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Reproductive Behavior of Pacific Cod in Captivity

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The reproductive behavior of Pacific cod (*Gadus macrocephalus*) was examined during captive experiments. The captive cod spawned demersal and slightly adhesive eggs, which dispersed and settled on the tank bottom. Ripe males and females did not display the ventral mounting behavior typically displayed in other gadid fishes during spawning. Neither sound production nor aggressive behavior occurred during the breeding period. The female released approximately all of her ripe eggs in a single spawning, which lasted less than 20 seconds. Spawning involved one female and one or more males in midwater of the tank. Just after release of eggs by a female, one or a few males followed the female and spread sperm on the eggs using tail beats. The eggs and milt slowly sank to the bottom.

The spawning behavior of Pacific cod differed from the single-pair spawning characterized by ventral mounting and multiple spawning over a several day period seen in walleye pollock and Atlantic gadid species.

Key words: Pacific cod, *Gadus macrocephalus*, spawning, reproductive behavior

The family Gadidae, with about 55 species, lives throughout the world, primarily in subarctic zones and at high latitudes.[1] Within Gadidae, the Genus *Gadus* is composed of three species: Pacific cod (*Gadus macrocephalus*), Atlantic cod (*G. morhua*), and Greenland cod (*G. ogac*). Pacific cod is widely distributed in the northern part of the North Pacific Ocean and adjacent waters, including 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 higher-trophic key species in the subarctic ecosystems.

Pacific cod inhabiting waters near northern Japan are known to migrate to spawning grounds characterized by shallow bay waters and silty or sandy bottoms.[3,4] Also, the spawning periods in the waters adjacent to the southern coast of Hokkaido and Mutsu Bay of the northern Honshu are assumed to be concentrated during December and January, based on analysis of the reproductive cycle.[5,6] Further, it is reported that the cod larvae and juveniles occurred in Mutsu Bay during spring and early summer and they fed on copepod nauplii, calanoid copepods and benthic prey items.[7]

Some studies on the nature of Pacific cod eggs were conducted, and it appears that Pacific cod spawn demersal and weakly adhesive eggs.[8,9] To date, there is no information about the reproductive behavior of Pacific cod in the natural habitat. A knowledge of the reproductive characteristics of Pacific cod is important for fisheries management, as it could assist the protection of spawning aggregations, the regulation of fishing seasons and area, and stock enhancement by the artificial propagation through ranching.

The present study aims to clarify the reproductive behavior of Pacific cod in captivity and compare it with the reproductive characteristics of other Pacific and Atlantic gadid fishes.[10-16] We were especially interested to know whether they produce sound when spawning as reported for other gadid fishes.

Materials and Methods

The breeding experiments of adult Pacific cod were carried out yearly during the spawning seasons from 1988 to 1991. All fish were collected from bottom set-nets off Usujiri and off Ohfune on the southwestern coast of Hokkaido, northern Japan. The fish were held in a 1,000 *l* circular tank and supplied with a flow of sea water during transport on a fishing boat to the harbor. The fish were transported from the harbor to a large maintenance tank at the Usujiri Fisheries Laboratory, Faculty of Fisheries, Hokkaido University using a 1,000 *l* tank on a truck.

The captive fish were measured for total body length (TL in mm), scale-covered body length (BL in mm) and total body weight (BW in g). The sex and maturity of individual fish were distinguished by inspection of germ cells sampled from the gonopore using a pipette. At the same time, females that had begun ovulation, evident by their fully expanded abdomens, were identified by the same method. Individuals were identified by tagging with thin vinyl color ribbon tags during 1988-1990 and anchor tags during 1990-1991 to the base of the dorsal fin before the fish were transferred to the large-sized maintenance tank (Table 1).

The living fish collected from the bottom set-nets were unable to swim to the bottom when placed in the tank, due to inflated swim bladders caused by decreased water pressure at the surface. Therefore, after being anesthetized by immersion in 0.1-0.2 ppm MS222 in sea water, the surplus gas in the bladder was released with a syringe. Syringes were inserted at the posterior dorsal side of the swim bladder, and special care was taken not to damage the swim bladder.

