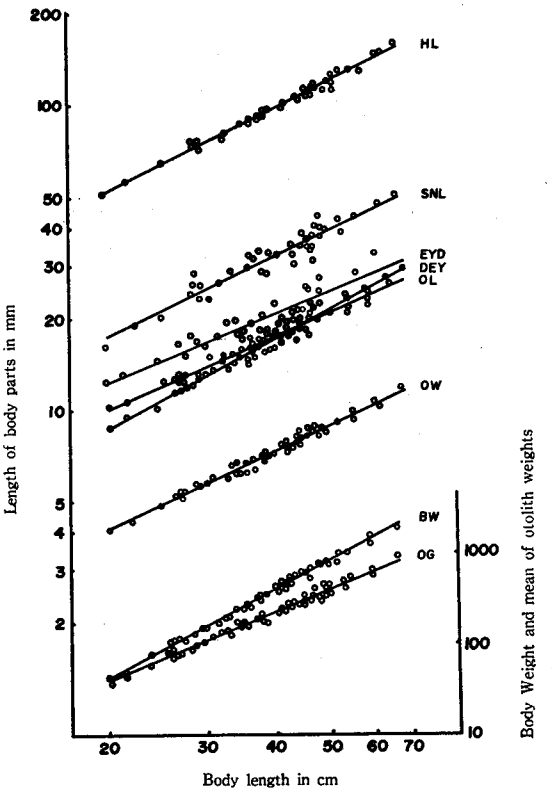


Fig. 3. Relative growth between body length and 14 other factors (*HL, SNL, EYD, DEY, BW, OLM, OLR, OLL, OWM, OWR, OWL, OGM, OGR, OGL*) for the samples from Rishiri-Rebun Island (Sp 7) illustrated by the X-Y Plotter System of FACOM 230-60 to examine the application of allometry equation.

inflection point can not be recognized in any combination. Correlation coefficients (r) are usually greater than 0.9 between two optional factors, in 105 combinations. Null hypotheses of Ho: $\rho=0$ were rejected at the 1% probability level (typical result appearing in Table 2). Due to the above reasons, it was preferrable to apply the allometry equation to the relative growth of all fifteen factors of walleye pollock.

Comparison between male and female

On pelvic fin length: It is difficult to sex specimens pollock from external characteristics. However some veteran fishermen do it just by looking at the fish abdomen. Pelvic fin lengths are also measured sometimes along with measurements of 12 other factors, and this factor was mainly useful to distinguish between male and female on the basis of their length and other characters. The female pelvic

Table 2. *Regression lines and results of statistical tests for the significance or regression coeffcients, to realize the relative growth of walleye pollock on the combinations between mutual fifteen parts in a sample from Kumaishi (Sp. 2).*

SET OF PARTS		REGRESSION LINE	DATA NO	CORREL. COEF.	CONFID. REG. LIMITS COEF.	T VALUE BETA=0	T VALUE BETA=1
BL	HL	Y=0.8043×+ −0.2833	34	0.9075	(0.2173 1.3914)	2.7910*	0.6790
BL	SNL	Y=0.7844×+ −0.7594	44	0.7787	(0.0323 1.5365)	2.1037*	0.5782
BL	EYD	Y=0.7004×+ −0.8167	43	0.8543	(0.1859 1.2149)	2.7483*	1.1758
BL	DEY	Y=1.1422×+ −0.5746	36	0.8690	(0.2366 2.0478)	2.5642*	0.3192
BL	BW	Y=2.6223×+ −1.4609	45	0.9482	(1.6212 3.6233)	5.2810*	3.2671*
BL	OLM	Y=0.6494×+ 0.2140	44	0.8047	(0.0926 1.2062)	2.3525*	1.2701
BL	OLL	Y=0.6559×+ 0.2015	43	0.8213	(0.1127 1.1991)	2.4381*	1.2788
BL	OLR	Y=0.6651×+ 0.1892	45	0.8011	(0.1000 1.2303)	2.3727*	1.1945
BL	OWM	Y=0.8700×+ −0.5152	44	0.8748	(0.3120 1.4280)	3.1447*	0.4700
BL	OWL	Y=0.8786×+ −0.5281	44	0.8746	(0.3148 1.4425)	3.1429*	0.4341
BL	OWR	Y=0.8818×+ −0.5343	44	0.8816	(0.3379 1.4257)	3.2701*	0.4384
BL	OGM	Y=2.4231×+ −1.3432	44	0.8450	(0.6484 4.1979)	2.7538*	1.6174
BL	OGL	Y=2.3930×+ −1.2937	44	0.8407	(0.6091 4.1768)	2.7058*	1.5750
BL	OGR	Y=2.5000×+ −1.4664	45	0.8488	(0.7361 4.2639)	2.8574*	1.7144
HL	SNL	Y=1.0967×+ −0.5981	36	0.8783	(0.1844 2.0090)	2.4440*	0.2155
HL	EYD	Y=0.8299×+ −0.5296	35	0.8393	(−0.0067 1.6666)	2.0186	0.4137
HL	DEY	Y=1.2816×+ −0.0351	31	0.8164	(−0.2707 2.8338)	1.6883	0.3709
HL	BW	Y=2.4610×+ 0.2658	34	0.8734	(0.1778 4.7443)	2.1956*	1.3035
HL	OLM	Y=0.7631×+ 0.4890	33	0.8731	(0.0132 1.5130)	2.0758*	0.6446
HL	OLL	Y=0.7696×+ 0.5215	33	0.8724	(0.0099 1.4493)	2.0680*	0.7664
HL	OLR	Y=0.6913×+ 0.5607	35	0.8102	(−0.0869 1.4695)	1.8078	0.8072
HL	OWM	Y=0.9872×+ −0.1117	34	0.8933	(0.1496 1.8249)	2.4009*	0.0310
HL	OWL	Y=1.0077×+ −0.1315	34	0.9011	(0.1901 1.8254)	2.5105*	0.0192
HL	OWR	Y=0.9151×+ −0.0401	35	0.8740	(0.1232 1.7069)	2.3516*	0.2182
HL	OGM	Y=2.9551×+ −0.4271	34	0.8886	(0.3874 5.5228)	2.3443*	1.5510
HL	OGL	Y=2.9262×+ −0.3972	34	0.8882	(0.3790 5.4733)	2.3401*	1.5404
HL	OGR	Y=2.8533×+ −0.3296	34	0.9052	(0.7234 4.9832)	2.7289*	1.7725

Table 2. (Continued)

SET OF PARTS		REGRESSION LINE		DATA NO	CORREL. COEF.	CONFID. LIMITS REG. COEF.		T VALUE BETA=0	T VALUE BETA=1
SNL	EYD	Y=0.4471×+	0.0910	44	0.5977	(−0.1655	1.0597)	1.4719	1.8208
SNL	DEY	Y=0.8996×+	0.8112	38	0.7206	(−0.1204	1.9196)	1.7886	0.1996
SNL	BW	Y=1.6863×+	1.9225	45	0.7313	(0.1004	3.2721)	2.1437*	0.8724
SNL	OLM	Y=0.5721×+	0.9708	42	0.7504	(−0.0024	1.1465)	2.0127	1.5056
SNL	OLL	Y=0.5650×+	0.9736	42	0.7685	(0.0288	1.1012)	2.1297*	1.6395
SNL	OLR	Y=0.4909×+	1.0112	44	0.6669	(−0.0649	1.0468)	1.7815	1.8473
SNL	OWM	Y=0.7015×+	0.5327	42	0.8154	(0.1605	1.2424)	2.6207*	1.1153
SNL	OWL	Y=0.7015×+	0.5342	42	0.8050	(0.1401	1.2629)	2.5253*	1.0745
SNL	OWR	Y=0.6870×+	0.5371	44	0.8033	(0.1708	1.2032)	2.6844*	1.2231
SNL	OGM	Y=1.9853×+	1.5623	43	0.7467	(0.0761	3.8945)	2.0995*	1.0420
SNL	OGL	Y=1.8872×+	1.6175	44	0.7138	(−0.0706	3.8449)	1.9443	0.9140
SNL	OGR	Y=2.0153×+	1.5463	44	0.7640	(0.2766	3.7541)	2.3378*	1.1778
EYD	DEY	Y=1.1084×+	0.9273	83	0.7272	(−0.3317	2.5484)	1.5609	0.1526
EYD	BW	Y=1.9593×+	2.1537	45	0.7275	(−0.2375	4.1560)	1.7981	0.8803
EYD	OLM	Y=0.6294×+	1.0680	41	0.8396	(0.1103	1.1485)	2.4515*	1.4435
EYD	OLL	Y=0.6119×+	1.0725	41	0.8385	(0.1049	1.1190)	2.4402*	1.5475
EYD	OLR	Y=0.6475×+	1.0633	42	0.8275	(0.0974	1.1977)	2.3789*	1.2948
EYD	OWM	Y=0.8456×+	0.6265	44	0.8295	(0.1602	1.5311)	2.4885*	0.4543
EYD	OWL	Y=0.8696×+	0.6200	44	0.8433	(0.2025	1.5366)	2.6294*	0.3944
EYD	OWR	Y=0.8715×+	0.6190	44	0.8381	(0.1814	1.5616)	2.5471*	0.3756
EYD	OGM	Y=2.5098×+	1.7938	44	0.8258	(0.4360	4.5836)	2.4410*	1.4684
EYD	OGL	Y=2.4916×+	1.8003	44	0.8265	(0.4384	4.5449)	2.4476*	1.4653
EYD	OGR	Y=2.5718×+	1.7758	45	0.8217	(0.4508	4.6928)	2.4445*	1.4940
EYD	BW	Y=1.5339×+	0.8340	38	0.8605	(0.7135	2.3543)	3.7918*	1.3198
EYD	OLM	Y=0.4195×+	0.7293	35	0.8006	(0.1166	0.7224)	2.8180*	3.9002*
EYD	OLL	Y=0.3803×+	0.7795	36	0.7544	(0.0717	0.6889)	2.5052*	4.0820*
EYD	OLR	Y=0.4318×+	0.7142	36	0.8005	(0.1296	0.7341)	2.9044*	3.8211*
EYD	OWM	Y=0.5042×+	0.2521	37	0.7825	(0.1364	0.8721)	2.7828*	2.7360*
EYD	OWL	Y=0.5219×+	0.2306	37	0.7967	(0.1589	0.8850)	2.9183*	2.6729*
EYD	OWR	Y=0.4811×+	0.2820	37	0.7782	(0.1304	0.8318)	2.7852*	3.0037*
EYD	OGM	Y=1.4304×+	0.7537	36	0.7858	(0.3815	2.4793)	2.7725*	0.8342
EYD	OGL	Y=1.4134×+	0.7761	36	0.7827	(0.3662	2.4605)	2.7440*	0.8025
EYD	OGR	Y=1.4898×+	0.6796	37	0.7943	(0.4619	2.5178)	2.9421*	0.9673

Table 2. (Continued)

SET OF PARTS		REGRESSION LINE		DATA NO	CORREL. COEF.	CONFID. LIMITS REG. COEF.		T VALUE BETA=0	T VALUE BETA=1
BW	OLM	Y=0.2119×+	0.6768	44	0.7448	(0.1341	0.2896)	5.4950*	20.4411*
BW	OLL	Y=0.2077×+	0.6874	44	0.7450	(0.1315	0.2839)	5.4989*	20.9744*
BW	OLR	Y=0.2154×+	0.6679	45	0.7363	(0.1361	0.2947)	5.4743*	19.9443*
BW	OWM	Y=0.2767×+	0.1243	44	0.7966	(0.1907	0.3628)	6.4887*	16.9573*
BW	OWL	Y=0.2797×+	0.1171	44	0.8034	(0.1947	0.3647)	6.6379*	17.0918*
BW	OWR	Y=0.2839×+	0.1050	44	0.8112	(0.1498	0.3679)	6.8149*	17.1936*
BW	OGM	Y=0.7720×+	0.4373	45	0.7439	(0.4913	1.0526)	5.5458*	1.6382
BW	OGL	Y=0.7623×+	0.4650	45	0.7396	(0.4816	1.0429)	5.4749*	1.7076
BW	OGR	Y=0.7982×+	0.3694	45	0.7685	(0.5319	0.1645)	6.9425*	1.5274
OLM	OLL	Y=0.9677×+	0.0403	44	0.9935	(0.8148	1.1206)	12.7690*	0.4261
OLM	OLR	Y=1.0324×+	−0.0404	44	0.9944	(0.8812	1.1836)	13.7719*	0.4318
OLM	OWM	Y=1.0403×+	−0.4251	43	0.8968	(0.3237	1.7569)	2.9311*	0.1136
OLM	OWL	Y=1.0311×+	−0.4126	43	0.8850	(0.2735	1.7887)	2.7479*	0.0830
OLM	OWR	Y=1.0557×+	−0.4445	44	0.8869	(0.2980	1.8134)	2.8103*	0.1482
OLM	OGM	Y=3.2231×+	−1.4939	44	0.9266	(1.4208	5.0254)	3.6070*	2.4879*
OLM	OGL	Y=3.1924×+	−1.4543	44	0.9235	(1.3656	5.0192)	3.5248*	2.4207*
OLM	OGR	Y=3.2535×+	−1.5333	44	0.9279	(1.4528	5.0542)	3.6442*	2.5241*
OLL	OLR	Y=1.0402×+	−0.0498	44	0.9759	(0.7115	1.3689)	6.3826*	0.2465
OLL	OWM	Y=1.0809×+	−0.4757	43	0.9055	(0.3532	1.8085)	2.9990*	0.2243
OLL	OWL	Y=1.0705×+	−0.4617	43	0.8929	(0.2947	1.8462)	2.7861*	0.1834
OLL	OWR	Y=1.0911×+	−0.4897	43	0.9057	(0.3574	1.8249)	3.0024*	0.2508
OLL	OGM	Y=3.2971×+	−1.5853	44	0.9207	(1.3144	5.2799)	3.3540*	2.3368*
OLL	OGL	Y=3.2646×+	−1.5459	43	0.9277	(1.3769	5.1523)	3.4917*	2.4221*
OLL	OGR	Y=3.3249×+	−1.6213	44	0.9211	(1.3313	5.3186)	3.3639*	2.3521*

Table 2. (Contenued)

SET OF PARTS		REGRESSION LINE		DATA NO	CORREL. COEF.	CONFID. LIMITS REG. COEF.		T VALUE BETA=0	T VALUE BETA=1
OLR	OWM	Y=0.9878×+	−0.3582	44	0.8680	(0.2412	1.7343)	2.6687*	0.0330
OLR	OWL	Y=0.9692×+	−0.3348	43	0.8664	(0.2203	1.7181)	2.6130*	0.0829
OLR	OWR	Y=1.0013×+	−0.3760	45	0.8705	(0.2654	1.7372)	2.7430*	0.0036
OLR	OGM	Y=3.1221×+	−1.3655	43	0.9318	(1.4849	4.7592)	3.8503*	2.6170*
OLR	OGL	Y=3.0629×+	−1.2877	44	0.9192	(1.3224	4.8034)	3.5495*	2.3906*
OLR	OGR	Y=3.1555×+	−1.4087	43	0.9344	(1.5367	4.7743)	3.9356*	2.6884*
OWM	OWL	Y=1.0053×+	−0.0039	44	0.9940	(0.8774	1.1333)	15.8473*	0.0842
OWM	OWR	Y=0.9945×+	0.0040	44	0.9938	(0.8659	1.1230)	15.6027*	0.0867
OWM	OGM	Y=2.6326×+	0.2366	44	0.9241	(1.3684	3.8968)	4.2002*	2.6048*
OWM	OGL	Y=2.6136×+	0.2543	44	0.9244	(1.3611	3.8661)	4.2088*	2.5985*
OWM	OGR	Y=2.6518×+	0.2188	44	0.9221	(1.3592	3.9444)	4.1379*	2.5775*
OWL	OWR	Y=0.9528×+	0.0400	43	0.9775	(0.7120	1.1935)	7.9903*	0.3962
OWL	OGM	Y=2.5889×+	0.2731	44	0.9199	(1.3222	3.8557)	4.1223*	2.5300*
OWL	OGL	Y=2.5760×+	0.2853	44	0.9222	(1.3368	3.8153)	4.1927*	2.5652*
OWL	OGR	Y=2.6017×+	0.2610	44	0.9157	(1.2913	3.9120)	4.0047*	2.4654*
OWR	OGM	Y=2.5902×+	0.2775	44	0.9160	(1.2699	3.9105)	3.9571*	2.4294*
OWR	OGL	Y=2.5648×+	0.3008	44	0.9141	(1.2405	3.8891)	3.9064*	2.3834*
OWR	OGR	Y=2.6547×+	0.2208	45	0.9158	(1.3303	3.9791)	4.0409*	2.5187*
OGM	OGL	Y=0.9927×+	0.0193	44	0.9991	(0.9765	1.0089)	123.7112*	0.9127
OGM	OGR	Y=1.0073×+	−0.0192	44	0.9992	(0.9913	1.0233)	126.8959*	0.9149
OGL	OGR	Y=1.0112×+	−0.0299	44	0.9966	(0.9782	1.0443)	61.7310*	0.6868

* significant at the 5% level

fins are considerably shorter and of light red colour during spawning migration in winter or early spring. On the other hand, the pelvic fins of the male are large, thick and blackish.

