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Maturation and Reproductive Cycle of Female Pacific Cod in Waters Adjacent to the Southern Coast of Hokkaido, Japan*1

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The maturation process and reproductive cycle of female Pacific cod *Gadus macrocephalus* were examined in the waters adjacent to the southern and southeastern coasts of Hokkaido, Japan, by collecting fish between April 1989 and September 1990.

Histological examination was made of the ovaries. During the course of ovarian maturation, a portion of the oocytes became isolated from immature oocytes at the yolk vesicle stage (less than 0.3 mm in diameter) and gradually developed into a group of yolky oocytes. When these oocytes reached the migratory nucleus stage (0.5–0.7 mm in diameter), they began to change into transparent mature eggs (0.8–0.9 mm in diameter) accompanied by hydration and yolk fusion. Following this, all of the mature eggs were simultaneously ovulated into the ovarian cavity. The maturity of female Pacific cod was histologically divided into nine grades from yolkless phase (I) to spent phase (IX). Ovaries gradually developed to the yolk vesicle phase from spring to summer. The onset of yolk formation and the most active yolk formation occurred from August through November. Females with ovaries at the migratory nucleus phase appeared during December and January. From the changes in maturity states and the gonadsomatic index (GSI values), the peak of spwaning in this region was assumed to occur during the period of late December through January. Also, the age of first maturation of female cod was estimated to be four years old.

The family Gadidae, with about 55 species, lives throughout the world, primarily in subarctic zones and high latitudes.[1] Within Gadidae, the Genus *Gadus* is composed of three species, Pacific cod *G. macrocephalus*, Atlantic cod *G. morhua*, and Greenland cod *G. ogac*. The Pacific cod is widely distributed in the northern part of the North Pacific Ocean and adjacent waters such as the Yellow Sea, the Sea of Japan, the Sea of Okhotsk, and the Bering Sea.[2] Pacific cod is important as a commercial resource and plays an important role in subarctic ecosystems.

Previous studies on some aspects of female reproduction in Pacific cod have been carried out using the gonadsomatic index (GSI values)[3] and macroscopic maturity.[4,5] Recently, Bowden *et al.*[6] microscopically described the oocyte growth and development of Pacific cod for correlation with macroscopic maturity of the ovary. The maturation process and the reproductive cycle of female Pacific cod based on histological examination, however, have not been made clear.

In this study, the process of Pacific cod oogenesis is described from fish collected in the waters off the southern coast of Hokkaido, Japan, throughout the year because Pacific cod in this region are regarded to be a homogeneous breeding group.[7] The reproductive cycle was studied by histological investigation of the ovaries, as well as GSI values and age determination.[8]

Materials and Methods

Female Pacific cod were mainly collected by angling, bottom trawl net, bottom long-line, bottom gill net, and bottom set net in the waters off the southern and southeastern coasts of Hokkaido (including the Tsugaru Straits and Mutsu Bay) from April 1989 to September 1990 (Fig. 1). Collections were made at depths of 50 to 300 m on the continental shelf and in shallow bay waters.

Body length (scale-covered length), total body weight, eviscerated body weight, and ovary

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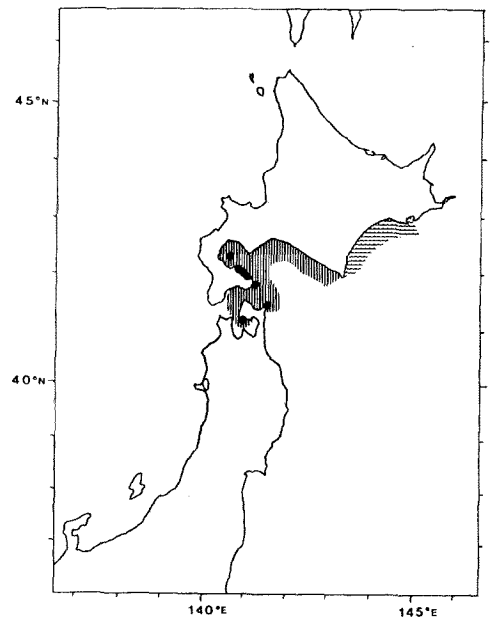