Table 1a. Measurements of captive Pacific cod used during the 1988–1989 experiment

No.	TL (mm)	BL (mm)	BW (g)	sex	tag	Remarks
1	676	628	3240	♀	S	not ovulated
2	668	623	3870	♀	Br	ovulated
3	650	608	3460	♀	3R	not ovulated
4	780	730	4800	♀	2R	not ovulated
5	755	712	5000	♀	3Y	ovulated
6	734	686	4800	♀	2Y	ovulated
7	735	696	4500	♀	1Y	not ovulated
8	714	666	4110	♀	3G	not ovulated
9	730	683	4400	♀	Re	not ovulated
10	583	545	2080	♂	Bl	sperm releasing
11	738	695	4200	♂	1R	sperm releasing

Measurements were carried out before spawning experiment on 19 December, 1988.

Table 1b. Measurements of captive Pacific cod used during the 1989–1990 experiment

No.	TL (mm)	BL (mm)	BW (g)	sex	tag	Remarks
1	704	663	4600	♀	1R	ovulated
2	720	678	4050	♀	1B	not ovulated
3	726	687	4500	♀	1Y	not ovulated
4	713	674	4600	♂	2Y	sperm releasing
5	690	636	3550	♀	2G	not ovulated
6	683	642	3700	♂	2B	sperm releasing
7	656	616	3000	♀	2R	ovulated
8	720	678	4350	♀	3G	not ovulated
9	693	553	3700	♂	3Y	sperm releasing
10	703	664	4400	♀	3R	ovulated
11	668	630	3450	♂	3B	sperm releasing
12	729	690	4550	♀	YY	not ovulated

Measurements were carried out before spawning experiment on 22 December, 1989.

Table 1c. Measurements of captive Pacific cod used during the 1990–1991 experiment

No.	TL (mm)	BL (mm)	BW (g)	sex	tag	Remarks
1	804	756	6550	♀	1	not ovulated
2	792	740	5750	♀	2	not ovulated
3	798	753	5680	♀	3	not ovulatod
4	784	726	4600	♀	4	ovulated
5	750	708	4400	♀	1-2	not ovulated
6	734	682	4850	♀	1-3	not ovulated
7	708	668	3300	♂	1-4	sperm releasing
8	721	671	4300	♂	2-3	sperm releasing
9	732	686	5320	♂	3-4	sperm releasing

Measurements were carried out before spawning experiment on 20 December, 1990.

Pacific cod were collected from the set-net off Usujiri and Ohfune.

The maintenance tanks used included a fabricated 5,000 *l* circular type during 1989–1990, and a raceway tank (5.5 m in length, 2.5 m in width, 1.2 m in depth, and 13,000 *l* in volume) during 1988–1989, and 1990–1991. The raceway tank had a semi-closed recirculating and filtering system, which allowed a continuous exchange of sea water to maintain water quality. Also, we attempted to imitate the muddy bottom found in the natural spawning ground to facilitate the spawning behavior by spreading brown-colored clothing and scattering muddy sand on the bottom of the tank during 1989–1991.

Experimental conditions including water temperature, salinity, pH and daily light cycle by artificial lighting with a timer were maintained at 6.4～7.6°C, 33～34‰, pH of 7.7～7.9 and 11L:13D, respectively. Moreover, we separated females from males by setting a opaque partition board at the center of the tank at night during 1990–1991, because we wanted to observe the spawning behavior of Pacific cod during the daytime.

Females were removed just after spawning from the tank, the body measurements were recorded, and the gonadosomatic indices (GSI=ovary weight × 100/total body weight) were calculated. The spawned eggs were used for the examination of fertilization rates. The behavior of the captive cods was recorded by three video-cameras (SONY, CCD-V900, 2 sets; National, Mackload VHS video-camera, 1 set).

In the winter of 1986, prior to this captive experiment at Usujiri laboratory, the sound production related to reproductive behavior was confirmed using a hydrophone (OKI, ST-8001) in a tank (30,000 *l* in volume) containing ripe Pacific cods (three females and five males) used for an artificial propagation at the Aquaculture Center of Aomori Prefecture.