The figure show the relationship of pelvic fin length with the body length in logarithms to clarify the difference between male and female of sample Abashiri (Fig. 4). The male points lie above those for females in the graph. There are also differences in lengths of pelvic fins between both sexes before sexual maturity, as this graph illustrates. Therefore, pelvic fin length was omitted from the usual measurements when comparing various samples in general. Fifteen factors, with emphasis on sex distinction, have been considered especially for five samples *viz.* Rishiri-Rebun (Sp 7), Belkina (Sp 18) in the Sea of Japan, Abashiri (Sp 24) in the Pacific. Many samples from Uchiura Bay did not show statistically significant differences from Ho: $\rho=0$ hypothesis, because of the shorter range of body length due to the selectivity of gill-nets. Furthermore, the sample of females from Belkina also had a wide confidence interval for the regression coefficient. However, the correlation coefficients (r) between certain two factors demonstrated enough big values in accordance with 1% significance level, for both male and females among five sample lots. Side by side statistical tests were carried out to detect, on all occasions, differences in morphometry between male and female.

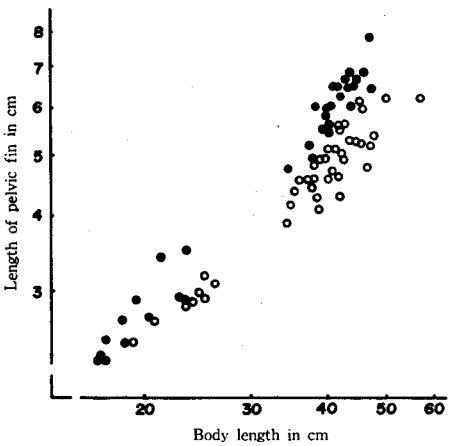


Fig. 4. Pelvic fin length on body length for male and female walleye pollock from Abashiri (Sp 24). Dots showing male, circle showing female.

Equilibrium constants (k) and adjusted means of log Y in the allometry equation are compared in paired samples for 15 factors using the analysis of covariance. Generally, significant differences between sexes is comparatively rare among sample tests (Table 3 shows a result of a statistical test between sexes from Uchiura Bay, Sp 41).

In the sample of Rishiri-Rebun Islands, the combinations based on snout length or eye diameter showed significant differences statistically. The reason for this significance might be due to the larger regression coefficients of the males (*BL-SNL*: ♀0.807, ♂0.971; *BL-EYD*: ♀0.656, ♂0.860) (Fig. 5-i). However no test yielded statistical differences in the four cases. Therefore, in general, the differences between male and female are realized only by variations in the snout length or eye

Table 3. *Calculated F values by covariance analysis between regression coeffcients (upper right) or adjusted means (below left) obtained from the mutual sets of the fifteen measurements of walleye pollock from Uchiura Bay (Sp 41).*

	BL	HL	SNL	EYD	DEY	BW	OLM	OLL	OLR	OWM	OWL	OWR	OGM	OGL	OGR
BL		0.994	0.436	2.375	5.407*	7.652**	0.304	0.431	0.173	0.012	0.093	0.027	0.551	0.458	0.844
HL	1.993		3.851	0.111	1.202	0.763	0.692	0.798	0.676	0.048	0.091	0.017	1.312	0.296	1.977
SNL	2.706	0.169		1.441	0.038	0.163	1.849	1.843	1.787	0.068	0.000	0.523	3.043	4.700*	5.235*
EYD	0.718	2.506	0.719		1.958	0.188	3.168	2.875	1.499	0.068	0.058	0.271	0.886	0.828	0.955
DEY	0.397	0.033	4.554*	19.027**		8.770**	10.458**	8.264**	3.093	1.640	1.098	3.266	1.651	1.929	3.891
BW	2.586	2.306	0.025	5.696*	0.045		1.992	2.984	2.088	0.451	0.696	2.047	2.493	2.916	2.984
OLM	0.828	2.203	4.214*	0.104	0.607	0.201		0.398	0.393	1.440	0.446	0.373	0.050	0.058	0.036
OLL	0.968	2.496	5.038*	0.282	1.543	1.279	0.543		0.335	1.675	0.502	0.549	0.009	0.015	0.002
OLR	1.018	2.474	4.354*	0.770	11.25	0.502	0.623	0.931		1.144	0.274	0.902	0.119	0.194	0.153
OWM	0.772	0.004	0.000	0.811	0.780	2.137	6.784*	7.329**	6.158*		1.636	1.641	1.211	1.350	1.225
OWL	0.121	0.415	1.549	1.463	2.197	3.877	4.884*	6.164*	4.568*	0.419		3.482	0.667	0.643	0.674
OWR	0.654	0.000	0.000	1.836	1.937	0.697	3.704	4.090*	7.164*	0.417	0.115		0.653	0.713	0.642
OGM	0.558	1.395	2.372	1.688	0.101	0.000	6.338*	7.013*	5.388*	0.007	0.017	0.023		0.015	0.014
OGL	0.708	3.039	0.134	1.420	0.022	0.006	6.302*	8.080**	5.404*	0.029	0.107	0.003	0.227		0.003
OGR	0.728	1.682	1.753	2.095	0.108	0.013	7.530**	8.125**	6.414*	0.002	0.062	0.024	0.000	0.000	

* significant at the 5% level of significance ** significant at the 1% level of significance

diameter. In the sample of Blekina (Sp 18), no significant difference were noted in the tests of regression coefficients, though differences are exhibited in a few cases based upon eye diameter, otolith width, and otolith weight (Fig. 5-ii). These differences are rare in the other four samples. In the sample from Abashiri (Sp 24), the combinations concerning head length, snout length, and eye diameter showed some statistical differences in the adjusted means (Fig. 6). This tendency was also found in the sample from Kushiro (Sp 46) in the Pacific region. During comparison between male and female, the significant differences of adjusted means were detected in the comparisons on snout length of eye diameter (Fig. 7). However these comparisons of the sample from Uchiura Bay mainly showed significant differences in the adjusted mean of combinations between otolith length and otolith width or weight.

The above account suggests that the sexes differed more often in the combinations of snout length and eye diameter than in any other combination of factors. For the snout length this phenomenon was detected in comparisons of samples from Rishiri-Rebun Islands, Abashiri, Uchiura Bay, and Kushiro. An actual sexual comparison of intrasample in these five sample lots followed the differences revealed by the above factors. However the statistical test of the Belkina samples showed no statistical differences as to regression coefficients or adjusted means. Significant differences between sexes would not be detectable constantly in the statistical tests of any sample.

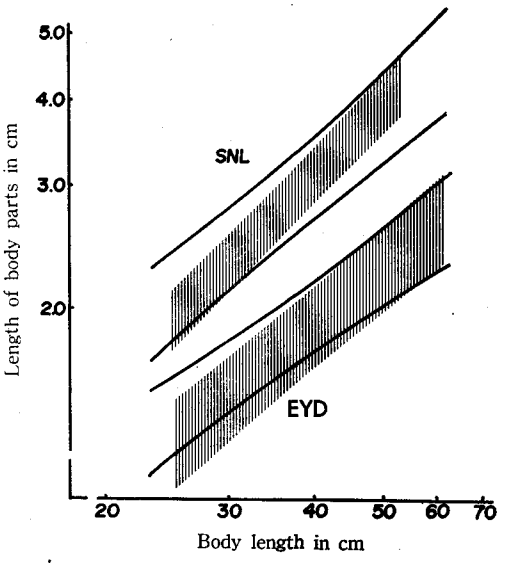


Fig. 5-i. Relative growth relationship of body length and snout length or diameter of eye between male and female in a sample from Rishiri-Rebun Islands (Sp 7). Shadow and curves showing 95% confiednce zones of male and female respectively.

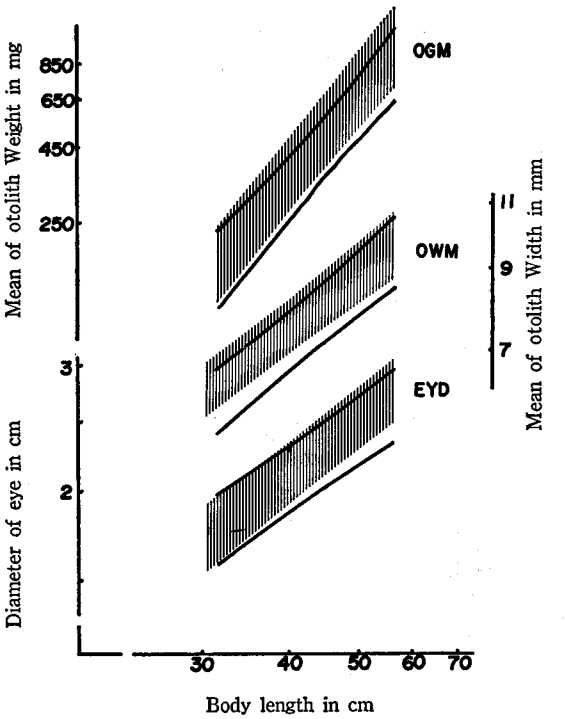


Fig. 5-ii. Relative growth relationship of body length and diameter of eye, mean of otolith width, or mean of otolith weight, between male and female in a sample from Belkina (Sp 18). Notes are the same as in Fig. 5-i.

The above facts clearly indicate that significant differences may be detectable, during the comparison between paired lots of males and females, but at the same time more detailed investigations seem necessary due to the obvious differences of body form between male and female. Therefor, these combination were excluded as far as possible, during the considerations on intersamples.

3. *k-log b Linear Relationship*

Two constants of equilibrium (k) and initial index ($\log b$) were examined in order to compare the characters of allometry equation in all samples. Lumer[68] found that a linear relationship exists between these two constants. Similar relationship was showed in greenlings incubated under different conditions.[69]

Twenty-nine paired constants of allometry equations as criterion of body length were examined, in which the constants were calculated only in the cases where the test showed significant difference from the null hypothesis of Ho: $\beta=0$. The

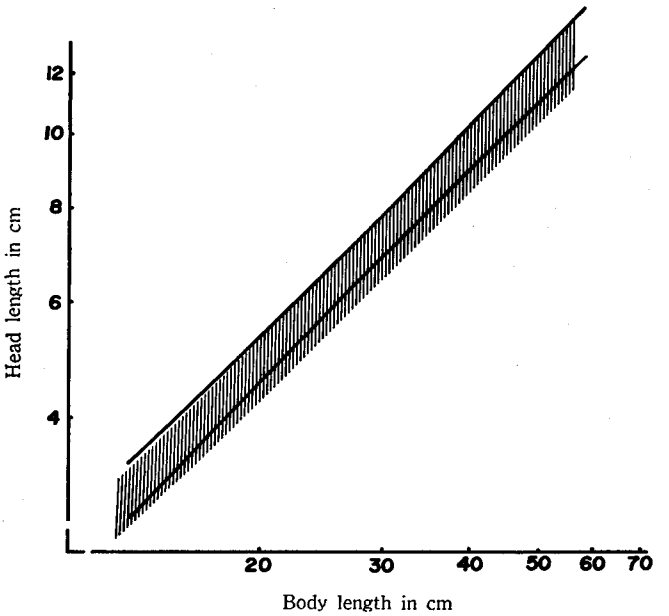


Fig. 6. Relative growth relationship of body length and head length, between male and female in a sample from Abashiri (Sp 24). Notes are the same as in Fig. 5-i.

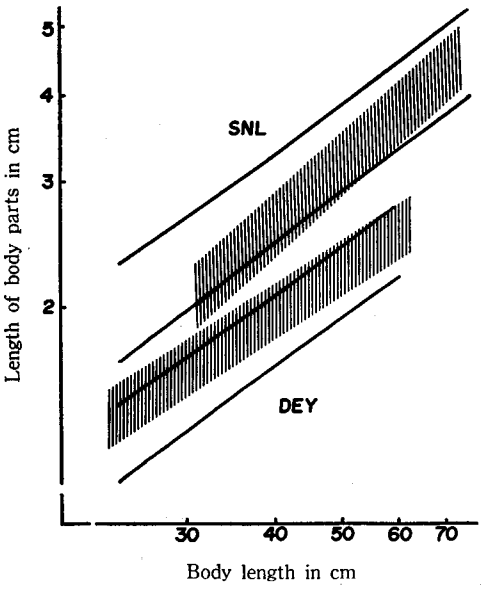


Fig. 7. Relative growth relationship of body length and diameter of eye, comparing between male and female in a sample from Kushiro (Sp 46). Notes are the same as in Fig. 5-i.