Fig. 1. Sampling areas off the southern coast of Hokkaido. Stripes indicate sampling area including sampling sites denoted by solid circles, and waves indicate sampling area investigated by trawl survey off the southeastern coast.

weight were collected and the gonadsomatic indices (GSI_1; ovary weight × 100/total body weight in g, GSI_2; ovary weight × 100/eviscerated body weight in g) were calculated for the 166 females.

Otoliths were kept in distilled water and were then used to determine age by sectioning.[8-10] Age is expressed as 1^+, 2^+, 3^+ . . . . on the assumption that January 1st was the date of birth of Pacific cod in the waters off the southern coast of Hokkaido.

The middle portions of ovaries from fresh fish were fixed in Bouin's solution. The fixed tissues were embedded in paraffin, sectioned at 8 μm by a standard method and stained with Delafield's haematoxylin and eosin. Prepared sections were examined under a light microscope.

Results

Characteristics of the Process of Oogenesis

The histological division of oogenesis in Pacific cod follows the oocyte growth of other gadoid fishes as has been reported in walleye pollock *Theragra chalcogramma*[11] and saffron cod *Eleginus gracilis*.[12] Previous authors have described twelve stages from oogonium to mature oocyte. The characteristics of Pacific cod oogenesis are described as follows.

Oogonia and oocytes in the chromatin-nucleolus stage exist in a cluster at the surface of the ovigerous lamella throughout the year (chromatin-nucleolus stage, Fig. 2A). At that time, the oocytes have a large nucleus and the very thin cytoplasm stain well with haematoxylin. The nuclei and oocytes are 25–50 and 40–80 μm in diameter, respectively. In early perinucleolus stage oocytes, the nucleus contains several nucleoli around the periphery of the nucleus (Fig. 2A). As maturation proceeds, the cytoplasm gradually increases in volume with oocyte growth, and the circular portion stain well with haematoxylin. This portion gradually moves from the edge of the nucleus to the periphery of the cytoplasm and the nuclei and oocytes are 50–100 and 80–200 μm in diameter, respectively (late perinucleolus stage, Fig. 2B). At an oocyte diameter of about 200–250 μm, small yolk vesicles occur on the periphery of the cytoplasm. The yolk vesicles increase in number and in volume with oocyte growth. The oocytes then become surrounded by the clear egg membrane (yolk vesicle stage, Fig. 2C). At an oocyte diameter of over 300 μm, circular yolk granules stained with eosin appear in the cytoplasm (primary yolk stage, Fig. 2D). They gradually accumulate and become distributed throughout the cytoplasm. Oocytes are 300–450 μm in diameter during the secondary yolk stage (Fig. 2E). At an oocyte diameter of about 500 μm, the yolk granules fill the cytoplasm. Oocytes are 700 μm in maximum diameter during the tertiary yolk stage (Fig. 2F). At the end of the vitellogenetic stage, the nucleus begins to displace toward the animal pole. The nucleus at this stage is an irregular half-moon shape. Oocytes are then 500–700 μm in diameter (migratory nucleus stage, Fig. 2G). After the migration of the nucleus to the periphery, the nuclear membrane disappears and no boundary is found between the nucleoplasm and the cytoplasm. Yolk granules begin to form a yolk mass and stain well with eosin. Oocytes are then 700–800 μm in diameter (pre-maturation stage, Fig. 2H). After that, the oocytes develop to 800–900 μm in diameter and complete fusion of yolk globules is seen (maturation stage, Fig. 2I). No adhesive substance was discernible between oocyte and follicular layer. Mature oocytes are thereafter ovulated into the ovarian cavity. Ripe eggs are the same in appearence