Results

Behavior of Pacific Cod before Spawning

Most of the male Pacific cod used were fully matured and could release sperm, and females were ready to ovulate or had already ovulated (Table 1). Captive Pacific cods did not form schools. Each individual swam slowly without making a shoal, and males sometimes followed females. In other words, during most observation periods, solitary swimming without aggressive or courtship behavior was common. The frequency of aggressive or courtship behavior between individuals was very low during the entire observation period.

Interactions between individuals of Pacific cod before spawning are described in brief as follows. Females did not follow or make contact with males, but swam slowly in the tank. The abdomen of a female before spawning fully expanded with the ovulation of hydrated ripe eggs into the ovarian cavity, and the female's gonopore conspicuously protruded just before spawning. At this maturation stage, females represented a up-and-down swimming behavior along the wall of the tank. Behavior evident of rank formation, like the pushing and prodding seen in other gadid species, was scarcely observed in the Pacific cod males. A few dorsal mounts between males were observed. The mount involved a male swimming beside another fish, and rubbing his ventral surface against the dorsal and occasionally lateral surface of another fish, as if holding the other fish with his pectoral fins. The mounts between males were performed by a male exhibiting the mount against a female.

A frequent and characteristic behavior displayed before spawning included a male following and approaching a female while performing an abrupt up-and-down swimming behavior. After this behavior, a few males were often observed to perform dorsal and lateral mounts of the female, but oviposition did not occur during these occasions. Although a male sometimes flaunted his body to a female after his approach and mount, there were no observations

Table 2. Frequency of aggressive (A) and courtship behavior (B) of male Pacific cod in captivity

A. Frequency of aggressive behavior to other males

Behavior*1	Beginning*2	Ending*3
Approach	0	0
Prodding or pushing	0	0
Dorsal mounting of a male	3	0
Lateral mounting of a male	0	0
Total	3	0

B. Frequency of courtship behavior to ripe females

Behavior*1	Beginning*2	Ending*3
Following after female	24	2
Flaunting display to female	2	0
Circling or leading	0	0
Dorsal mounting of a female	5	0
Total	31	2

*1 See the text for details.
*2 Observation (total 30 minutes) of behavior at beginning of experiment on 25 December 1989 (5 males and 2 ripe females).
*3 Observation (total 30 minutes) of behavior at ending of experiment on 8 January 1990 (3 males and 1 ripe female).

of spawning after performing the flaunting display to a female.

We compared the cod behavior patterns at the beginning and the end of a spawning season. As shown in Table 2, the following of females by males was observed only two times at the end of the experiments. At the beginning of the experiments, there were only 3 instances of dorsal mounting of a male by another male. There were 5 instances of dorsal mounting of a female by a male, 2 instances of flaunting display of the male before a female, and 24 instances of the male following and approaching a female.

From these results, it appears that the behavior of Pacific cod before spawning is characterized by slow swimming of fish, with males following and approaching females.

Spawning Behavior of Pacific Cod

Five spawning bouts including the release of milt and eggs, were observed and recorded by video-cameras during the experimental period from 1988 to 1991. Details of the spawning behavior witnessed on 26 December 1990, are described below (Fig. 1). The figures drawn were traced from photographs.

The behavior of Pacific cod just before spawning was characterized by following and approaching a ripe female by a male, and up-and-down swimming behavior by the female. The female began up-and-down swimming 16 minutes before spawning. Eleven minutes before spawning the female slowly swam near the surface, making a large circle. The diameter of this circle gradually decreased to about 1 m in diameter. Although males followed the ripe female, aggressive behavior between males was not observed. When the female began to release eggs and beat her tail at the surface (Fig. 1-A), one male responded by approaching the female, and as soon as his snout touched the spawned eggs (Fig. 1-B), milt was released by the male accompanied by powerful tail beats (Fig. 1-C, D). The time lag between the release of eggs and sperm release was about 8 seconds. Afterwards, the male continued releasing sperm for several seconds (Fig. 1-E). The mass of eggs and sperm appeared to form a large dense cloud in the water, sank slowly, and scattered on the bottom. The spawning act was completed in about 18 seconds, and the fertilization rate of eggs was 89.2%. Individuals not involved in the spawning swam to the bottom as if avoiding the cloudy water mass.