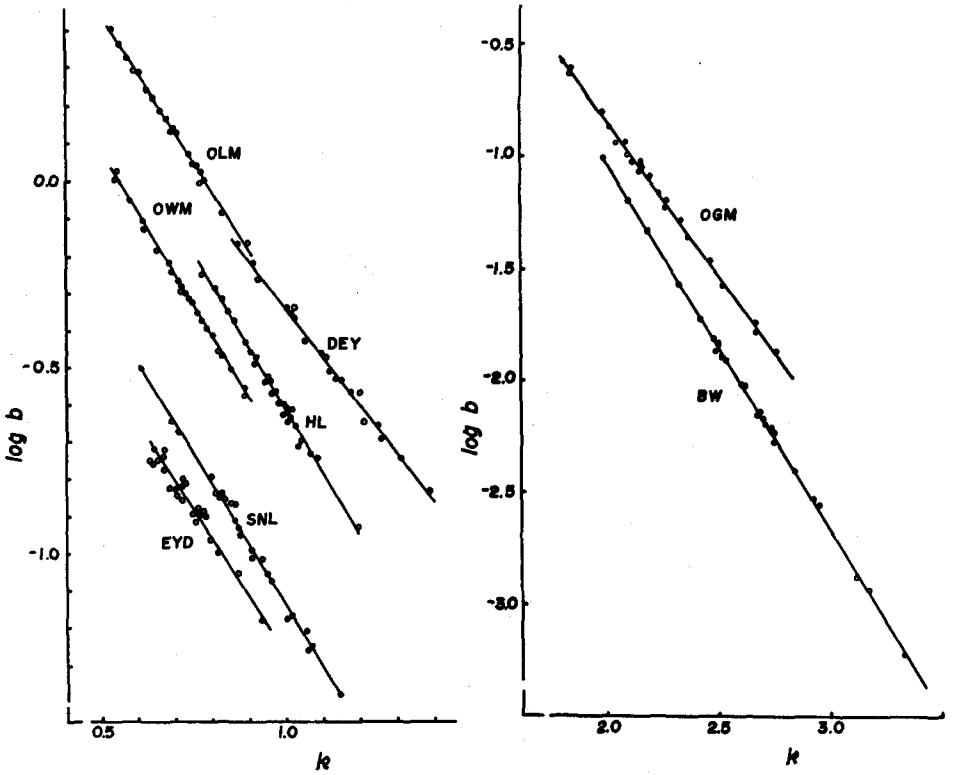


Fig. 8–i Fig. 8–ii

Fig. 8. k-log b relation of body parts relating to body length. Circle showing one sample.

figures (Fig. 8) illustrate good fitness with the linear equation for eleven relationships of *BL-HL*, *BL-OLM*, *BL-OLR*, *BL-OLL*, *BL-OWM*, *BL-OWR*, *BL-OWL*, *BL-OGM*, *BL-OGR*, *BL-OGL*, and *BL-BW*. Three rejective curves for the lines *BL-SNL*, *BL-EYD*, and *BL-DEY* were wider than the above eleven rejective zones.

Equilibrium constants (k) changed within certain ranges as described in Table 4. Relative growth of body parts with respect to body length showed specific characters within the stage of treated fish. Eye diameter, otolith length, otolith weight showed negative allometry ($k<1$ in length or 3 in weight). The other three factors of *SNL*, *DEY*, and *BW* did not exhibit significant differences by isometry ($k=1$). The position of samples in the graph do not show a trend, for samples from a certain region to concentrate together. The rejective limits were also calculated at the 1% significance level. No sample was rejected. Therefore all samples from the vicinity of Japan to Alaska had their peculiar values within the limits of specific variation.

Table 4. *Dispersion ranges of equilibrium constant (k) of allometry equations of 29 samples.*

relationships	dispersion range			
	k		$\log b$	
BL-HL	0.78	1.17	−0.26	−0.87
BL-SNL	0.46	1.63	−0.50	−1.36
BL-EYD	0.68	0.92	−0.75	−1.17
BL-DEY	0.86	1.36	−0.14	−0.82
BL-BW	2.22	3.52	1.19	−3.39
BL-OLM	0.54	0.91	0.41	−0.19
BL-OWM	0.53	0.87	0.02	−0.53
BL-OGM	1.95	2.82	−0.59	−1.95

4. *Comparison between Samples*

Regression coefficients and adjusted means, for pairs of the 15 measurements, were preferred to compare the morphological characteristics of the samples. The test of significant difference between regression coefficients or adjusted means of allometry equation were computed by the analysis of covariance. All 105 F values were calculated for both regression coefficients and adjusted means, for the selected pairs of the 355 combinations. The statistical differences at the 5% significance level were counted and are listed in Table 5. These numbers were changed to percentages, which were normalized with the arcsine transformation to standard distribution. The analysis of rejective limits was made to judge the total differences between samples. The level of significance, which is marked by underlines in Table 5, was selected as 25% probability, because these percentages of differences counted for approximately 25% for sexual comparisons in a given sample mentioned above.

In the Sea of Japan, the values were small, thus indicating some morphological homogeneity among the samples in this area. All rejectable values, in both regression coefficients and adjusted means, concentrate on the left side in normal distribution. In the Okhotsk Sea, the samples from Rausu showed unique characteristics in body form, and were noted for their significant differences against all other samples, depending upon regression coefficients or adjusted means at 25% level. Three Aniva Bay samples showed relatively small variation of values and no significant difference could be detected. Significant difference could not be found among the samples in the areas of western and eastern parts of the Okhotsk Sea. In the Pacific Ocean, the samples from Uchiura Bay distinguished themselves significantly from others, and the detected differences were in agreement with earlier findings.

Table 5. *Number of significant differences between certain combinations in the analysis covariance.*

		SAMPLE	2	3	7	12	15	17	18	19	21	22	24	28	26	27	30	34	37	38	41	42	46	52	55	60	61
Sea of Japan	2	Kumaishi		4	24	27	25	55	24	42	**83**	69	28	45	18	18	12	54	68	42	39	53	26	24	39	18	20
	3	Kudo	5		11	14	6	62	20	16	71	**82**	34	43	37	15	5	45	78	17	48	67	23	14	31	11	17
	7	Rishiri-Rebun	44	44		23	25	67	37	5	**85**	**93**	26	64	57	48	6	70	**90**	27	72	82	12	15	48	27	36
	12	Kholmst	39	37	28		10	51	14	25	69	86	34	44	42	14	12	38	68	45	41	70	26	1	14	12	16
	15	Il'insky	41	46	7	17		18	68	32	32	**81**	86	48	34	30	2	52	86	30	49	67	42	20	43	11	35
	17	Staritsa	65	72	63	56	81		53	68	61	36	66	12	40	34	51	32	29	23	19	68	46	34	36	41	56
	18	Belkina	44	57	62	32	62	60		36	37	**81**	46	31	28	5	7	36	25	42	43	33	55	4	16	65	11
	19	Belkina	70	68	48	63	38	75	56		**80**	**87**	39	61	45	42	11	69	72	15	**75**	**87**	10	14	46	12	29
Okhotsk Sea	21	Rausu	72	49	57	59	55	69	63	83		22	**84**	36	55	59	72	51	5	**85**	42	15	**87**	**79**	68	63	72
	22	Rausu	60	77	65	**84**	77	88	75	88	22		**95**	39	67	71	68	62	10	94	46	11	**83**	**81**	63	65	**90**
	24	Abashiri	77	69	48	74	**87**	82	74	20	**85**	**89**		66	54	51	21	70	**86**	38	72	**86**	22	26	57	27	31
	28	Aniva Bay V	31	28	37	35	58	47	25	34	69	83	54		13	10	31	18	32	51	30	25	63	34	31	26	51
	26	Aniva Bay X	65	54	49	73	64	57	66	74	52	58	72	63		5	19	35	58	50	27	49	58	48	45	19	12
	27	Aniva Bay XII	49	45	43	46	50	52	40	49	32	37	70	35	59		2	18	49	57	22	43	35	16	15	4	8
	30	Terpenia Bay	60	60	42	68	60	76	51	32	**85**	**84**	12	37	72	60		47	**74**	37	41	32	8	31	27	7	17
	34	Magadan	43	40	58	29	50	55	40	66	74	70	68	47	69	48	59		44	71	19	42	57	41	26	28	49
	37	West Kamchatka	53	54	57	47	66	62	62	54	72	82	76	45	76	44	73	29		**90**	21	22	**85**	**75**	59	65	**77**
	38	West Kamchatka	48	52	44	55	57	76	72	66	34	50	64	49	19	26	64	19	52		**87**	**85**	47	28	68	58	56
Pacific	41	Uchiura Bay	81	78	73	50	71	37	66	72	**89**	**85**	63	68	70	72	28	70	86	67			69	43	36	38	53
	42	Uchiura Bay	72	66	62	68	72	**85**	75	69	**93**	**92**	66	60	69	56	59	74	88	67	19	19	**82**	**78**	50	55	68
	46	Kushiro	69	66	70	**91**	**93**	72	63	**85**	**84**	87	64	65	78	71	33	71	76	74	54	65		19	45	22	25
	52	North Kuril I.	72	83	82	75	69	88	64	69	**89**	**94**	49	86	84	82	42	79	83	78	63	58	45		25	11	41
	55	Inkanyush Cape	65	73	72	61	80	76	60	51	**90**	**99**	62	76	83	72	42	71	**94**	81	56	46	50	54		13	40
	60	Kodiak	40	59	59	61	66	82	59	45	78	**85**	46	59	80	68	31	62	58	59	44	58	56	48	42		7
	61	Dry Bay, Juncau	81	72	74	83	75	82	87	72	**84**	**95**	57	74	74	81	65	80	80	71	71	75	61	78	79	55	

F value for regression coefficients

F value for adjusted means

Bold-face figures showing rejectable values at the 25% significance level.

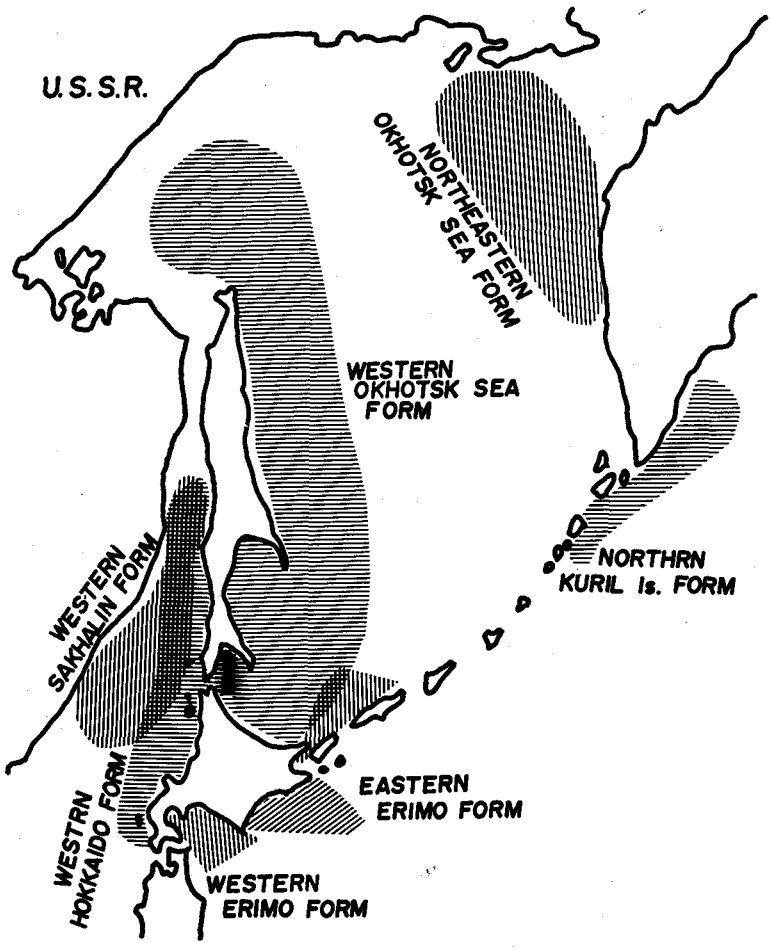


Fig. 12. Map showing the estimated distribution of local forms defined by morphometrical analyses in walleye pollock in the vicinity of Japan.

5. *Discussion*

Allometry equations were fitted to the comparison of various samples of not only body length and partial length or weight, but also for other combinations of measurements in this study. This fitness was proved by the *X-Y* PLOTTER results and correlation coefficients.

Sexual differences on body form were examined for 16 measurements including pelvic fin length. The relationship between pelvic fin length and body length satisfactorily distinguished males from females, as illustration of the sample from Abashiri denoted. However, no dimorphism was regularly detected when comparing regression coefficients or adjusted means of all 15 factors in five examined

samples.

The k-log$b$ linear relationships[63),64)] showed good fit in all samples collected from the northeastern to the northwestern Pacific. These results may show a specific attribute of walleye pollock. No sample was omitted by rejection curves of 1% significance level.

An analysis of covariance among thirty samples showed considerable differences for a certain combination lot. The sum of the statistical differences between 15 parameters of certain combination of samples were judged by the methods of rejective limits with 25% probability level. The results of morphological differences suggested that there were two local forms in the Pacific region, three forms in the Okhotsk Sea, and one in the Sea of Japan.

On the population of this species, Kyushin *et al.*[53)] previously reported the presence of two morphologically differing groups, inhabiting, sympatrically, Uchiura Bay, based on investigations of relative growth between body length and otolith weight or diameter of orbit. Hashimoto and Koyachi[50),51)] while analyzing relative growth between body length and other 10 measurements, used the B-type group from Uchiura Bay as the standard form for the comparison among samples. In this study, by means of a computer, all parameters were analyzed simultaneously, in contrast to early analysis where body length was fixed as standard parameter. However, studies are required to ascertain each probability for more detail analysis.

IV. Analysis of the Number of Vertebrae

Few studies investigated the number of vertebrae as an indicator of the walleye pollock populations. Ogata[55)] reported that in the eastern Sea of Japan, pollock had less vertebrae than in the Pacific region. Furthermore, he analyzed the mean number of vertebrae between samples for 9 years with the t-test, and classified the populations as follows:

1 Northern group along Honshu: Aomori prefecture — Bay of Toyama (small population, small migration)
2 Western group along Honshu: Western region from Noto Peninsula (small population)
3 Primorskaya Province group: Eastern Korea — along USSR (large population, large migration)
4 Western Hokkaido group: (vertebral number was similar to the western group along Honshu)

Hashimoto and Koyachi[50),51)] also investigated this category. They avoided presuming the population distribution, and described only the statistical results. They showed that the fish from Lopatka in the southern Kamchatka Peninsula and from the Bering Sea had higher mean counts than other samples. According to

the data of body length, modal number of vertebrae and tagging experiments, it was suggested that only one population occupied the northern Sea of Japan.[23] Iwata and Hamai[70] studied the population in the vicinity of Japan and proposed eight local forms, which will be discussed as the key subject in this chapter.

1. Materials and Methods

A total of 1877 specimens of walleye pollock were collected from 42 stations in three regions around Hokkaido: 15 samples in the Okhotsk Sea; 15 samples in the Sea of Japan; and 12 samples in the Pacific Ocean (Fig. 1). Most samples were collected during the spawning season, from late autumn to spring, with gill-nets, trawls and long-lines. The collecting period extended from November 1968 to September 1970 (Table 1).

The samples, except for Mashike (Sp 5), consisted of several age groups of adults, 37 to 60 cm long, that would contribute to reproduction. However, the year classes could not be classified because of the uncertainty of age determination.

The fish were boiled to separate the flesh from the vertebral column, and then the number of abdominal and caudal vertebrae were counted separately. The caudal vertebrae counts began with the centrum having the first closed haemal arch. The urostyle was excluded. The total number of vertebrae included the number of abdominal and caudal vertebrae.

Fisher's F-test and Student's *t*-test were used for determining significant differences among variances and means. When the variance test showed a significant difference, the method by Cochran & Cox was employed in place of the *t*-test for the difference of means.

2. Basic Investigations

The caudal vertebrae counts of the walleye pollock ranged from 29 to 33; the abdominal vertebrae counts from 17 to 20; and the total vertebrae counts, 47 to 54. Usually, the range of vertebral counts in a sample was three centra for abdominal vertebrae, and three to five for caudal and total vertebrae.

To determine whether or not these variations of vertebral counts occur in a local form, the distribution curve and the statistical differences between males and females were examined in the combined samples from Mashike (Sp 5) to Kholmsk (Sp 12) in the northern Sea of Japan. Spawning shoals in this area apparently belong to a single population.[23),24] Figure 9 illustrates the results of the normal probability paper method[71] applied to the frequency distributions of each sex. They seem to be normal, and no significant difference between sexes is detected in the statistical tests of means and variances except one case (Table 6). Therefore, the sexes were combined for the following analysis.