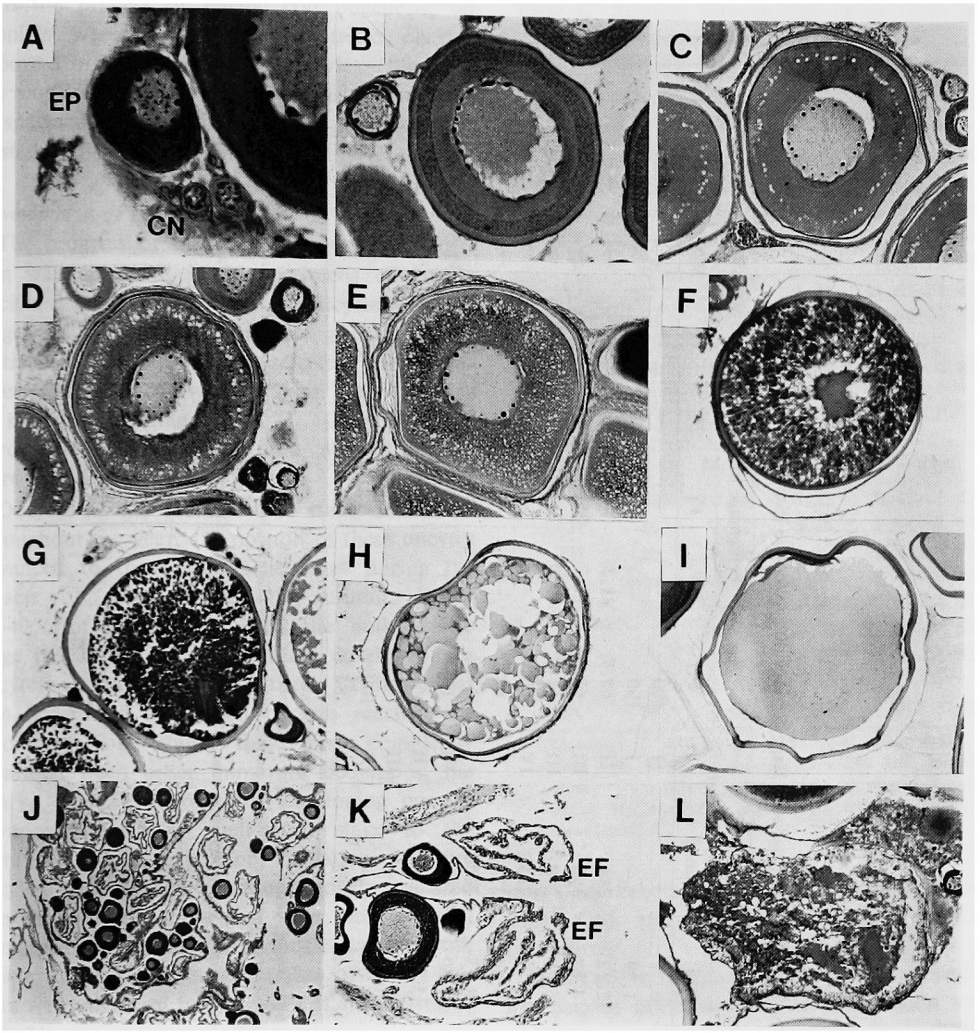

Fig. 2. Photomicrographs obtained from sections of Pacific cod ovary.

A: Oocytes at the chromatin-nucleolus stage (CN), and oocyte at the early perinucleolus stage (EP). ×373.
B: Oocyte showing the phenomenon of cytoplasmic zoning at the late perinucleolus stage. ×187.
C: Oocyte at the yolk vesicle stage. ×93.
D: Oocyte at the primary yolk stage. ×93.
E: Oocyte at the secondary yolk stage. ×93.
F: Oocyte at the tertiary yolk stage. ×37.
G: Oocyte at the migratory nucleus stage. ×37.
H: Oocyte at the pre-maturation stage with massed yolks. ×37.
I: Oocyte at the maturation stage. ×37.
J: Empty follicles in the ovary after spawning. ×37.
K: Empty follicles (EF). ×187.
L: Atretic oocyte. ×37.

as at the maturation stage except for the lack of an enclosing follicle. Eggs are adhesive in the ovarian cavity, and become 900–1000 μm in diameter. After ovulation, many empty follicles are observed in the ovigerous lamella (Figs. 2J–2K).