Thus, the spawning behavior of Pacific cod in captivity does not include ventral mounting by the males, a common behavior of walleye pollock and Atlantic gadid species. In general, the spawning behavior of Pacific cod involves one or several males following a single female. The spawning of Pacific cod in captivity was observed to occur at the surface, and the spawned eggs sank slowly at a speed of 7.5 cm per second. When the water clouded by milt became clear after about an hour, spawned eggs were settled and dispersed on the bottom and lost their weak adhesiveness, and the post-spawning female rested on the bottom near the corner of the tank. From these observations, it appears that spawned eggs do not have a strong adhesive substance on the egg membrane that attaches to substratum, such as algae, and settle separately on the bottom.

During observation of spawning behavior in 1986, we examined whether sound was produced by ripe females and males during the reproductive period, including before and after spawning, but no sound production related to reproductive behavior was confirmed.

Reproductive Characteristics of Spawning of Pacific Cod

The period from ovulation to spawning was examined during each breeding experiment (Fig. 2). The ovulation of females was confirmed by inspection of germ cells sampled from the gonopore using a pipette and estimated from the condition of the fully expanded abdomen. Most spawning occurred 3 to 5 days after ovulation, with a maximum of 8 days. If more than 11 days passed after ovulation, females could not spawn because the eggs ovulated in the ovarian cavity became overripe. It is estimated that a female will spawn ripe eggs within a week after ovulation. Fifteen of the 21 spawnings observed during the experimental period from 1988 to 1991 occurred continuously, and others occurred individually (Fig. 3). It is suggested that a ripe female would spawn synchronously if several ripe females were present at the same time and placed at the natural spawning ground. Also, almost all ripe eggs are released in a single spawning. The number of unspawned ripe eggs in the ovarian cavities of spent females were very low and the GSI values of spent females ranged from 5 to 6 (Table 3), which is a little higher than that of naturally spent fish.[5]

Based on the results of spawning experiments shown in Fig. 3, the spawning dates of Pacific cod in experiments during 1988–1989, and 1989–1990 were examined (Fig. 4). The data from experiments in 1990–1991 were not included because females were separated from males by an opaque board placed in the center of the tank at night. Spawning dates were concentrated in late December and early January, especially during 25 December to 2 January (12 of 16 spawnings). Also, many spawnings occurred at