Table 6. *Significance test for the difference of mean number of vertebral centra between male and female.*

section	sex	mean	s^2	n	F	t
abdominal	male	17.98	0.1721	117	1.1807	0.8351
	female	18.03	0.1708	100		
caudal	male	31.15	0.6059	114	1.9753*	$t'=0.38$
	female	31.18	0.3610	97		
total	male	49.10	0.5206	182	1.0983	1.1474
	female	49.18	0.4637	186		

Asterisk shows the significant difference at the 5% level.

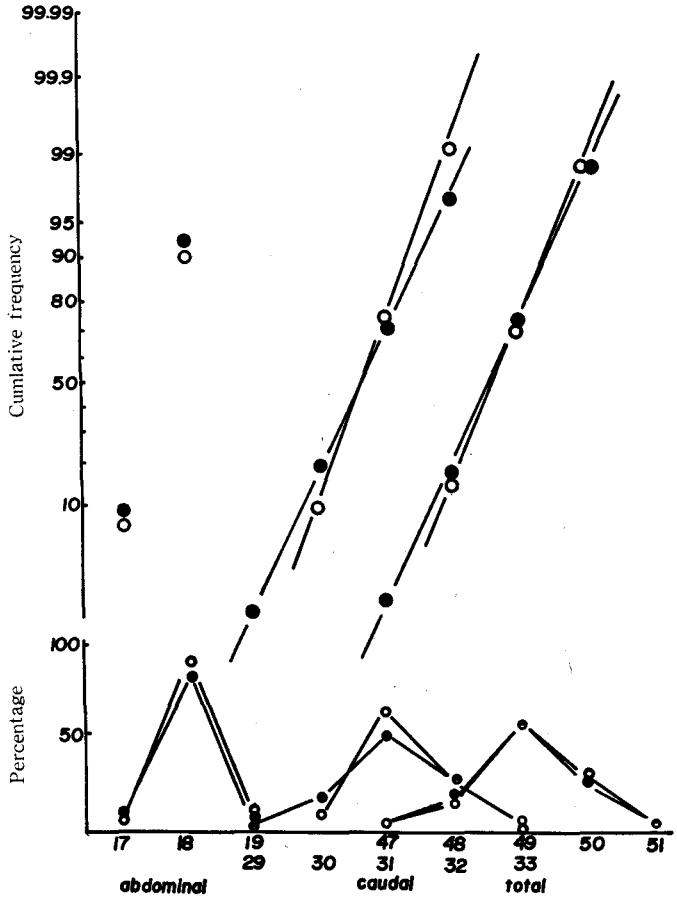


Fig. 9. Frequency distributions of abdominal, caudal and total vertebrae numbers for the walleye pollock in the Sea of Japan; and the cumulative percentage plotted in the normal probability paper. ○: female, ●: male.

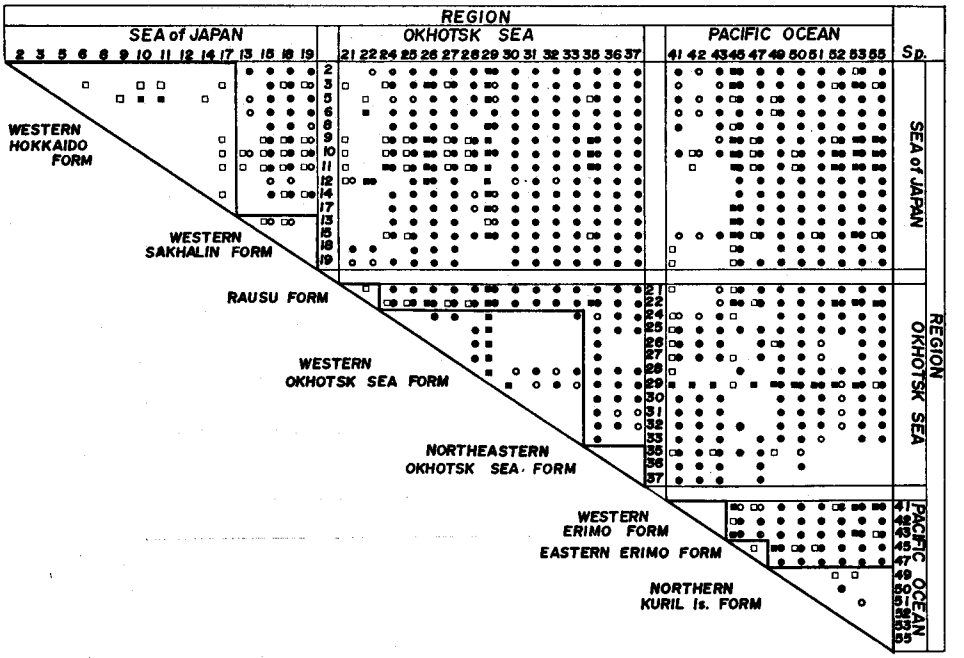


Fig. 10. Significance of differences between the mean total numbers of vertebrae and their variances at various stations and the estimated groups of stations showing a local form with a thick lined triangle.
○: significant at the 5% level of significance in the means
●: significant at the 1% level of significance in the means
□: significant at the 5% level of significance in the variances
■: significant at the 1% level of significance in the variances

3. *Comparisons of Mean Vertebral Counts among Samples*

The Sea of Japan

Based upon the above results, the geographical variations of the number of vertebrae were compared among 41 samples. As seen in Fig. 10, the means of total vertebrae from four samples, i.e. Kholmsk (Sp 12), Il'inskiy (Sp 15) and Belkina (Sp 18, 19), in the northern area of the Sea of Japan showed higher values than all samples (Sp 2, 3, 5, 6, 8, 10, 11) in the southern area, with statistical significance at the 1 or 5% significance level. That is, the northern Sea of Japan can be separated into two areas, i.e. a southern area adjacent to Hokkaido, and a northern area off Sakhalin Island, and Primorskaya Province. However, the means of three samples (Sp 13, 14, 17) in March were more similar to the samples of the southern area than those of the northern area. Also the samples from the southern area showed no statistical difference from the samples of Rausu (Sp 21, 22), in the Okhotsk Sea.

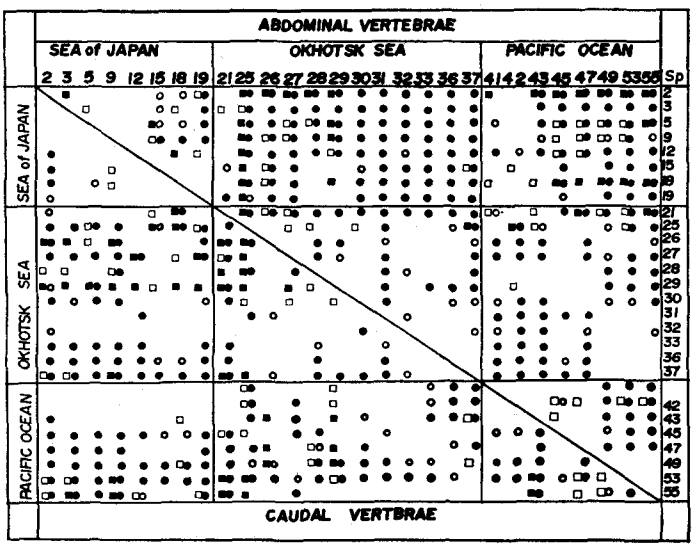


Fig. 11. Significance of differences among means and variances of abdominal and caudal vertebral numbers in various stations. Notations are the same as those in Fig. 10.

The mean numbers of abdominal vertebrae for three samples (Sp 15, 18, 19), in the northern area were clearly different from those in the southern area, as illustrated in Fig. 11. Sample 12 was included in the group from the southern area in this comparison. Further, in the case of caudal vertebrae, it was demonstrated that those four samples (Sp 12, 15, 18, 19) were separable from sample 2 in the southern area.

Similar results for both abdominal and caudal vertebrae counts supported the possibility of separation between the northern area and the southern area in the Sea of Japan. On the basis of the above results, the walleye pollock stock in the northeastern Sea of Japan can be segregated into the *Western Sakhalin form* and the *Western Hokkaido form*, as schematically demonstrated in Fig. 12.

Although the Western Hokkaido form is separated from the Western Sakhalin form, some samples of these forms are close to the samples from Rausu (Sp 21, 22), or the samples in May and July from Aniva Bay (Sp 25, 19). Aniva Bay lies near the habitat of the Western Sakhalin form, and a sample (Sp 29) from this bay in July showed a significantly larger variation in total vertebral counts (Table 7). These results suggest that there are two local forms deduced from the numbers of vertebrae, and the possibility of mixing between the Western Sakhalin form and the fish of Aniva Bay during their feeding period.

Okhotsk Sea

Fifteen samples were collected in this sea during all seasons except winter,

when the fishing was closed by ice. Out of them, twelve samples were collected from the western continental shelf and three from the northeastern part of this sea.

From the results of *t*-test (Fig. 10), four remarkable groups of means were identified. Two samples from Rausu (Sp 21, 22) formed the first group with significantly lower means than those of the other samples. As described previously, this Rausu group had similar values to the Western Hokkaido form. The second group is composed of eight samples (Sp 24, 25, 28–33) which are indicated by the thick lined triangle in figure 10. The means of total vertebral counts of this group all fell within the range of 50.12–50.43. All of these samples were collected within a narrow band on the continental shelf along the western Okhotsk Sea from north to south. The third group from the same region consisted of two samples (Sp 28, 29) from Aniva Bay. These did not correspond to the second group, but showed similar mean values to the Western Sakhalin form. These two samples were collected in May and July, when the feeding migration had begun following spawning. The fourth group included three samples from the northeastern Okhotsk Sea. They showed significantly higher values than all others in this sea.

Therefore, it would appear that in the Okhotsk Sea there are three indigenous groups called the *Rausu form*, the *Western Okhotsk Sea form* and *Northeastern Okhotsk Sea form*. The fishes from the Western Hokkaido form seem to appear in this region during the feeding season.

Pacific Ocean

Eleven samples were collected from three areas in the Pacific region. These areas are distant from each other. The samples from Uchiura Bay and Kushiro were collected during the spawning season (from winter to spring) in 1969 and 1970, while those from the north Kuril Island area were caught during the prespawning stage.

The habitat of each walleye pollock group might differ seasonally due to migration, but the statistical tests successfully detected local forms. The samples from Uchiura Bay possessed the lowest counts of abdominal, caudal and total vertebrae compared with those from the other two areas, and conversely, the counts for the northern Kuril Island samples were highest. In every case, the differences of mean of vertebral counts among three areas were statistically significant for all three counts.

Accordingly, in the Pacific region, three geographical groups of Walleye pollock were designated: the *Western Erimo form*, the *Eastern Erimo form*, and the *Northern Kuril Island form*.

Table 7. *Number of observed fish (n), mean number of centra of abdominal, caudal and*

		Sample number and area*	Date of collection	Abdominal	
				n	mean
Sea of Japan	2	Kumaishi	5 II '70	47	18.04
	3	Kudô	23 I '70	49	18.02
	5	Mashike	29 III '69	49	18.00
	6	Teuri Yagishiri Is.	29–30 XII '69		
	9	Northwest Wakkanai	6 XII '69		
	8	North Wakkanai	17 I '69	65	18.09
	10	Moneron Is.	7 XII '69		
	11	Moneron Is.	29 III '69		
	12	Kholmsk	25 XII '69	83	17.98
	13	Kholmsk	26–27 III '69		
	14	Il'inskiy	27–29 III '69		
	15	Il'inskiy	23–25 V '69	40	18.28
	17	Staritsa	24–29 III '69		
	18	Belkina	4 XII '69	73	18.19
	19	Belkina	18 XII '69	100	18.26
Okhotsk Sea	21	Rausu	8 IV '69		
	22	Rausu	21 IV '79	96	18.07
	24	Abashiri	10–11 IV '69		
	25	East from Sôya	21 X '69	29	18.52
	26	Aniva Bay	23 X '69	48	18.73
	27	Aniva Bay	19 XII '69	63	18.60
	28	Anvia Bay	24 V '69	50	18.36
	29	Aniva Bay	20 VII '69	39	18.38
	30	Terpeniya	24 V '69	26	18.58
	31	Northern Sakhalin	30 VIII '70	26	19.04
	32	Northern Sakhalin	2I X '70	31	18.65
	33	Northern Sakhalin	3I X '70	37	18.76
	35	Magadan	9 IX '70	29	18.86
	36	Magadan	21 XI–2 XII '70		
	57	Western Kamchatka	2 I '70	87	18.91
Pacific Ocean	41	Uchiura Bay	18 I '69	26	18.27
	42	Uchiura Bay	18 I '69	25	18.20
	43	Uchiura Bay	30 I '70	83	18.28
	45	Kushiro	8 V '69	24	18.50
	46	Kushiro	18 IV '70	60	18.35
	49	Northern Kuril Is.	10–17 X '69	40	18.85
	50	Northern Kuril Is.	16–23 XI '68		
	51	Northern Kuril Is.	23–27 XI '68		
	52	Northern Kuril Is.	19–21 VII '69	29	19.00
	53	Northern Kuril Is.	21–28 XI '69	87	18.86
	55	Inkanyush Cape	14 IV '70		
		Total number		1441	

4. *Correlative Variation of Abdominal and Caudal Vertebrae*

Since the total number of vertebrae is the sum of abdominal and caudal vertebrae, these values are not independent from each other (Table 8). Each frequency distribution was normal, and the variance of caudal vertebrae was

total vertebrae, and its variance in 41 samples of the walleye pollock in 1968–70.

	Caudal			Total		
variance	*n*	mean	variance	*n*	mean	variance
0.1285	47	30.94	0.4089	47	48.98	0.4996
0.2704	49	31.16	0.3894	49	49.18	0.4052
0.1667	46	31.00	0.5333	46	49.02	0.5996
				25	48.96	0.7900
				29	49.07	0.4950
0.1789	65	31.14	0.3711	65	49.23	0.3991
				30	49.03	0.3093
				30	49.20	0.3034
0.1945	83	31.34	0.4945	83	49.33	0.5393
				30	49.23	0.5310
				30	49.20	0.3584
0.3582	40	31.38	0.5992	40	49.65	0.6505
				28	49.29	0.7300
0.1572	73	31.42	0.6089	73	49.62	0.6564
0.2347	100	31.21	0.4908	100	49.48	0.6360
				48	49.19	0.6662
0.1736	96	31.16	0.3648	96	49.23	0.3891
				66	49.89	0.6809
0.4729	29	31.79	0.2414	29	50.31	0.6896
0.2868	48	31.67	0.9504	48	50.40	0.7974
0.2677	62	31.79	0.5946	62	50.44	0.6433
0.2759	50	31.22	0.6649	50	49.58	0.6371
0.3482	38	31.47	1.1749	38	49.87	1.6371
0.2140	26	31.54	0.4984	26	50.12	0.5060
0.4824	26	31.19	0.8816	26	50.23	0.5846
0.4366	31	31.52	0.5247	31	50.16	0.8731
0.3281	37	31.52	0.7808	37	50.43	0.8078
0.1946	29	31.83	0.5746	30	50.73	0.4784
				18	50.83	0.9706
0.2240	87	31.99	0.6627	87	50.90	0.7683
0.2844	26	31.23	0.5844	26	49.50	0.3400
0.1667	25	31.25	0.5233	25	49.44	0.5900
0.2516	83	31.20	0.4088	83	49.48	0.4960
0.2478	24	31.79	0.6070	27	50.26	1.1996
0.3161	60	31.52	0.4235	60	49.87	0.6430
0.2846	40	32.43	0.3679	40	50.98	0.4351
				29	51.31	0.5789
				28	50.89	0.5437
0.3571	29	31.69	0.8646	29	50.69	0.7932
0.2830	87	32.20	0.7172	87	51.06	0.8423
				29	51.10	0.8403
	1436			1856		

approximately twice as large as that of abdominal vertebrae (Table 7). Therefore, if the abdominal and caudal vertebral numbers are plotted on rectangular coordinates, the points are expected to be distributed in an ellipse of which the long axis corresponds to the count of caudal vertebrae. In the same manner, sets of these means of samples extracted from a definite local form are also expected to be

distributed in an ellipse which represents a probability density of the normal bivariate population. Hereupon, in order to make the relation of these variates to the total number of vertebrae clear, the means of abdominal and caudal vertebrae were plotted on Cartesian co-ordinates intersecting at an angle of 60° (Fig. 13). The origin was fixed conveniently at the points 18.5 and 31.5, respectively, on the abdominal and caudal axis to scatter uniformly all the points about the origin. Accordingly, values for the total vertebrae can be read rectangularly on the bisector of the two axes.