Table 1. The change of the oogenetic stage composition in female Pacific cod

Date	Loc.*1	Body length (mm)	GSI*2		Number of oocytes examined	Mat.*3	Percentage of oocytes at each stage*4							
			GSI_1	GSI_2			PN	YV	1Y	2Y	3Y	MN	PM	M
4 Apr., '89	UJ	461	0.49	0.71	—	I	100	—	—	—	—	—	—	—
18 Apr., '90	EN	617	1.04	1.29	—	I	100	—	—	—	—	—	—	—
7 Aug., '90	EN	624	2.16	2.52	214	II	68.7	31.3	—	—	—	—	—	—
6 Sep., '90	EN	640	3.92	4.68	198	III	62.6	11.7	25.7	—	—	—	—	—
27 Oct., '89	KN	658	4.58	5.78	270	III	61.1	10.0	28.9	—	—	—	—	—
27 Oct., '89	KN	655	5.43	6.73	213	IV	60.6	—	—	39.4	—	—	—	—
24 Nov., '89	EN	668	7.92	9.24	222	V	68.0	—	—	—	29.7	—	—	—
24 Nov., '89	EN	751	13.33	18.17	255	V	57.2	2.3	—	—	42.7	—	—	—
21 Dec., '89	OF	775	22.95	34.52	166	VI	67.5	—	—	—	—	32.5	—	—
23 Dec., '89	WW	670	24.46	35.49	114	VII	64.4	—	—	—	—	—	35.6	—
21 Dec., '89	OF	624	38.77	72.78	—	VIII	(++			Ovulation				++)
23 Jan., '90	EN	689	1.72	2.07	—	IX	100	—	—	—	—	—	—	—
23 Jan., '90	EN	760	1.90	2.24	182	IX	84.1	15.9	—	—	—	—	—	—

*1 Location: UJ (off Usujiri), EN (off Esan), KN (off Kinaoshi), OF (off Ohfune), WW (off Wakinosawa).

*2 Gonadsomatic index: GSI_1 = ovary weight × 100/total body weight; GSI_2 = ovary weight × 100/eviscerated body weight.

*3 Maturity: I, yolkless phase; II, yolk vesicle phase; III, early yolk formation phase; IV, middle yolk formation phase; V, late yolk formation phase; VI, migratory nucleus phase; VII, maturation phase; VIII, spawning phase; IX, spent phase.

*4 Oogenetic stage; PN, perinucleolus stage; YV, yolk vesicle stage; 1Y, primary yolk stage; 2Y, secondary yolk stage; 3Y, tertiary yolk stage; MN, migratory nucleus stage; PM, pre-maturation stage; M, maturation stage.

In the process of Pacific cod oogenesis, oil droplets were not observed. Atretic oocytes appeared in part of the yolky oocytes (Fig. 2L). We considered that most mature eggs would be spawned, however, because few atretic oocytes existed.

Development of Ovary

The progress of the oogenetic stage composition was examined in 50 specimens of female Pacific cod. The counting of oocytes at each stage was only carried out on eggs with clearly distinguishable nuclei and selected from continuous sections of ovary to avoid the possibility of replicate counting (Table 1). Oocytes at the chromatin-nucleolus stage and atretic oocytes were excluded from this analysis.

Oocytes at the perinucleolus stage dominated throughout the year. A portion of these oocytes advanced to the yolk vesicle stage during the season of summer through autumn. When 30–40% of oocytes achieved the yolk vesicle stage, part of the oocytes gradually developed into oocytes of the vitellogenic stage. Yolk formation progressed and when oocytes reached the secondary yolk stage, they were completely separated from other immature oocytes in the ovary. Their synchronously developing oocytes advanced from the vitellogenic stage to the maturation stage just before ovulation. Mature oocytes were thereafter simultaneously ovulated into the ovarian cavity and were then released. Immature oocytes at the perinucleolus and yolk vesicle stages and a large number of empty follicles were observed in the ovary of spent females (Fig. 2J).