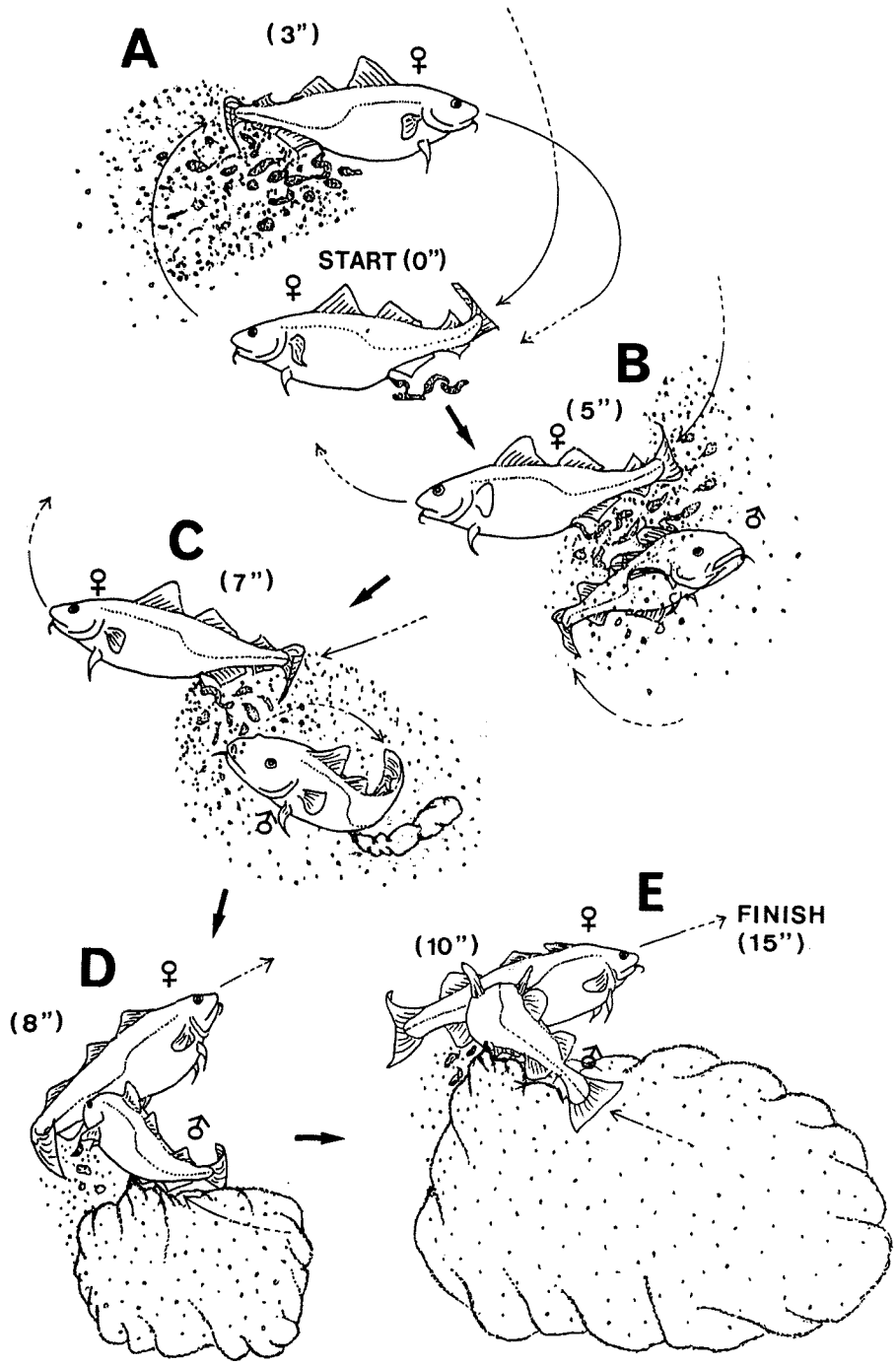

Fig. 1. Spawning behavior of Pacific cod in captivity observed in December 1990.
The figures were traced from photographs. Number in parentheses indicates the time (in seconds) after egg release by the female. See the text for details.

night (12 of 16 spawnings).

Discussion

Despite the long history of the fishery, we have little knowledge about the biology, especially reproduction, of Pacific cod in northern Japan. However, spawning aggregations that occur in winter allow the identification of several populations among the coast of Notojima in the middle of the Sea of Japan, and elsewhere,[4] and the spawning grounds are known to be characterized by shallow bay waters and silty or sandy bottoms.[3]

A relatively well-known stock is the so-called Pacific stock inhabiting the Pacific coast of Hokkaido Island. The distribution of this stock extends widely from off the northeast of Hokkaido to Mutsu Bay, northern Honshu Island, and the seasonal migratory route is known from tagging experiments.[17] The peak of spawning of this stock is

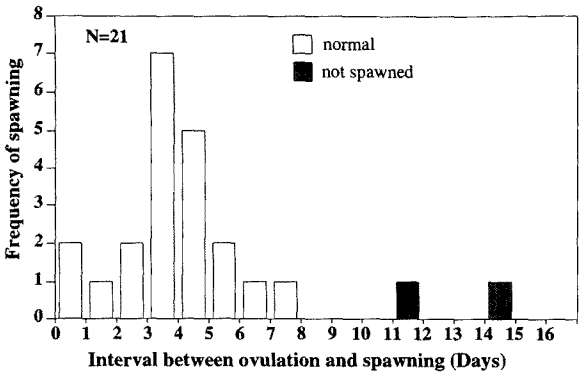

Fig. 2. Interval between ovulation and spawning of captive Pacific cod in the 1988–1991 experiments.

