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Author(s)	Sakurai, Yasunori; Ishii, Kiyohiko; Nakatani, Toshikuni; Yamaguchi, Hidekazu; Anma, Gen; Jin, Masato
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15. Reproductive Characteristics and Effects of Temperature and Salinity on the Development and Survival of Eggs and Larvae of Arctic Cod (*Boreogadus saida*)

Yasunori SAKURAI¹⁾, the late Kiyohiko ISHII, Toshikuni NAKATANI¹⁾,
Hidekazu YAMAGUCHI¹⁾, Gen ANMA¹⁾ and Masato JIN²⁾

¹⁾ Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041-8611, Japan

²⁾ Aomori Prefectural Asamushi Aquarium, Babayama 1-25, Aomori 039-35, Japan

Abstract

In the summers of 1991 and 1992, live Arctic cod (*Boreogadus saida*) captured by bottom trawling south of St. Lawrence Island were transported to a laboratory at Hakodate, Hokkaido, Japan, when they were maintained in a small aquarium at -0.2 to 3.0°C until they spawned or were used for artificial fertilization. The embryonic development and survival of larvae were examined at five temperatures (-1.0 to 9.0°C) at 32-33 psu and six salinities (3.3 to 62.6 psu) at 1.5°C. Female released all ripe eggs during spawning. Eggs were non-adhesive, pelagic and ranged in diameter from 1.5-1.7 mm. Most spawned females and males stopped feeding, weakened and died, but a few survived and spawned again one year later. Normal embryonic development occurred between -1.5 and 3.0°C, with highest embryonic survival rates (> 65%) occurring between 0.5 and 3.0°C. The number of days to 50% hatching were 75 at -1.0°C, 44 at 1.5°C, and 35 at 3.0°C. At 1.5°C, normal embryonic development occurred at salinities between 12.9 and 51.6 psu, with highest survival rates (>70%) occurring at 32.1 and 40.8 psu, and lowest survival rates (<20%) occurring at 12.9, 22.5, and 51.6 psu. Newly hatched larvae survived longer at temperatures below 0.5°C and at a wide range of salinities from 12.9 to 40.8 psu.

Key words: long-term maintenance, captive spawning, artificial fertilization, normal embryonic development, optimum temperature and salinity range

Introduction

Arctic cod (*Boreogadus saida*) is abundant throughout circumpolar arctic seas and a key component in arctic marine food webs (Hobson and Welch, 1992; Hop et al., 1997a), such as in arctic Canadian, Alaskan and Russian waters (Ponomarenko, 1968; Wolotira et al., 1977; Lowry and Frost, 1981; Welch et al., 1992). Despite the importance of Arctic cod in arctic marine food webs, little is known about its natural history, particularly regarding reproduction and its early life stages (Hop et al., 1995), since Arctic cod typically spawn under the ice in the darkness of the Arctic winter (Rass, 1968). Spawning occurs from late December to late March with a peak occurring in January-February in the Barents Sea (Rass, 1968), northern Alaskan waters (Craig et al., 1981) and arctic Canadian waters (Hop et al.,

1995).

Arctic cod eggs develop near the surface, beginning under the ice cover and ending near the surface in ice-free areas after melting of the ice cover (Rass, 1968). Environmental conditions under the ice where embryonic development occurs are uniformly cold ($\leq 0^{\circ}\text{C}$). However, the early life stages after hatching must be tolerant of widely fluctuating temperatures and salinities that occur with ice breakup and melting (Drolet et. al., 1991; Pondon and Fortier, 1992; Gilbert et al., 1992). The reproductive success of Arctic cod will depend on physical and biological conditions at the spawning and nursery grounds, including the distribution of ice and the location of the ice edge. To clarify the environmental factors controlling the reproductive success of boreal and arctic fishes, laboratory experiments have been conducted to examine the influence of temperature and salinity on mortality in the critical early life stages from fertilization to after hatching (Holliday and Blaxter, 1960; Laurence and Rogers, 1976).