Thus, Pacific cod exhibit a clear bimodal distribution of oocyte composition. This development form of oocytes is typical of the "group-synchronous oocyte development" type, as shown in rainbow trout *Onchorynchus mykiss*[13] and saffron cod.[12]

State of Maturity of Ovary

Since the form of development of oocytes of Pacific cod was typical of the "group-synchronous oocyte development" type, maturity was based on the oocytes of the most developed stage and was defined by nine grades, from yolkless to spent. The GSI_1 and GSI_2 values at each phase are given in Table 2 and the characteristics of each phase are as follows.

I. Yolkless phase: Oocytes at the perinucleolus stage have a diameter of less than 200 μm. Mean GSI_1 and GSI_2 values are 0.72 and 0.84, respectively.

II. Yolk vesicle phase: The group of developing oocytes progresses to the yolk vesicle stage when the oocyte diameter ranges from 200 to 250 μm. Mean GSI_1 and GSI_2 values are 1.96 and 2.22, respectively.

III. Early yolk formation phase: Developing oocytes reach the primary yolk stage when the oocyte diameter reaches 300 μm. Mean GSI_1 and GSI_2 values are 3.72 and 4.50, respectively. This phase corresponds to the time when immature fish recruit to the maturing fish group.

IV. Middle yolk formation phase: Developing oocytes reach the secondary yolk stage when the oocyte diameter becomes 300–400 μm. Mean GSI_1 and GSI_2 values are 4.60 and 6.24, respectively. The developing oocytes are visible with the naked eye, and are completely separated from immature oocytes.

V. Late yolk formation phase: Developing oocytes reach the tertiary yolk stage. The

Table 2. Relation between GSI values (GSI_1 and GSI_2) and maturity of female Pacific cod

Maturity*	N	GSI_1		
		Mean	S.D.	Range
I	47	0.72	0.19	0.35– 1.19
II	46	1.96	0.75	0.96– 4.11
III	10	3.72	1.17	2.24– 6.32
IV	4	4.60	1.73	1.91– 6.61
V	28	12.15	2.69	7.30–17.17
VI	7	20.84	4.31	11.47–24.79
VII	9	28.75	2.80	24.46–33.81
VIII	1	38.77	—	—
IX	14	2.55	0.89	1.55– 4.42

Maturity*	N	GSI_2		
		Mean	S.D.	Range
I	47	0.84	0.23	0.41– 1.43
II	46	2.22	0.74	1.10– 4.54
III	10	4.50	1.47	2.73– 7.98
IV	4	6.24	2.88	2.42–10.43
V	28	16.22	4.03	9.03–24.41
VI	7	30.09	7.00	15.08–36.68
VII	9	45.68	6.42	35.49–56.62
VIII	1	72.78	—	—
IX	14	3.01	1.07	1.91– 5.42

* *Maturity*: I, yolkless phase; II, yolk vesicle phase; III, early yolk formation phase; IV, middle yolk formation phase; V, late yolk formation phase; VI, migratory nucleus phase; VII, maturation phase; VIII, spawning phase; IX, spent phase.