Table 8. *Correlation coefficients among abdominal, caudal and total vertebral centra between male and female.*

section	r	P (H_0: $\rho=0$)
abdominal	0.705 (0.613-0.779)	0.01
caudal	0.359 (0.192-0.526)	0.01
total	0.816 (0.753-0.864)	0.01

d.f.=139. Figures in parenthesis show the confidence interval of r.

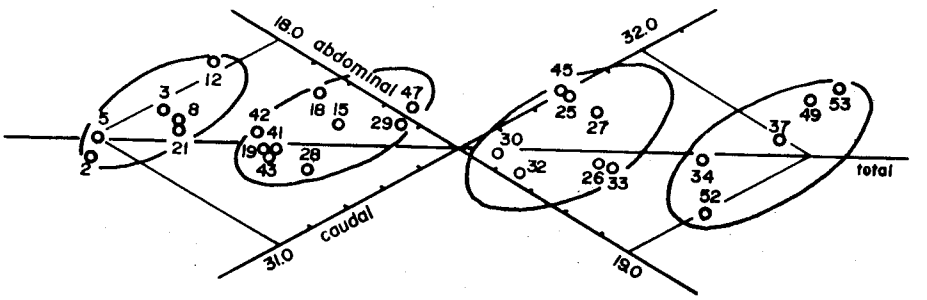


Fig. 13. The means of abdominal and caudal vertebral counts plotted on Cartesian co-ordinates of 60°. The figures show the station numbers.

The points of 27 samples are distributed in four clumps which are in rows like stairs along the total-vertebrae axis. On the abdominal axis, the points concentrate on four levels — 18.0, 18.3, 18.65, and 18.95. These clumps may be enclosed with respective probability ellipses. The Western Hokkaido form and the Rausu form are contained in the first clump; the Western Sakhalin form, the May and July samples of Aniva Bay, and the Western Erimo form are in the second group; in the third clump are included the Western Okhotsk Sea form and the Northern Kuril Island form; and the Northeastern Okhotsk Sea form are in the fourth clump. But the Eastern Erimo form is divided into the second and the third clumps.

5. *Inclination of Means of Vertebral Number to Latitude*

In general, it is known that fish from higher latitudes tend to have a larger number of vertebrae than the fish from lower latitudes. So the relationship between the mean vertebral numbers and the degree of latitude were analyzed by regions (Fig. 14). In order to extend the range of latitude, fifteen means of the total vertebrae in nine coastal areas of Honshu, published by Ogata[55], and Hashimoto and Koyachi[50], were added to the present data.

The regression lines were calculated for three counts of vertebral numbers, i.e. total, abdominal, and caudal, in each region, and the significance test for the slopes of these lines were also calculated (Table 9). Result of the tests showed that the slopes were significantly positive at the 5% significance level, exclusive of the caudal vertebrae in the Okhotsk Sea, and the abdominal vertebrae in the Sea of Japan. Then the significance of differences of the adjusted means and regression coefficients between the regions were tested by the analysis of covariance.

The adjusted mean number of total vertebrae of the Sea of Japan was significantly lower than those of two other regions. In the caudal vertebrae, the adjusted mean of the Pacific region is higher than that of the Sea of Japan at the 1% level of significance. The adjusted means of abdominal vertebrae are

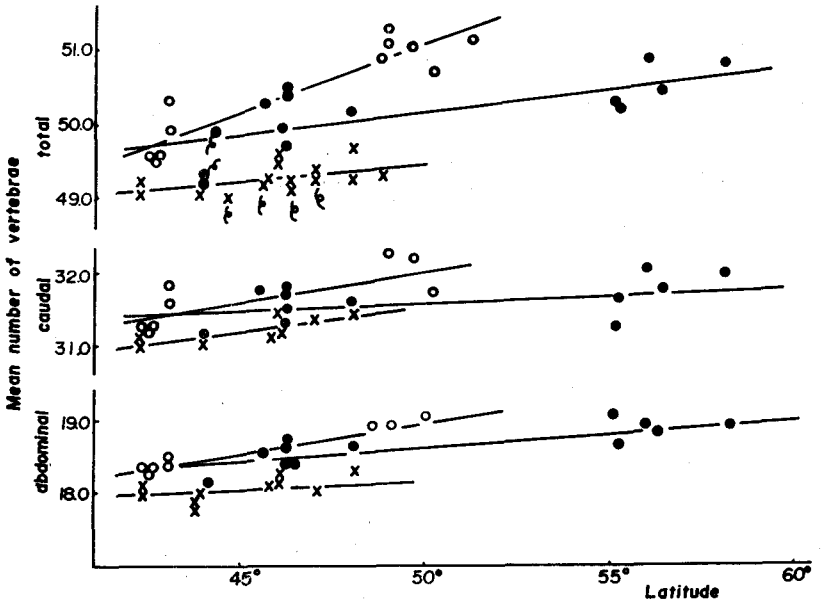


Fig. 14. Regression lines of the means for abdominal, caudal and total vertebrae in the walleye pollock with regard to latitudes in the regions. ○: Pacific region, ●: Okhotsk Sea, ×: Japan Sea region, spiral marks from Ogata, Hashimoto and Koyachi.

Table 9. *Constants a and b in the regression equation ($V=a+bL$, where V means the number of vertebrae and L the degree of latitude) and comparison of b and the adjusted means between regions.*

	Region	b	F-test for difference of b	a	Adjusted mean (μ)	F-test for difference of μ
Total vertebrae	Pacific Ocean	0.1873**	F=27.841	41.67	50.341	F=4.544
	Okhotsk Sea	0.0476*	df=1, 25	47.84	49.954	df=1, 26
			P<0.001			0.025<P<0.05
	Okhotsk Sea	0.0476*	F=0.423	47.84	50.035	F=2.407
	Sea of Japan	0.0372**	df=1, 30	47.48	49.194	df=1, 31
			P>0.1			P<0.01
	Sea of Japan	0.0372**	F=54.592	47.48	49.194	F=2.041
	Pacific Ocean	0.1873**	df=1, 33	41.67	50.341	df=1, 17
			P<0.01			P>0.01
Caudal vertebrae	Pacific Ocean	0.0841*	F=95.36	27.83	31.726	F=2.041
	Okhotsk Sea	0.0164	df=1, 12	30.75	31.504	df=1, 13
			P>0.1			P>0.1
	Okhotsk Sea	0.0164	F=0.788	30.75	31.726	F=2.041
	Sea of Japan	0.0841*	df=1, 16	28.29	31.265	df=1, 17
			P>0.1			P>0.05
	Sea of Japan	0.0841	F=0.818	29.29	31.201	F=18.21
	Pacific Ocean	0.0841*	df=1, 12	27.83	31.624	df=1, 13
			P>0.1			P<0.01
Abdominal vertebrae	Pacific Ocean	0.0822**	F=3.655	14.83	18.690	F=3.483
	Okhotsk Sea	0.0386**	df=1, 16	16.68	18.614	df=1, 17
			P>0.05			P>0.05
	Okhotsk Sea	0.0386	F=0.050	16.68	18.545	F=15.784
	Sea of Japan	0.0322	df=1, 17	16.65	18.216	df=1, 18
			P>0.1			P<0.01
	Sea of Japan	0.0322	F=3.427	16.65	18.538	F=57.194
	Pacific Ocean	0.0822**	df=1, 12	14.83	18.109	df=1, 13
			P>0.05			P<0.01

The asterisk shows the significance level for the test of H_0: $\beta=0$,
* $0.01<P<0.05$, **$P<0.01$

significantly different at the 1% level between the Seas of Okhotsk and Japan, and between the Sea of Japan and the Pacific. Consequently the regression lines of the Pacific region generally show the highest position in each count of vertebrae and those of the Okhotsk Sea follow after. For the regression coefficients, significant differences were noted for the total vertebrae between the Pacific region and the Sea of Okhotsk or the Sea of Japan.

These results suggest that there is a positive linear relationship between the latitude and the numbers of total, abdominal and caudal vertebrae. The slope was steeper, and the vertebral counts higher, in the Pacific region.

6. *Discussion*

Although the present samples are insufficient to represent all the local forms

of the walleye pollock, the statistical comparison of the mean number of vertebrae suggests that some local forms occur in geographically restricted waters within the present study area. In the northern region of the Sea of Japan there are two groups of walleye pollock showing different mean numbers of abdominal and total vertebrae. One is a group designated as the Western Sakhalin form in the northern area and the other is the Western Hokkaido form in the southern area. These two forms overlap off the southwest coast of Sakhalin Island. In the Okhotsk Sea, the Western Okhotsk Sea form is distributed from the eastern coast of Hokkaido to the area northward of Sakhalin Island along the eastern coast of this island, and is readily distinguished from the Rausu form. In this sea there is another group, the Northeastern Okhotsk Sea form, distributed in the northeastern part of the sea. In the Pacific region there are three local forms, *viz.* the Western Erimo form, the Eastern Erimo form and the Northern Kuril Island form.

In the diagrammatic analysis of correlative variations between the abdominal and caudal vertebrae, four clumps were distinctly found. Taking separately each region into account, each clump coincides with each local form, excluding the samples from Aniva Bay in May and July and a sample of the Eastern Erimo form (Sp 47). Although this discontinuity is expected to represent the discontinuity among local forms, some clumps contain together several samples from geographically distant areas, and consequently it is difficult to accept that each clump represents the homogeneity of a local form. Probably these mixtures are due to the geographical inclination of vertebral counts with latitude.

It is also indicated that abdominal, caudal and total vertebrae counts show normal distributions, and both the means and variances of samples within an area are about the same. The mean tends to increase with increasing latitude. Thus, the local form classified by phenotype can be defined in a given region as follows: (1) the vertebral counts are normally distributed with a certain specific hereditary range within each environmentally homogeneous area; (2) the mean vertebral counts have a relative position and a particular regression coefficient within each region with respect to latitude, and accordingly their variation is related to particular environmental and geographical factors in each respective region.

So the various studies on fish population must be reviewed, with respect to the phenotypical characteristics employed by previous authors, and then the validity must be considered for the concept of "local form" proposed here. Earlier, Jordan's papers drew attention to a correlation between the temperature conditions on the globe and the number of vertebrae in the different groups of fishes, and Heincke's investigations[72] on the racial characters of the Atlantic herring, *Clupea harengus*, aroused great interest in fisheries research, for the use of meristic characters in delimiting the so-called races in many different groups of fishes (*vide*

Tåning).[73] Numerical variations in vertebral counts with respect to latitude have been investigsted by Schmidt[74] for cod (*Gadus callarias*) by Tester[75] for herring (*Clupea pallasii*), and by Kubota & Ono[76] for loach (*Misgurnus anguillicaudatus*). These authors concordantly showed an increase of vertebral counts from warmer waters to colder waters or from south to north in the northern hemisphere. Yokota and Furukawa[77] reported a negative linear relationship between the vertebral number and water temperature at the hatching period of the anchovy (*Engraulis japonicus*). A temperature sensitive phase was found by Tåning[73],[78],[79] during early ontogeny in the sea trout (*Cynoscion regalis*). This phase is regarded to be the same for herring.[80] The results do not contradict the results of the present paper. Considering the circumstances for the reproduction of the walleye pollock, the following conclusions have been attained.

Spawning shoals of the walleye pollock migrate on the continental shelf as much as 120 miles or more from south to north along western Hokkaido.[22],[23] These spawning shoals migrate one shoal after another from January to March. The oceanographical environment changes considerably during this period and it must influence the early development of the fish. These evidences will support the abovementioned hypothetical items (1) and (2) assume a continuous changing environment in an oceanic region.

It is considered that in the walleye pollock the variation in number of vertebrae occurs through the organogenesis of ontogeny encountered with changeable environmental conditions. It can be reliably stated that fish having similar phenotype, which is acquired by particular external conditions, form a homogeneous group in response to the environment. Their phenotype can be distinguished from that of other groups which developed under different environmental conditions, without the consideration of the innate structures of fish population. However, the population, as a unit of resource, has to be recognized with diagnostic features which reflect the structure of reproduction and growth. It is, therefore, quite proper to call the homogeneous group a "local form" which means the group of identical individuals in respect to phenotypic variation.

On the other hand, Hempel and Blaxter[80] suggested that the difference in the mean vertebral counts of Scottish and German spring-spawning herring was genetic, based on experiments involving changing incubation temperature and cross fertilization. But at present nothing has been shown to prove any genetic relationship among different groups in the walleye pollock, although it is necessary to define the population which is an infallible unit of fish resource. For this reason the term "local form" is applied to the geographical variations of the phenotypic characteristics, until the system and mechanism which produce the variations are better clarified. After that, the phenotypic characters will be recognized as a standard for the classification of populations.

V. Genetic Identification

Morphometric and meristic analysis based on the concept that all individuals in a unit of reproduction belong to a proper genetic system and are exposed to similar environment, is still the backbone of the studies being made on population identification. But during the last decade, knowledge obtained through these means has been reinforced considerably by biochemical data derived from a direct structural analysis of the proteins. Of a number of techniques is use, starch gel electrophoresis has been widely accepted as one of the most useful tools to analyse large numbers of samples simultaneously.[81)-83)] Using this technique, Wieland and Pfleiderer found five bands of lactate dehydrogenase isozymes in rat tissue. Also, Markert[84)] proved experimentally that two subunits made five kinds of lactate dehydrogenase isozymes combined as a tetramer.

Then practical identifications were carried out by Møller in gadoid fishes with transferrin since the middle of the nineteen-sixties.[85)-87)] Tetrazolium oxidase (TO) isozyme was pointed out to be significant as a probable tool to identify the genetic polymorphism biochemically.[88)] Later on, a number of other studies[89)-93)] further emphasized the usefulness of such an approach. Independent verification of these differences based on chemotaxonomic methods appeared to be desirable for the studies of walleye pollock. A preliminary electrophoretic investigation[94)] revealed a potential use of TO polymorphism in the study of walleye pollock stocks.

1. Materials and Methods

Samples of walleye pollock for isozyme analysis were obtained from fourteen localities around Hokkaido and two areas in the northeastern Bering Sea (Table 1, Fig. 1). Spawning migration of this species lasts about four months, that is from winter to spring in certain areas, but it might begin earlier in the lower latitudes than the higher ones. The sampling times were selected to match the duration of this migration. Commercial and research vessels were used to collect the samples.