Recent laboratory experiments on Arctic cod have examined feeding (Hop et al., 1997), spawning energetics (Hop et al., 1995), reproduction and larval biology (Graham and Hop, 1995). Experimental work has also focused on embryonic and larval development, and its relation to temperature, salinity and food consumption (Doroshev and Aronovich, 1974; Aronovich, 1974; Altukhov, 1981; Graham and Hop, 1995). However, no study has determined the optimum temperature and salinity range for embryonic and larval development and survival. In this study, we examined the reproductive characteristics and the effects of temperature and salinity on the development and survival of Arctic cod embryos and larvae reared after captive spawning and artificial fertilization.

Materials and Methods

During Chukchi Sea and Bering Sea surveys by the T/S *Oshoro Maru* of the Faculty of Fisheries, Hokkaido University in the summers of 1991 and 1992, Arctic cod were caught by bottom trawling south of St. Lawrence Island, near 63°N , 173°W . Depths and temperatures of the sampled area ranged between 41-50 m and -1.0 to -1.6°C , respectively. Live Arctic cod ($n=23$ in 1991, size range 143-185 mm in BL; $n=20$ in 1992, size range 122-190 mm) collected in late July of both years were kept for about 3 weeks in a 80-L holding tank at about 3°C on board as they were transported live to the Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, Japan. The fish became accustomed to feeding on chopped frozen shrimp (*Argis lar*) fillets within a week after being caught.

In 1991, two Arctic cod (male and female) were kept at a laboratory in Hakodate (H), and 21 were transported from Hakodate to the Asamushi Aquarium (AA), Aomori, Japan. We used the same shipping method as described by Hop et al. (1997b). The transit time to AA was about 6 hrs, and there was no mortality during transport. In 1992, eight adult Arctic cod were maintained at H and 12 were kept at AA. The fish were kept in a 20-L tank (in 1991) and 40-L tank (in 1992) in a incubator at H and in a 180-L tank at AA (in 1991

and 1992). Water temperatures ranged from 1.0 to 3.0°C at H and -0.2 to 3.0°C at AA. Salinities ranged from 32 to 34 psu. Water quality in tanks was maintained by a filtering system and by adding filtered seawater *ad libitum*. Fish were fed chopped frozen shrimp (*Pandalus borealis*) fillets at LH and frozen krill (*Euphausia superba*) and frozen fish fillets (*Pleurogrammus azonus*) at AA, three or four times per week until they spawned or were used for artificial fertilization. two fish at H and five fish at AA were maintained through spawning, which occurred in February 1992. five fish at H survived after spawning in 1993. eight fish at AA did not spawn in 1993, although five of these fish survived after spawning in 1994.

Table 1. Summary of female Arctic cod (*Boreogadus saida*) spawned or used for artificial fertilization during captive experiments from 1991 to 1995. BL: Body Length. BW: Body Weight. Age: Age in years.

No.*	Date of spawning	Date of death	BL (mm)	BW (g)	Age	Lab.**
1	9 February 1992	15 June 1992	190	58.3	5	AA
2	14 February 1992	15 June 1992	157	30.2	4	AA
3	17 February 1992	14 April 1992	153	17.9	4	H
4	23 February 1993	6 April 1993	194	40.8	6	H
5	1 March 1994***	5 June 1995	220	-	?	AA

*No.1, 2 and 3 fish were collected in late July of 1991, and No.4, 5 fish were collected in late July of 1992, south of St. Lawrence Island.

** AA: Asamushi Aquarium, Aomori, Japan, H: Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, Japan.

***Date of artificial fertilization.

Captive spawning of Arctic cod, collected in the summer of 1991 occurred at H on 17 February 1992, and two females at AA spawned on 9 and 14 February (Table 1). One fish (185 mm in BL) collected in 1992 spawned at H on 23 February 1993. In 1993, about 8,000 newly fertilized eggs at the first cleavage stage were collected with a small plankton net from the tank and kept in a separate aquarium to examine the effects of temperature on embryonic development and larval survival. Two 2-L plastic jars containing about 500-1,000 eggs at first cleavage stage were maintained in incubators at -1.0, 0.5, 3.0, 5.0, 7.0 and 9.0°C (Table 2). Temperatures were maintained within $\pm 0.2^\circ\text{C}$ and salinities ranged from 32 to 33 psu. The fertilization rate at the start of the experiment was 54%.