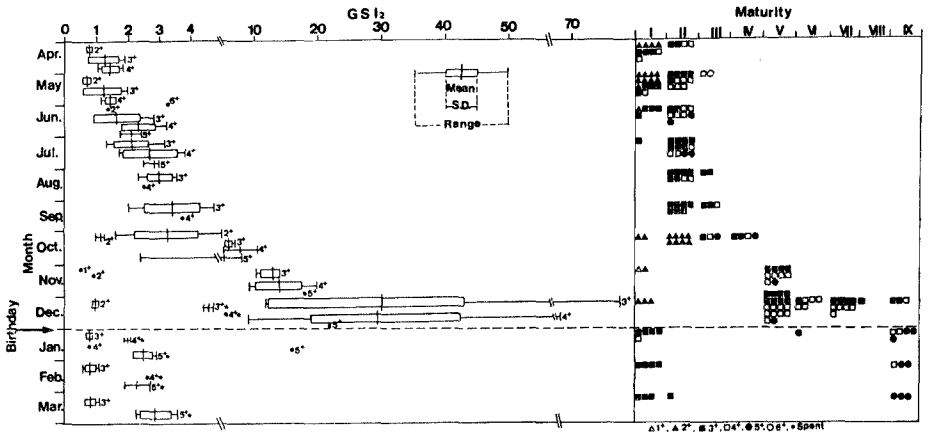

Fig. 3. Seasonal changes of GSI_2 values and maturity of female Pacific cod in the waters off the southern coast of Hokkaido.

Table 3. Comparison of the GSI_2 values and maturity of adult female Pacific cod in the waters adjacent to the southern coast of Hokkaido during the period December through February

	Date	Loc.*	N	Body length (mm)		GSI_2 value		Number of maturity				
				Mean	S.D.	Mean	S.D.	V	VI	VII	VIII	IX
1	Dec., '89	EN	5	625.0	60.2	11.09	5.06	5	0	0	0	0
14	Dec., '89	EN	2	655.5	—	18.25	—	2	0	0	0	0
19	Dec., '89	EN	8	665.0	35.6	20.11	2.47	8	0	0	0	0
21	Dec., '89	OF	9	685.6	59.1	32.72	16.74	3	4	1	1	0
23	Dec., '89	WW	13	681.6	38.6	34.74	17.71	0	2	8	0	3
23	Jan., '90	EN	6	695.2	35.6	4.44	4.77	0	1	0	0	5
22	Feb., '90	EN	3	716.7	47.2	2.44	0.37	0	0	0	0	3

* Location: EN (off Esan), OF (off Ohfune), WW (off Wakinosawa).

oocyte diameter ranges from 500 to 700 μm. Mean (maximum) GSI_1 and GSI_2 values are 12.15 (17.17) and 16.22 (24.41), respectively.

VI. Migratory nucleus phase: Ovaries are characterized by developing oocytes of the migratory nucleus stage, whose diameter is between 500 to 700 μm. Mean (maximum) GSI_1 and GSI_2 values are 20.84 (24.79) and 30.09 (36.68), respectively.

VII. Maturation phase: Developing oocytes reach the pre-maturation stage or the maturation stage, when the oocyte diameter ranges from 700 to 900 μm. Mean (maximum) GSI_1 and GSI_2 values are 28.75 (33.81) and 45.68 (56.62), respectively. The oocytes are transparent and are not ovulated into the ovarian cavity.

VIII. Spawning phase: Developing oocytes are ovulated into the ovarian cavity. The ripe eggs are recognizable with the naked eye. Under microscopic observation, the ripe eggs and many empty follicles are observed. GSI_1 and GSI_2 values are 38.77 and 72.78, respectively.

IX. Spent phase: After spawning, the ovarian capsule becomes thick and forms folds. The oocytes are then at the perinucleolus or the yolk vesicle stage, and many empty follicles can be observed by microscopic observation. Mean GSI_1 and GSI_2 values are 2.55 and 3.01, respectively.

Reproductive Cycle of Female Pacific Cod

Seasonal changes of GSI_2 values (GW×100/eviscerated body weight) and maturity were examined (Fig. 3). Because GSI_1 values are influenced by the change of stomach content weight, GSI_2 values were used in this analysis. Also, the age of each individual was used to examine the age at first maturation.