Sample tissues were used either fresh, or after being frozen rapidly within one hour after capture and stored at −20°C. No significant differences could be detected between fresh and frozen samples. Extracts from eye, brain, gill, heart muscle, pyloric caecum, kidney, gonad, and skeletal muscle were made with a glass homogenizer. A sample tissue was homogenized with distilled water (1:1) and centrifuged for 20 minutes at 2°C and 20,000G. The supernatants were absorbed on filter paper pieces (4×6 mm, TOYO No. 2) and were inserted into starch gel slits. Horizontal electrophoresis (250×120×6 mm) was conducted with hydrolysed potato starch (JOKO SANGYO) in a discontinuous buffer system,[95),96)] consisting 0.06 M lithium hydroxide and 0.3 M boric acid for both electrode

buffer vessels. The gel buffer was prepared by adding 1 ml of electrode buffer to each 100 ml of 0.03 M boric acid for both electrode buffer vessels. The gel buffer was prepared by adding 1 ml of electrode buffer to each 100 ml of 0.03 M Tris [tris(hydroxymethyl)aminomethane] and 0.005 M citric acid. A constant current of 1.5 mA/cm^2 was applied for about 14 hours at 4°C. The gel was then sliced with a stainless steel mandoline cord and TO achromatic zones were visualized by incubating for about 2 hours at 35°C in a solution containing 20 mg nitro-blue tetrazolium and 14 mg phenazine methosulfate per 100 ml of distilled water. The staining methods and buffer systems used here are described as follows.

Staining Methods

Lactate dehydrogenase (LDH): after Markert and Faulhaber[97]
45 ml 0.2 M, pH 8.0 Tris-HCl buffer
9 ml 0.5 M, Sodium lactate
5 ml 1 mg/ml Nitro-blue tetrazolium
5 ml 1.6 mg/ml Phenazine methosulfate
2 ml 10 mg/ml NAD

Tetrazolium oxidase (TO):
20 mg Nitro-blue tetrazolium
14 mg Phenazine methosulfate
per 100 ml distilled water, modified from Johnson *et al.*[90]

Buffer Systems

Tris – borate – EDTA (T–B–E) system, Markert and Faulhaber.[97]

Stock Solution	*1 liter*
Tris (0.9 M)	109 gm
H_3BO_4 (0.5 M)	31 gm
2Na-EDTA (0.02 M)	6.7 gm

Use 1/20 dilution for gel buffer; 1/5 and 1/7 dilution for electrode buffer of cathodal and anodal chambers.

Tris – citric acid system, Ridgway *et al.*,[95]

Electrode Buffer	*1 liter*
LiOH (0.06 M)	2.5 gm
H_3BO_4 (0.3 M)	18.6 gm

Gel Buffer	*1 liter*
Tris (0.03 M)	3.6 gm
Citric acid (0.005 M)	1.05 gm

Gels are made with a 99% gel buffer and 1% electrode buffer mixture.

2. *Lactate Dehydrogenase Isozyme*

Several buffer systems (Clayton and Gee[98]; Williscroft and Tsuyuki[99]; Fine *et al.*[101]; Karlsson and Carlsson;[102] and Markert and Faulhaber[97]) were subject to examination to investigate the fitness for the electrophoresis in lactate dehydrogenase (LDH) of walleye pollock.

The migrating distances of the fastest band were measured in each buffer system (Table 10). LDH of walleye pollock was most mobile in the citric acid – phosphate buffer system, but the clearness of zymogram in T-B-E system was better than the others. Also in the T-B-E system, the migration distances in increased in the higher pH in experimented range. Various tissues of many specimens were investigated, and certain tissues showed a certain zymogram consistently (Fig. 15, 16). Six bands of LDH were observed in the retina extract. Though retina extract included seven bands in Ridgway's system, no variation was found (Fig. 17).

Table 10. *Investigations of buffer systems in starch gel electrophoresis for lactate dehydrogenase isozymes of walleye pollock.*

buffer system				electrophoresis condition			migration distance of quick band
in starch gel	in electrode chambers			current (mA/cm²)	time (hr)	temperature (C)	
citric acid 0.002 M adjusted to pH 8.0 with Tris at 22°C	citric acid 0.04 M adjusted to pH 8.0 with Tris at 22°C			1	8	4	12
0.2 M citric acid 7 ml 0.2 M sodium phosphate dibasic 50 ml, pH 7.0 at 24°C	0.2 M citric acid 20 m 180 ml distilled water adjusted to pH 7.0 with phosphate			0.5	16	4	49
Tris-borate-EDTA buffer systems stock solution	dilution ratio for						
	gel	anode	cathode				
Tris 0.9 M boric acid 0.3 M EDTA 0.02 M pH 8.89 at 25°C	1:20	1:7	1:5	0.5	16	4	42
Tris 0.5 M boric acid 0.207 M EDTA 0.016 M pH 8.82 at 24°C	1:20	1:7	1:5	0.5	16	4	40
Tris 0.9 M boric acid 0.5 M EDTA 0.02 M pH 8.70 at 25°C	1:20	1:7	1:5	0.5	16	4	39
Tris 0.9 M boric acid 0.6 M EDTA 0.02 M pH 8.6 at 25°C	1:20	1:7	1:5	0.5	16	4	36

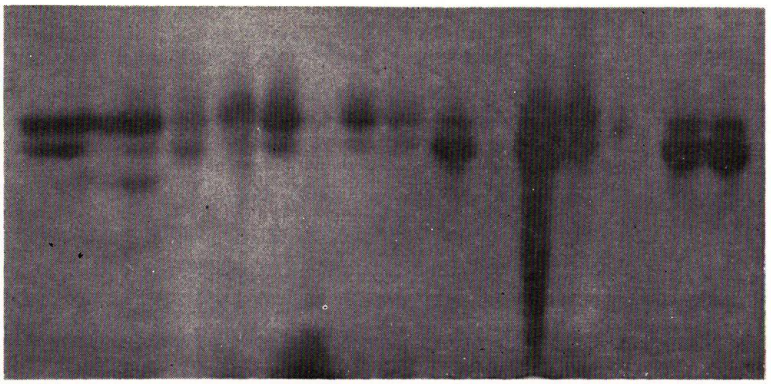


Fig. 15. Zymogram of lactate dehydrogenase from various tissues of walleye pollock, with Tris-boric acid-EDTA buffer system.

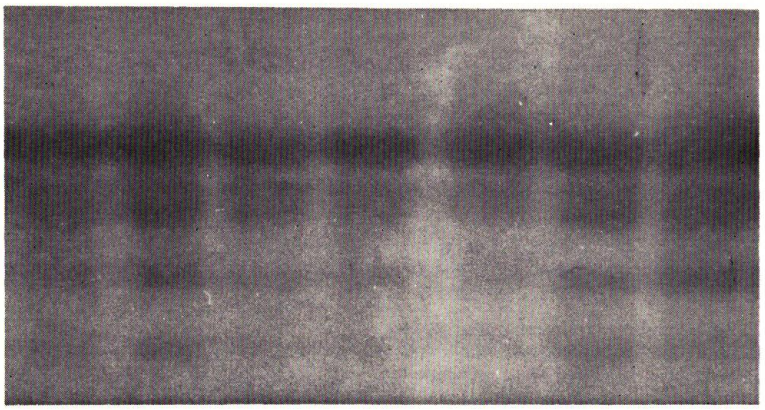


Fig. 16. Zymogram showing no variation among individuals as to lactate dehydrogenase from retine of walleye pollock with T-B-E buffer system.

3. *Tetrazolium Oxidase Isozyme* (*TO*)

Preliminary experiments were carried out in order to prove the fitness of this analysis. TO activity bands appeared as achromatic regions against non-specific dark blue background after about 2 hours. In Ridgway's buffer system all the bands of TO isozyme possessed slow electrophoretic mobilities in comparison with LDH. For example, the fastest band of TO moved 17 mm from the origin, whereas the fastest band of lactate dehydrognease migrated 35 mm.

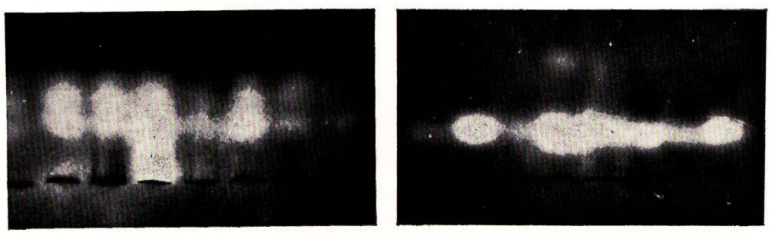
Preliminary experiments on 16 specimens from Sahara (Sp 44) showed relative visibility of achromatic zones to be better in the extracts of the liver, kidney, and brain, but zymograms of all eight tissues (eye, heart muscle, pyloric caecum, gonad, and skeletal muscle, plus the above three tissues) were qualitatively identical in a

specimen (Fig. 18). Therefore brain tissue was selected for the following experiments because of easy extraction. In the second series of experiments the zymograms of tissues frozen for ten and twenty days were checked. Some faint bands were observed in these zymograms, and these bands were excluded from consideration. In the third series of experiments on 44 specimens from Sahara and 94 from Kumaishi (Sp 1), only extracts of liver and brain were used. Three phenotypes were detected in all tissue samples (Fig. 19). These phenotypes were designated as S (slow), F (fast) and SF. The zymogram patterns indicated that TO have a dimeric construction which is controlled by two codominant alleles (TO^s and TO^f) at the pollock *TO* locus. The observed frequencies were tested for goodness-of-fit to the expected distributions according to the Hardy-Weiberg equilibrium (Kumaishi: $\chi^2=0.378$; Sahara; $\chi^2=0.642$). These Chi-square values show that observed frequencies of each allele fitted with the expected frequencies, that is, two TO alleles equilibrate in each fish group.

Fig. 17. Zymogram of lactate dehydrogenase in various tissues of walleye pollock with Ridgway's buffer system.

(a) *Comparison between male and female*

Considering the importance of assigning the TO locus on the chromosomes for a better analysis of detectable phenotypes, statistical computation of TO



A B

Fig. 18. Two phenotypes in eight tissues from specimens A(SF) and B(S). Examined tissues are eye, brain, heart muscle, pyloric caecum, kidney, gonad, and skeletal muscle from right to left.

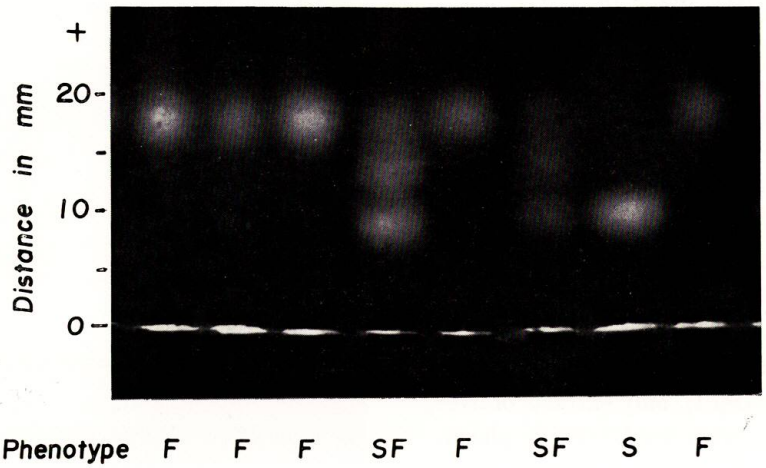


Fig. 19. Clear zymogram of tetrazolium oxidase was actualized by the electrophoresis in 12% starch gel in discontinuous Ridgway's buffer system for 6.5 hours of 1.5 mA/cm² direct current.

phenotypes frequencies between males and females was performed. A number of specimens in three TO phenotypes of five sample lots from Hachinohe (Sp 39), Northern Wakkanai (Sp 9), Western Sakhalin (Sp 16), Belkina (Sp 20), and Iturup Island (Sp 48) was shared by both sexes. The observed frequencies were tested for fitting goodness to the expected distribution according to the Hardy-Weinberg law (Table 11). As for the females from Iturup Island (Sp 48), the maximum Chi-square value was 1.2114 (d.f.=2). The probability level for all Chi-square values was more than 0.5. Snedecor and Cochran[67] suggested that it was sufficient to apply the Chi-square test, if the expected frequencies are larger than 1.0. But the expected frequencies in the present data were smaller than 1.0 in those two cases.

The combination of probability test was also applied in order to clarify the existence of dimorphism on TO allele without the variation of probabilities in the five samples. Fisher has shown that in the formula:

$$-\frac{1}{2}\chi^2 = \log_e P_i$$

the density function of χ^2 has a χ^2 distribution with 2n degrees of freedom. The value of Chi-square, thus, becomes:

$$\chi^2 = -2\sum \log_e P_i$$

where P_i stands for probability level. Consequently the Chi-square value is 6.62 and the probability as $0.8>P>0.7$, pointing out that sexual dimorphism has no bearing on the TO polymorphism.

Table 11. *Significance test for the frequency difference of tetrazolium oxidase phenotypes between male and female.*

	Location	Sex	No. of fish	Phenotypes			Allelic frequency			χ^2
				S	SF	F	TO^s	TO^f	χ^2	
39	Hachinohe	male	39	7 (5.69)	17 (15.55)	15 (17.88)	0.3974	0.6026	0.9232 (0.7>P>0.5)	1.5552 P=0.46
		female	57	7 (8.31)	21 (22.56)	29 (26.13)	0.3070	0.6930	0.6319 (0.9>P>0.7)	
9	Northern Wakkanai	male	39	6 (5.20)	23 (22.10)	10 (11.70)	0.4487	0.5513	0.4067 (0.9>P>0.7)	1.1621 P=0.56
		female	21	2 (2.80)	11 (11.90)	8 (6.30)	0.3471	0.6429	0.7554 (0.7>P>0.5)	
16	Western Sakhalin	male	30	7 (8.00)	14 (15.00)	9 (7.00)	0.4667	0.5333	0.7631 (0.7>P>0.5)	1.5262 P=0.47
		female	30	9 (8.00)	16 (15.00)	5 (7.00)	0.5667	0.4333	0.7631 (0.7>P>0.5)	
20	Belkina	male	30	6 (5.00)	16 (17.08)	8 (7.92)	0.4667	0.5333	0.2696 (0.9>P>0.7)	0.4622 P=0.79
		female	42	6 (7.00)	26 (23.91)	11 (11.08)	0.4405	0.5595	0.1926 (P>0.9)	
48	Iturup Is.	male	31	6 (5.06)	17 (15.82)	8 (10.12)	0.4677	0.5323	0.7078 (0.7>P>0.5)	1.9192 P=0.38
		female	18	2 (2.94)	8 (9.21)	8 (5.89)	0.3333	0.6667	1.2114 (0.7>P>0.5)	

(b) *Comparison between samples*

The rates of TO^s or TO^f allele, and the goodness of fit to the expected frequencies were calculated for 942 specimens from fourteen sample lots (Table 12). Phenotype S did not appear in the eastern Bering Sea region, therefore the expected frequencies were less than 1.0. Although the fitness may not be accurate, to match the frequencies of two phenotypes, the Chi-squares were computed by an ordinary method and marked with asterisks. The observed frequencies in fourteen samples matched the expected values, and the maximum probability was 0.44 (χ^2=0.648). It may, therefore, be assumed that tetrazolium oxidase isozymes are controlled by two codominant alleles on the autosomes of walleye pollock.