On 2 March 1994, we artificially fertilized eggs extracted from a 210-mm BL female at AA, that had been collected in 1992, to examine embryonic development and larval survival in different salinities at 1.5°C. About 14,000 eggs were collected, of which about 90% were fertilized. Some fertilized eggs were transported from AA to H. Eggs were put in a plastic bag that contained about 2-L of seawater. The bag was filled with oxygen prior to

Table 2. Arctic cod embryonic development at different temperatures and salinities, 1993-94.

Mean temp (°C)	Mean salinity (psu)	Fertilization date	Female BL (mm)	No. eggs	Survival(%) at 50% hatching	Development
Temperature experiments						
- 1.0	32.5	23 February 1993	185	1,058	38.8	normal
0.5	32.5	23 February 1993	185	915	68.0	normal
1.5	32.1	1 February 1994	210	3,696	82.3	normal
3.0	32.5	23 February 1993	185	1,192	67.5	normal
5.0	32.5	23 February 1993	185	2,072	0.1	abnormal of caudal part
7.0	32.5	23 February 1993	185	1,200	0	none after the second cleavage
9.0	32.5	23 February 1993	185	1,006	0	none after the second cleavage
Salinity experiments						
1.5	3.3	1 March 1994	210	1,409	0	none after the second cleavage
1.5	12.9	1 March 1994	210	1,618	6.2	delayed hatching
1.5	22.5	1 March 1994	210	1,716	31.3	normal
1.5	32.1	1 March 1994	210	3,696	72.7	normal
1.5	40.8	1 March 1994	210	1,934	85.2	normal
1.5	51.6	1 March 1994	210	1,906	13.4	normal
1.5	62.6	1 March 1994	210	1,616	0	none after Stage-I

sealing and placed inside a 10-L insulated cooler that had a layer of snow on the bottom. The shipping time to Hakodate was about 5 hrs. After arrival at H, a few 1-L glass jars containing about 500-1000 eggs at the first cleavage stage were maintained in incubators at 1.5°C in seven salinity units (3.3, 12.9, 22.5, 32.1, 40.8, 51.6 and 62.6 psu) (Table 2). Low salinity water was made by adding distilled water to filtered seawater. High salinity water was made by adding sodium chloride to filtered seawater. Salinities for each incubation jar were determined at the beginning and end of each incubation period to monitor any changes. Hatchlings of the incubation unit at 32.1 psu and 1.5°C in 1994 were used for temperature experiments in 1993.

During the 1993 and 1994 experiments, the water in these jars was changed once a day, at which time the development stages were observed and the dead eggs and larvae, and

unfertilized eggs were counted and removed. The incubation jars were covered to minimize evaporation. Embryonic developmental rates were compared at different temperatures and salinities. Embryos were classified within the scheme of developmental stages for Arctic cod given by Altukhov (1981) and walleye pollock (*Theragra chalcogramma*) by Yusa (1954). The staging classification used in this study is as follows:

Stage- I First gastrula stage

Stage- II The germ ring reaches over the equator. The germinal ring and embryonic axis are formed.

Stage- III Length of the tail reaches over the equator. The pupils are visible in both eyes.

Stage- IV Length of the tail reaches three-quarters of the egg circumference and the heart starts pulsating.

Stage- V Embryo fills the whole egg and the tail touches the head.

Stage- VI First hatching. Length of the tail is beyond the head Pigment bands on tail become prominent.

Stage- VII 50% hatching. The number of hatched embryos equals the number of live unhatched embryos (Laurence and Rogers, 1976; Sakurai et al., 1996).

Stage- VIII 100% hatching.