We found that the maturity of female Pacific cod gradually shifted from the yolkless phase to the yolk vesicle phase from April through August. Through these seasons, GSI_2 values also slowly

increased. In August, part of the 3^+ age group advanced in maturity to the early yolk formation phase, which showed the onset of active maturation. In October, the maturity of individuals over the 3^+ age group shifted to the active vitellogenic stage (middle yolk formation phase), but the maturity of females below the 2^+ age group remained at the yolk vesicle phase. In November, the GSI_2 values of the individuals over the 3^+ age group rapidly increased to 10–20, and their maturities reached the late yolk formation phase, the final stage of active vitellogenesis. After this, the GSI_2 values of individuals over the 3^+ age group rapidly increased to about 30 and the maturity of spawners shifted from the late yolk formation phase to the spent phase from early to late December (Table 3). In late December (21 and 23 December), individuals at the migratory nucleus phase, maturation phase, spawning phase, and spent phase were observed. By 23 January, the maturity of most spawners had shifted to the spent phase. By 22 February, no ripe females were observed.

From this analysis, the peak of Pacific cod spawning in this region was assumed to be from late December through January. Mature and spent conditions were not observed in fish below the 3 age group (2^+ age group before 1 January and 3^+ age group after 1 January). In other words, the age at first maturation of the female Pacific cod was estimated at four years.

Discussion

In this report, we describe the oogenesis and maturity of female Pacific cod based on histological examination. Also, the developing form of Pacific cod oocytes was thought to belong to the "group-synchronous oocyte develompent" type. This spawning cycle is the same as that of rainbow trout[13] and pelyad, *Coregonus peled*.[14] In the familiy Gadidae, those of saffron cod,[12] walleye pollock,[11] and Atlantic cod[15-17] belong to the "group-synchronous oocyte development" type. However, the change of oogenetic composition in Pacific cod was similar to that of saffron cod,[12] and was more synchronous than that of walleye pollock, which had a few oogenetic stages in the same ovary.[11] Pacific cod and saffron cod release all ripe eggs in a single spawning,[12,18] but walleye pollock spawn repeatedly with intervals of a few days during the spawning season.[19,20] Accordingly, differences of developing forms between the species would be reflected in the modes of spawning.

Using GSI values and maturity, we examined the reproductive cycle of female Pacific cod in the waters adjacent to the southern coast of Hokkaido. In this region, the ovaries of individuals at first maturation (3^+ age group) and the ovaries of individuals at the recovery stage (over 4^+ age group) gradually advanced to the yolk vesicle phase from spring to summer. The recruitment of individuals of the 3^+ age group occurred in October. The onset of yolk formation was synchronous among the individuals over the 3^+ age group, and the most active yolk formation occurred from October through November. After that, the maturity of spawners synchronously shifted from the late yolk formation phase to the spent phase during the period from early December through late December. In January, the maturity of most spawners shifted to the spent phase. Accordingly, the peak of Pacific cod spawning in this region was assumed to occur during the period from late December through January. Such a very short spawning season would imply that maturity between individuals is the same and synchronous. In this region, it is supposed that the main spawning ground is in the waters off Wakinosawa (Mutsu Bay, Aomori Prefecture) and part of the spawning ground is in the waters off Ohfune (Funka Bay, Hokkaido).

On the other hand, the spawning season of Pacific cod in other Japanese waters has been studied,[7,21-25] and the period of spawning seasons is longer than that found in our study. Recently, it was found that the spawning season in the Musashi Tai Region (Sea of Japan) is during February and the beginning of March.[3] The spawning season in the Musashi Tai Region is later than that on the Pacific Ocean side. It would be reasonable to assume that there are different stocks in the Sea of Japan and the Pacific Ocean, because the catch of this species in the Sea of Japan decreased but that of the Pacific Ocean increased during the 1960's and the 1980's.[18] Foucher and Westrheim[26] reported that the spawning season was relatively short and only slightly later in high latitudes such as the west coast of Canada. The tendency towards later spawning seasons in high latitudes was recognized in Japanese waters, as well.

It is likely that the variety of spawning seasons results from the exsistence of local stocks,[27] which are separated by the synchronous process

of ovarian development and a short spawning season.

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