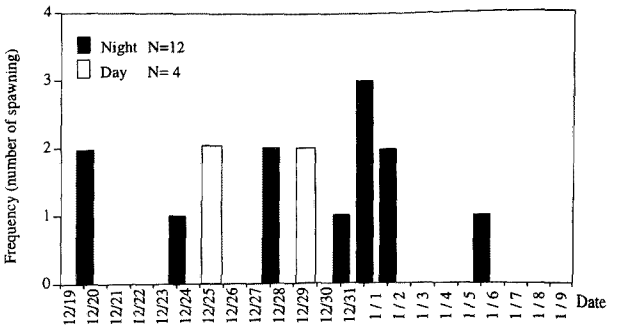

Fig. 4. Spawning dates of captive Pacific cod in the 1988–1990 experiments.

assumed to occur in the mouth and inner part of Mutsu Bay during late December through January.[3,5,6] The dominant spawning age groups are composed of 4-, 5- and 6-year olds (about 500–850 mm in BL).[18,19] In this study, the age composition of the captive cod observed in the spawning experiments were estimated to be 4 and 5 years, based on the range of 545 mm to 760 mm in BL.

Thus, the spawning of Pacific cod in the natural habitat is characterized by the aggregation of ripe fish in shallow coastal waters having a silty-sandy bottom during a short period in winter. In this study, we observed that Pacific

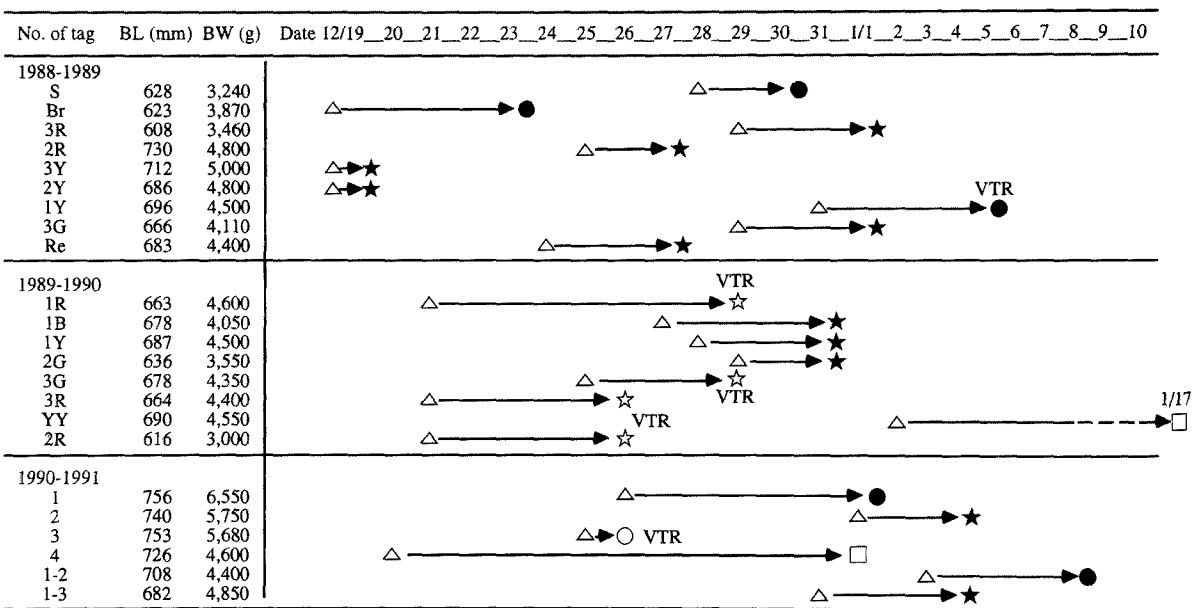

Fig. 3. Summary of observations of spawned female pacific cod, showing the dates of ovulation and spawning in the 1988–1991 experiments.