Table 12. *Observed and expected (in parentheses) frequencies of tetrazolium oxidase phenotypes in walleye pollock from the vicinity of Japan and from the eastern Bering Sea.*

Sample number and area		No. of fish	Phenotypes			Allelic frequency		
			S	SF	F	TO^s	TO^f	χ^2
39	Hachinohe	96	14 (11.3)	38 (43.3)	44 (41.4)	0.344	0.656	1.443
40	Usujiri (Uchiura B.)	59	8 (10.2)	33 (28.7)	18 (20.2)	0.415	0.585	1.358
44	Sahara (Uchiura B.)	60	12 (12.5)	33 (29.9)	15 (16.6)	0.475	0.525	0.634
45	Kushiro	48	8 (7.9)	23 (23.2)	17 (16.7)	0.406	0.594	0.002
48	Iturup Is.	49	8 (8.6)	25 (23.8)	16 (16.6)	0.418	0.582	0.129
1	Kumaishi	94	26 (24.5)	44 (46.9)	24 (22.6)	0.511	0.489	0.378
4	Ofuyu	145	26 (26.5)	72 (71.0)	47 (47.5)	0.428	0.572	0.030
8	Northern Wakkanai	60	8 (10.4)	34 (29.2)	18 (20.4)	0.417	0.583	1.648
16	Western Skhalin	60	16 (16.0)	30 (30.0)	14 (14.0)	0.517	0.483	0.002
20	Belkina	72	12 (14.7)	41 (35.7)	19 (21.7)	0.451	0.549	1.615
23	Rausu	108	19 (20.9)	57 (53.2)	32 (33.9)	0.440	0.560	0.545
59	Northern Unimak Is.	31	0 (0.3)	6 (5.4)	25 (25.3)	0.097	0.903	0.357*
57	Western Pribilof Is.	30	0 (0.1)	4 (3.7)	26 (26.1)	0.067	0.933	0.153*
56	Western St. Matthew Is.	30	0 (0.1)	4 (3.7)	26 (26.1)	0.067	0.933	0.153*

Table 13. *Chi square values and significance of difference between the observed frequencies of tetrazolium oxidase S, SF, and F phenotypes (right upper), and between the frequencies of TO^s and TO^f allele (left below).*

Sample number and ares		39	40	44	45	48	1	4	9	16	20	23	59	57
39	Hachinohe		4.304	6.816*	1.435	2.404	9.901**	4.429	4.705	8.759*	6.901*	5.766	12.515**	23.005**
40	Usujiri	1.601		1.064	0.691	0.298	4.170	0.849	0.007	3.301	0.406	0.464	21.170**	25.435**
44	Sahara	5.327*	0.860		1.395	0.834	1.367	0.561	1.088	0.749	0.247	0.452	25.656**	36.802**
45	Kushiro	1.079	0.018	1.021		0.103	2.653	1.162	0.828	2.580	1.222	0.524	16.600**	24.118**
48	Iturup Is.	1.552	0.002	0.699	0.029		2.442	0.068	0.384	2.167	0.585	0.152	18.508**	22.309**
1	Kumaishi	10.817**	2.646	0.372	2.777	2.198		3.485	4.375	0.163	3.189	2.949	31.030**	37.745**
4	Ofuyu	3.400	0.052	0.774	0.135	0.018	3.167		1.022	2.758	1.109	0.276	23.132**	30.474**
9	Northern Wakkanai	1.681	0.000	0.826	0.024	0.001	2.594	0.041		3.417	0.393	0.545	21.702**	26.365**
16	Western Sakhalin	9.126**	2.459	0.417	2.612	2.091	0.011	2.717	2.411		1.959	2.140	27.070**	33.168**
20	Belkina	4.008*	0.345	0.149	0.395	0.258	1.146	0.222	0.321	1.117		0.506	26.808**	31.571**
23	Rausu	3.927*	0.188	0.386	0.306	0.106	2.023	0.076	0.169	1.830	0.047		26.679**	31.714**
59	Northern Unimak Is.	14.074**	19.430**	25.837**	17.713**	18.931**	33.063**	24.003**	19.637**	30.795**	24.128**	24.508**		0.403
57	Western Pribilof Is.	17.494**	23.114**	29.770**	21.326**	24.378**	37.261**	27.921**	23.335**	34.882**	28.007**	28.422**	0.367	

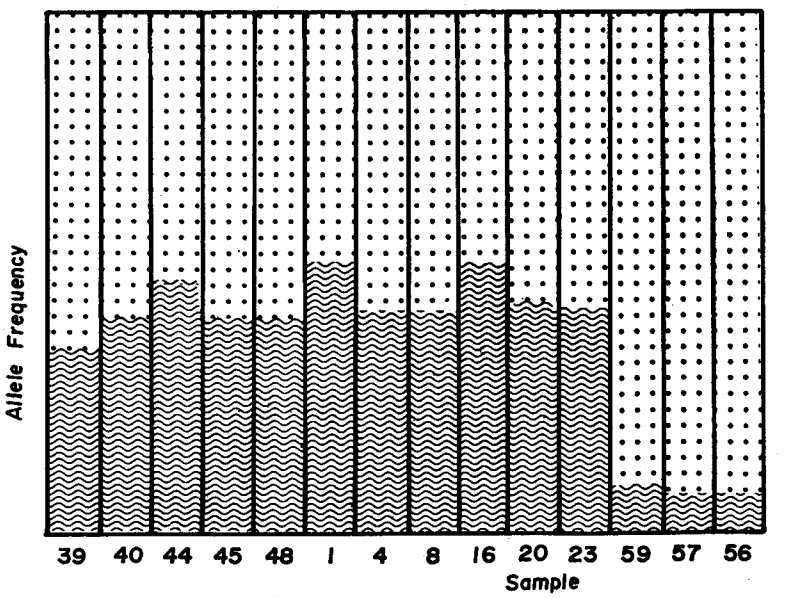


Fig. 20. Frequencies of tetrazolium oxidase allele in fourteen samples: shaded and dotted columns show the rates of TO^s and TO^f respectively.

The rates of TO^s and TO^f remained around 0.5. The TO^s allele was dominant among three samples from the eastern Bering Sea (Fig. 20). The Chi-square test was applied to the calculated frequencies and observed frequencies of three phenotypes (Table 13). Statistically, three samples in the eastern Bering Sea showed significant differences with all other samples collected from nearby Japanese regions. Furthermore, the sample collected off Hachinohe showed some significant differences among the phenotype frequencies, in comparison with the other four samples from the vicinity of Japan. When calculated on a phenotype basis or allele basis, the differences were found to be approximately the same.

Walleye pollock taken from the Gulf of Alaska also appear to fall into the eastern Bering Sea group on the basis of TO allelic frequencies.

4. Discussion

The results of experiments suggest that tetrazolium oxidase isozymes of walleye pollock are composed of dimerous usbunits under the control of two codominant alleles on autosomes. No significant differences were noted between the observed frequencies of TO phenotypes of males and females, and all of the frequencies were homologous to the expected ones calculated from the Hardy-Weinberg law of equilibrium. Single band phenotypes of S and F consist of two homologous subunits (S-S and F-F), and three bands of heterozygote phenotype SF, which are

heterogeneous and composed of two different subunits.

The above assumption is in full agreement with the studies made on other vetebrates. For example the polymorphism of tetrazolium oxidase in dogs has been explained as dimerous construction.[103] Johnson *et al.*,[90] who found three electrophoretically separable TO polymorphs among fifteen species of *Sebastodes* also gave the same explanation. For the bluefin tuna from the Atlantic, a similar report is available.[91] However, five patterns of TO phenotype were found in black rockfish, and it was suggested that the dimerous TO isozymes are controlled codominant alleles.[93]

Although 942 specimens of walleye pollock were analyzed for the tetrazolium oxidase phenotype, no exception has so far been found. Fourteen samples fitted well for the Hardy-Weinberg equilibrium based on the assumption that tetrazolium oxidase is controlled by two codominant alleles.

Accordingly, these results suggest that there is little possibility of genetic interchange between the walleye pollock in the eastern Bering Sea or the north-eastern Pacific Ocean, and in the seas in the vicinity of Japan. Since the two habitats are far apart, walleye pollock may be considered in a state of reproductive isolation through their long history.

Following Simpson[104] and Imaizumi,[105] the walleye pollock species can be defined to have at least two "lineages".

VI. Synthetic Discussion

Analyses along three lines following different concepts were made during this study of population identification. The results are illustrated in figure 21. Both morphological analysis and the classification by vertebral counts led to similar conclusions, but the results of the analyses on tetrazolium oxidase differed with them, considerably.

For the sake of comparison, other studies made so far, will be discussed in detail. Tsuji[24] has summarized the investigations on this species made by Hokkaido Fisheries Experimental Stations. He noted that only one population inhabits the northern Sea of Japan excluding Kumaishi and Kudo, while the population distributed in the areas from Abashiri to Terpenia Bay in the Okhotsk Sea was separate. Every other group in Rausu remained to be identified. Tsuji and Hayashi[106] separated the fish groups of the Pacific region into the Western Erimo Group and the Eastern Erimo Group.

Formerly, when pollock fishery was not so developed, four populations were recognized around Hokkaido *viz.* the Sea of Japan population, the Okhotsk Sea population, Western and Eastern Erimo populations founded on a hypothesis that migrating interchange among various regions was very rare.[44] A population transition occurred in the Western Erimo region, and the A-middle group mixed

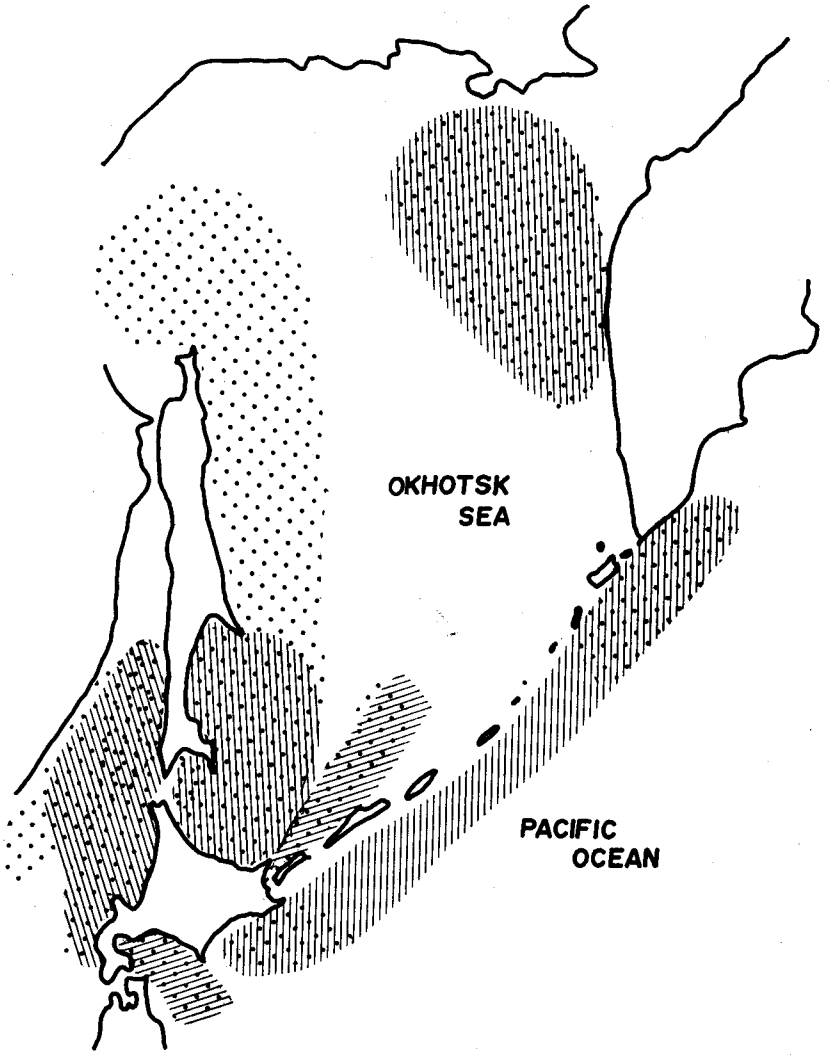


Fig. 21. Schematic pile of estimated distributions of walleye pollock local forms which were classified by morphometric and meristic analyses. shadow: analysis of morphometry, dots: analysis of vertebral counts.

with the declining A-large group. But afterward both types decreased and the B-type later appeared in this region.[50]

In all above studies the term "population" was used to denote the local forms identified by the analyses of the vertebral counts and other morphometric descriptions like the one utilized in the present study. The present study showed that two local forms, the Western Hokkaido local form and the Western Sakhalin form, exist in the northern Sea of Japan, contrary to the findings of Tanaka[23] or

Tsuji[24].

Secondly, the present study also demonstrates that the geographical range of the feeding migration after spawning in the Okhotsk Sea is extensive, a conclusion matching former reports.[24] For instance the feeding shoals of the Western Sakhalin form migrate to Aniva Bay in late spring and summer, whereas another local form of the Western Okhotsk Sea, usually spawn on the continental shelves along Hokkaido or southern Sakhalin Island. The fish in summer may penetrate the northern areas off Sakhalin Island.

Though the exact identification of the spawning group off Rausu is uncertain, it was found that forms and counts of vertebrae were obviously different from those of the fishes of the Western Okhotsk Sea or the Eastern Erimo form. The Rausu form is usually regarded as an independent local form coming from some adjacent area. The Western Okhotsk Sea form has also been separated from the Eastern Okhotsk Sea form due to the same reason.

Of the local forms in the Pacific region investigated here, the "Northern Kuril Island form" should be separated from the "Eastern Erimo form" due to a statistical discontinuance of vertebral counts, though the morphometric analysis based on body form did not reveal this difference. Both analyses, however, suggested the independence of the "Western Erimo form" from the "Eastern Erimo form" and the local forms of the Sea of Japan.

Following the above discussion, walleye pollock may be concluded to have eight local forms in the vicinity of Japan as classified below.

Northern Sea of Japan	Western Hokkaido form
	Western Sakhalin Island form
Okhotsk Sea	Eastern Okhotsk Sea form
	Western Okhotsk Sea form
	Rausu form
Pacific region	Northern Kuril Island form
	Eastern Erimo form
	Western Erimo form

If we see the seasonal migration of certain local forms, it can be easily imagined that their migration occurs within a very wide range and, sometimes this movement is speedy. From evidence, the results of tagging experiments are arranged in figure 22. The releasing points were mainly in the waters off Abashiri and Rausu in the Okhotsk Sea. Of the released fishes ten specimens tagged during the late spawning period, moved 150–180 miles north after only one week to two months.[107] Three specimens crossed the Okhotsk Sea, as spawners, to western Kamchatka or eastern Kamchatka, after one year. From the same area off Abashiri, two specimens were caught in the Pacific waters off Iturup Island during the spawning season. After one year, two immature fishes entered the Sea of

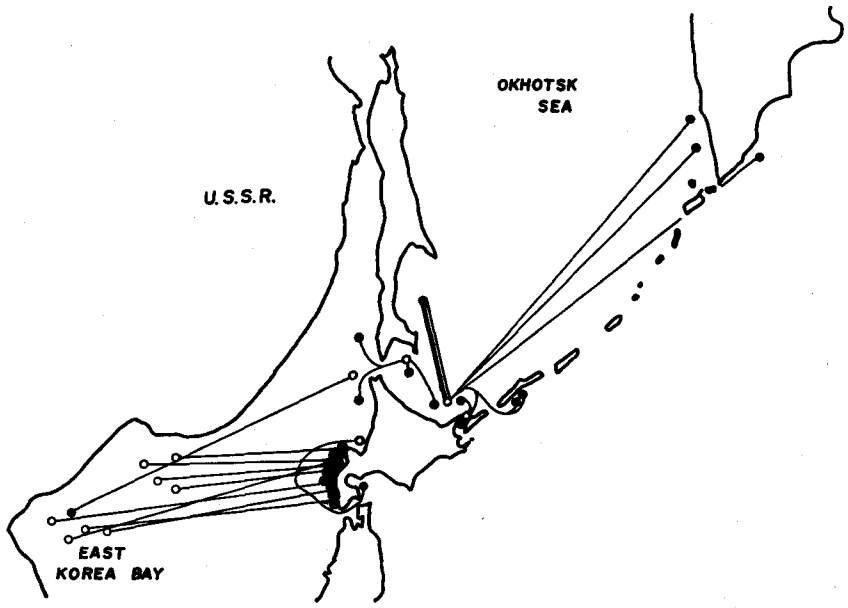


Fig. 22. Tagging experiments reported by Korea Fish. Exp. Station (*vide* Ogata, 1956); Tsuji, 1973; and Kondo *et al.*, 1973. circle: release point, dot: recapture point.