Table 3a. Measurements of female Pacific cod after spawning experiment in 1989–1990

Tag no.	Date of measurement	TL (mm)	BL (mm)	BW (g)	Liver W.	Gonad W.	Gutted W.	GSI	age	Remarks
1R	1/4/90	708	666	3220	200	160	2600	4.97	—	spent fish

Table 3b. Measurements of female Pacific cod after spawning experiment in 1990–1991

Tag no.	Date of measurement	TL (mm)	BL (mm)	BW (g)	Liver W.	Gonad W.	Gutted W.	GSI	age	Remarks
1	1/2/91	—	760	5150	410	300	4100	5.83	5	spent fish
3	12/26/90	802	760	4550	240	250	3800	5.49	5	just after spawning
1-2	1/9/91	750	705	3600	160	210	3050	5.83	5	spent fish
1-3	1/5/91	740	689	4080	300	248	3320	6.08	5	spent fish

cod females release approximately all of their eggs, which are demersal and slightly adhesive, in a single spawning within 20 seconds, and spawn synchronously when several ripe females are present with ripe males. Also, we observed that a female will spawn ripe eggs within a week after ovulation, with most female spawning 3 to 5 days after ovulation. This delay from ovulation to spawning might be caused by captive stress. Further, the pre-spawning behavior involved a single female and one or several males in the midwater of the tank and after spawning, eggs and milt slowly sank, and were scattered on the bottom. Therefore, Pacific cod require a suitable bottom type, namely silt or sand, as well as suitable conditions in the water column (e.g. temperature and salinity) to ensure successful reproduction. Spawning groups must then aggregate in the limited areas with suitable physical conditions, so the duration of spawning will be concentrated in a short period.

We compared the reproductive characteristics among Pacific and Atlantic gadid species. Based on the nature of spawned eggs and the reproductive styles, these fishes can be grouped into two types. The first type includes those which produce pelagic and separate eggs. This type includes Atlantic cod, *Gadus morhua*,[20-23] haddock, *Melanogrammus aeglefinus*,[10,24] and walleye pollock, *Theragra chalcogramma*.[12-14,25] In these species, spawning behavior is characterized by a typical ventral mounting behavior with vent-to-vent contact between a male and female pair. In addition, these fishes are multiple spawners, which spawn eggs at intervals of a few days over a few months. During spawning, these species produce sound using drumming muscles attached to swim bladder[10,11,15,16,26,27] and exhibit body color changes. In addition, each species has species specific courtship patterns, and displays aggressive behavior.

The second type includes Pacific cod and saffron cod, *Eleginus gracilis*, which lay slightly adhesive demersal eggs that settled on the sea bottom. The fishes of this type do not display the ventral mounting behavior during the spawning act. Neither sound production nor aggressive behavior occurs during spawning. Pacific cod and saffron cod[28] release most of their ripe eggs in a single spawning within a few minutes. Further, the spawning behavior of these two species involves a single female and one or more males. After release of ripe eggs by the female, one or several males spread sperm on the eggs using tail beats. These distinct characteristics are considered remarkable different from those of the single-pair spawning behavior, characterized by ventral mounting, in walleye pollock[12-14] and other Atlantic gadid species.[10,21]

Within the same genus *Gadus*, it is interesting to note that the reproductive characteristics of *G. morhua* of the North Atlantic Ocean and *G. macrocephalus* are extremely different. However, the reproductive characteristics of *G. ogac*, which lives in the fjords and coastal waters of Greenland, are not well-known, except that the species spawns demersal eggs.[29] This species has been called a morphological sister species of *G. macrocephalus*.[30] Grant and Ståhl[31] reported that Pacific cod experienced a severe population bottleneck that led to the loss of gene diversity and gene expression, based on an allozyme investigation in Atlantic and Pacific cod. They also suggested that Pacific cod dispersed into the Pacific Ocean soon after the Bering Strait opened in the mid-Pliocene. The reproductive characteristics of Pacific cod may have drastically shifted from those of Atlantic cod during the process of species differentiation.

Recently, Pacific cod resources have been given much attention regarding stock enhancement and restocking in the coastal waters of Japan, including artificial propagation and fisheries management. The results of this study may help in the enhancement of the stocks and management of the fishery.

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