Japan. Of the "Rausu form" and the "Western Okhotsk Sea form", three spawners in the Rausu area migrated to the area off Abashiri during the feeding season. Another three specimens were recaptured in the area off Rausu, as spawners. Next year two other mature adults also homed in. Other tagging experiments showed that one specimen migrated from the Sea of Japan to Uchiura Bay during 1968–'70 (unpublished data).

In the western Bering Sea, eleven specimens were recaptured, and four pollock among them migrated over 100 miles at the adjacent area of the releasing point. Noteworthy another specimen migrated from Cape Olytolsky to a water off Cape Navarin.[25] Another tagging experiments in the eastern Bering Sea proved that seven specimens moved about in this region, and two of them interchanged between eastern and western areas near Pribilof Islands.[108]

With the help of tagging experiments, we know that walleye pollocks move rapidly to feeding areas after spawning, and sometimes migrate distances of several hundred miles. This species does not always dwell on the bottom, but should be considered as a pelagic migrator, transfering habitat at various spawning grounds, from winter to early spring, and feeding in certain areas from late spring to autumn.

It is quite probable that pollock groups interchange between the regions where more than one local form live. These findings of tagging experiments should

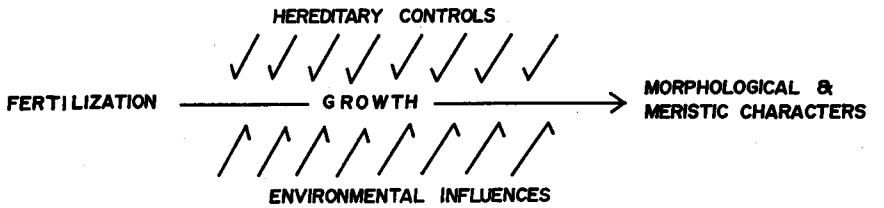


Fig. 23. Control system of morphological and meristic characters. Hereditary controls and environmental influence reflecting contrarily.

clarify to some extent, the controversies related to the identification of local forms and lineages, proposed under genetic and evolutionary concepts. Moreover, a simultaneous study, dealing with three different concepts, that is, morphometry, meristic analysis and population genetics, should further improve these understandings.

Firstly the body form is the cumulative value depicting an individual's history, till it is caught. Not only the direct control by the inherited from its parents and population, but also the surrounding environments have an effect on its morphological formation during the entire process of its growth (Fig. 23). Genetic control acts upon the individual in a manner similar to the morphological characteristics of population and parents. However environmental factors which are highly changeable act upon the fish unilaterally, contrary to genetic control. The effect does not depend on the internal conditions of the fish, but selects the adaptable individuals, or controls the growth of the cell number, which is the base of absolute growth. In other words, the time dimension coincides with the period of an individual's life. Hamai and Kyushin[69] actually showed controls exerted by artificially controled water temperature during the incubation of greenlings. Similar morphological differences were also realized among groups of rainbow trout kept under controled temperature waters.[61] In this experiment, Martin suggested an important hypothesis that growth rate was not correlative to body form, but the control of initial growth might act importantly upon it. If Martin's hypothesis is reasonable, we may recognize that morphological formations are similar to the determination mechanisms of meristic characters. In the incubation experiments of *Cyprinus carpio*, however, the absolute growth and relative growth have changed more in the half diet group than in the full diet one.[109] These results suggested the possibility that there are some other factors also affecting the fish form.

Secondly about formation mechanisms of meristic characters, discussed in context of vertebral counts, Tåning found a temperature sensitive phase of meristic characters in the early ontogenesis.[73),78),79] Therefore the meristic characters of a fish were determined during the short term of ontogenesis by the environments and

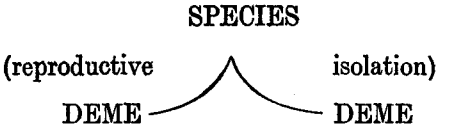
genetic information together. Meristic characters may become standards after supposing that environments and genetic information are common within certain populations.

Thridly, genetic information from both parents is summed up at the time of fertilization and materialized during growth. The Hardy-Weinberg law, used in the present study, were introduced by Dobzhansky[110),111)] and Crow & Kimura[112)] as, "realization of a gene pool", which is the smallest unit evolutionary process. It is supposed that sexual mating occurred at random in this unit. If so, the alleles have codominant importance. Since this occurs early in animal life as compared with the other two affecting factors, it might not have been so variable during the long evolutionary period in a certain population.

Boughey[113)] explained that the mutation rate of an allele may be apploximately 10^{-5}, but it is reversible; that is, there is a back mutation. The chances of mutation for a fixed allele in a population were calculated to require the period of 300 generations.[114)] In the case of walleye pollock, the period may have been about 1200 years as their recruit cycle is 4 years. Furthermore, experimental results showed that the reason for artificial mutations were temperature, radioactivity and medicines, though it was hard to produce mutations artificially.[115)] Therefore it can be considered reasonable that the experimental results dealing with tetrazolium oxidase in walleye pollock reflect the genetic differences which were fixed in the evolutionary course.

It is clear from the above discussion of those three basic concepts, being followed in the present study, that the control idea involved in the analyses by vertebrae and morphometry is very similar as far as determination mechanisms are concerned. That is, the environment acts as an important factor to determine the formation during the early stage of ontogeny. But the concept of genetic analysis seems more distinguishable than the other two concepts.

Present taxonomists generally agree about the categories from Kingdom to subspecies. However the taxa of lower categories are not well established due to the differences in taxonomists's viewpoints. Mayr's concept was based on (1) a reproductive community; (2) an ecological unit; and (3) a genetic unit, when he defined species. He considered that "The species definition that results from this theoretical species concept is: Species are groups of interbreeding natural populations that are reproductively isolated from other such groups". Natural population explained by Imaizumi[105)] as a "deme": is defined as "every individual taking a position in a certain group inhabiting an area, that can produce the next generation by mating". He further stated a smallest unit consisting of specimens that frequently exchange their genes, though this group is isolated geographically from other groups. Therefore, the next vertical relationship under species can be outlined as in the following:



Special emphasis, now, will be given to marine fishes. It is well known that the "species" can not be fixed, but they are in the process of infinite evolution. It has been pointed out that the herring had separated from their mother population in the Atlantic Ocean at the tertiary period. Species should be accepted as a taxon which is on the way to speciation and divergence.

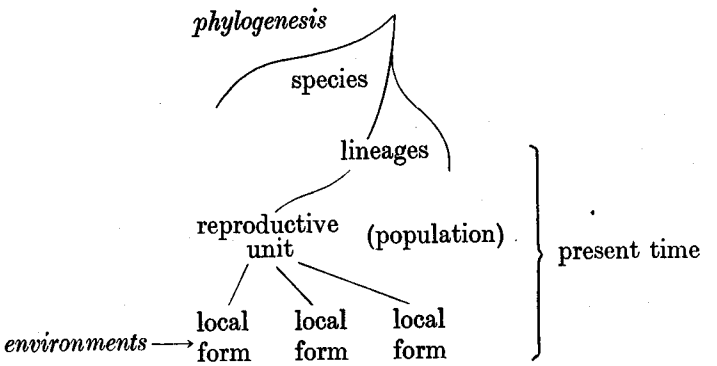
An evolutionary unit is not an individual, but a reproductive unit, that is, deme. If we can distinguish the little differences among demes, they might not evolve independently. Moreover it is more reasonable to consider that these demes construct a group, so that we can recognize more differences between groups. These groups must have parted from one another a longer time ago than the separation among demes. For example, Charles Darwin pointed out that the finches in Galapagos Island could speciate due to inhabiting the isolated islands, though they might have originated from common species. The process of speciation may be on a same level. Boughey writes in this context: "From time to time a mutation occurs in a segment of a polytypic species, such as an ecotype or a subspecies, that limits its ability to exchange genes with other segments of the parent species.[113] The population that develops from the mutant is *reproductively isolated* and is commonly recognized as a separate species population, distinctively from the original species". Simpson[104] explained that the evolving group which is reproductively isolated from other groups in "an evolutionary species is a *lineage* (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies. — Lineages slowly diverging or speciating at first have minimal morphological distinction but in most cases, at least, the distinction increases constantly as time passes."

Imaizumi thought that the lineage was constructed from the demes as a result of segmentation. As described above, breeding is the standard of distinction between one deme and the other. However, it is too hard to apply this standard for the marine fishes. The investigation of geographical distribution of a group that migrate extensively within broad regions is difficult. Consequently, in the present study other distinctive observations including morphology and meristic characters were also made, to distinguish the samples from the spawning grounds where the species was maintained by gene exchange. The genetic analysis was used to ascertain independent lineages. From this discussion, we can propose the definition of taxa below species as follows.

SPECIES
↓
LINEAGES
↓
LOCAL FORMS

If we consider the management of fishery resources, we should not consider a species as a homogeneous identity. At first, each lineage must be separated from others, because they are all independent in their evolutional history. Secondly, we should recognize that the local form is a category different from the reproductive unit, since both morphological and meristic characters may vary from generation to generation. Namely, the reproductive units are "sympatric and reproductive units during mating behavior", if we assume that accidental isolations between them occurred through several generations. The fertilized eggs met with highly changeable environments that changed their characters, in the cases of long spawning periods, as in walleye pollock. The fact that a group migrate over 120 miles during its spawning behavior also supports a hypothesis that a few local forms may occur in a reproductive unit.

Therefore the author would propose the taxa for marine fishes should be as in the following sequence, which is applicable for the understanding of walleye pollock, which the present study deals with.



Based on this understanding, the author believes that the managements of fisheries resource of walleye pollock, and probably other marine fishes, should be remodelled.

Summary

1. Sixty-one sample lots were analyzed by three methods along three lines of different concepts, which include a morphometrical analysis, a statistical analysis of vertebral counts, and an isozymic identification based on genetics.

2. Fitness of allometry equation proposed by Huxley, Teissier, and Nomura

was recognized on the comparisons among 15 measurements *viz.*, *BL, HL, SNL, EYS, DEY, BW, OLM, OLR, OLL, OWM, OWR, OWL, OGM, OGR, OGL* (see text).

3. On the pelvic fin length, the morphological differences between sexes were detected, but the above 15 factors showed monomorphism.

4. Regression coefficients (k) and initial indices ($\log b$) fit in the hypothesis of Lumer's k-log b linear relationship.

5. Morphological comparison of intersamples were carried out with the analysis of covariance and the analysis of rejective limits. Therefore six local forms were hypothesized; there are those of the northern Sea of Japan, Uchiura Bay, the region eastward from Kushiro to the eastern Kamchatka, Rausu area, western and eastern Okhotsk region.

6. Frequency distribution of vertebral counts on total, abdominal, and caudal parts were recognized as monomodal distribution for each sex.

7. No significant difference between male and female is indicated statistically in the vertebral counts.

8. Statistical comparisons of vertebral counts delimited eight local forms in the vicinity of Japan.

9. The abdominal and caudal vertebral numbers were plotted on Cartesian co-ordinates (60°). Four ellipses were detected concerning local forms.

10. Positive linear relationship between the latitude and the number of total, abdominal and caudal vertebrae were recognized, also the inclination was steeper and the vertebral counts higher in the Pacific region.

11. Fourteen sample lots were examined for the genetic analysis. Lactate dehydrogenase (LDH) and tetrazolium oxidase (TO) were investigated by horizontal electrophoresis with Markert & Faulhaber's, and Ridway's buffer systems.

12. No variation of LDH phenotype among individuals was found in the various tissues.

13. Tetrazolium oxidase isozymes of walleye pollock are composed of dimerous subunits under the control of two codominant alleles on autosomes.

14. The frequencies of tetrazolium oxidase (three phenotypes) showed good fitness to the Hardy-Weinberg law.

15. No significant differences could be recognized on the comparisons of frequencies of TO phenotypes between male and female.

16. Two lineages depending on population genetics were detected separately from the vicinity of Japan and the eastern Bering Sea or the Gulf of Alaska.

17. Taxa below species were discussed in detail, and the terms lineage, reproductive unit, and local form were proposed for population identification and managements of marine fishes.

Acknowledgements

I would like to express my gratitude to Professor Ikusô Hamai for his solemn guidance throughout this study.

Obligations are due to Professors Tsuneyuki Saito, dean of Faculty, Hidejiro Niiyama, Tokimi Tsujita of Faculty of Fisheries, Hokkaido University; Drs. Fred M. Utter and Allyn G. Johnson of National Marine Fisheries Service (U.S. Dept. of Commerce), Dr. Ken-ichi Numachi of the University of Tokyo, and Professor Kazuo Fujino of Kitasato University for their encouragement and useful advice during this study.

I also express my thanks to Mr. S. Jergen Westrheim (Fish. Res. Bd. Canada, Nanaimo, B.C.), Dr. Alan Jamieson (Ministry of Agr., Fish. and Food, Lowestoft, Suffolk, England), Professor Toshiro Kuroki (University of Tokyo), Professor Kenichiro Kyushin, Mr. Tetsuichiro Kinoshita, Dr. Tsuneo Nishiyama, Professor R. Kawashima, Mr. K. Amagai, Dr. Takeshi Shibata, Dr. Naoyuki Uchida, Mr. Hajime Okisu, Dr. Hideo Fukuoka, Mr. Absar ul Hasnain (Faculty of Fisheries, Hokkaido Univ., Hakodate) for their informative and fruitful suggestions.

The staffs of the following organization: Hokkaido Fisheries Experimental Stations; Hokkaido, Tohoku, and Far Sea Regional Fisheries Laboratory (Fisheries Agency); T/S Oshoro-Maru and Captain Takeji Fujii; and R/V Commando (Washington Univ.), also the following persons: Mr. Robert Meyer (National Marine Fisheries Service, Kodiak, NOAA, USA); Dr. Jay C. Quast (N.M.F.S., NOAA, Auke Bay); Mr. Kenji Shimazaki, and Mr. Haruo Ogi (Hokkaido Univ.) deserve special acknowledgement for their valuable help in securing samples and other relevant pieces of information. Thanks are due to Dr. Osamu Kibesaki (Dean of Seikai Reg. Fish. Lab.) and Mr. Yutaka Kitano (Hokkaido Reg. Fish. Lab.) for opening an unequalled opportunity of Sepcial Scientific Program of Department of Agriculture and Forestry.

Finally, I would like to thank my parents and my wife for their understanding, help and subsidy.

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