Results

Reproductive characteristics

Arctic cod collected in 1991 spawned during 9-17 February 1992 and fish collected in 1992 spawned on 23 February 1993 (Table 1). Females released most of their eggs in a single spawning at night, but fecundity could not be calculated because some of the released eggs were lost during collection. These spent females and males survived after spawning, but gradually stopped feeding, weakened and died in April 1992, or by June in 1993. Eight fish did not spawn in 1993, and five fish of these survived to the following year. Because the body lengths of Arctic cod collected in 1992 ranged from 122 mm to 190 mm, most of captive fishes were assumed to be immature. Captive Arctic cod spawned during the same month as wild fish, despite the different light regimes (H: continuous darkness, AA: approximately 12L and 12D cycle) and temperatures.

Interactions between individuals (three females and two males) before spawning are described below, but actual spawning was not observed. The abdomen of a female gradually began expanding one month before spawning, and fully expanded with the ovulation of hydrated ripe eggs into an ovarian cavity. Males occupied the central part of the tank. The fish swam slowly and did not form schools. The color of the abdomen of dominant males was whitish, but the body surface color of the other males and females was uniformly black. Males often followed and approached females before spawning. Spawned eggs were non-

adhesive, contained no oil globule, pelagic and ranged in diameter from 1.5-1.7 mm. The newly hatched larvae, at 50% hatching, were 5-6mm long in TL.

Effects of temperature on egg and larval development

Fertilized eggs spawned at 2°C in 1993 were gradually acclimated to each temperature unit between -1.5 and 9°C, using intermittent temperature units. Temperature acclimation was not done for artificially fertilized eggs at 1.5°C in 1994 since this temperature was maintained during experiments. Normal early development to Stage- II occurred between -1.5 and 5°C, but at 7°C and 9°C, egg development stopped at the first or second cleavage stage and the eggs died (Table 2). Embryonic development was highly temperature dependent (Fig.1). Normal development to 100% hatching (Stage- VIII) occurred at -1.0 and 3°C. At 5°C, most development ceased at Stage- II, but a few embryos survived through hatching. In these embryos, organogenesis was delayed and abnormal, particularly in the development of the embryonic caudal parts.

The number of days from fertilization to 50% hatching (D) against incubation temperature (T) was compared to similar data for Saffron cod (*Eleginus gracilis*) (Chen, 1989) and walleye pollock (Nakatani and Maeda, 1984) (Fig.2). The relationship between temperature and embryonic development can be expressed as an exponential function: $T=59.53EXP(-0.16D)$. The number of days from fertilization to 50% hatching was 75 at -1 °C, 54 at 0.5°C, 44 at 1.5°C, and 35 at 3°C. The sequential changes in egg and larval mortality at temperatures from -1.0 to 5°C are shown in Fig 3. Through this temperature range, mortality rates before 50% hatching were below 30% from 0.5 to 3°C, but over 60% at -1°C and over 99.9% at 5°C. During embryonic development, high mortality at each temperature unit occurred by Stage- III, partially at Stage- II.

The survival rate for unfed larvae from the 50% hatching date until 70 days post-hatching was temperature dependent (Fig.4). At 20 days after 50% hatching it was 80% at 1.5°C, and it was about 70% at 0.5 and 3°C, or similar to the rates at 50% hatching. However, survival of larvae between -1.0 and 3.0°C after 30 days from 50% hatching was high only at the cold temperature range below 0.5°C, and 10% of the larvae still survived after 70 day at -1°C.

The effects of salinity on egg and larval development

Egg and larval mortality rates at salinities between 12.9 and 62.6 psu at 1.5°C are shown in Fig.5. Normal embryonic development to 100% hatching (Stage- VIII) occurred at salinities between 12.9 and 51.6 psu, with higher survival rates occurring at 32.1 (72.7%) and 40.8 psu (85.2%), and lower survival rates occurring at 12.9 (6.2%), 22.5 (31.3%), and 51.6 psu (13.6%) (Table 2). Egg development at 3.3 psu stopped after the second cleavage stage, and embryos kept at 62.6 psu did not develop past Stage- I . High mortality during embryonic development occurred before Stage- II, especially at 12.9, 22.5, and 51.6 psu.

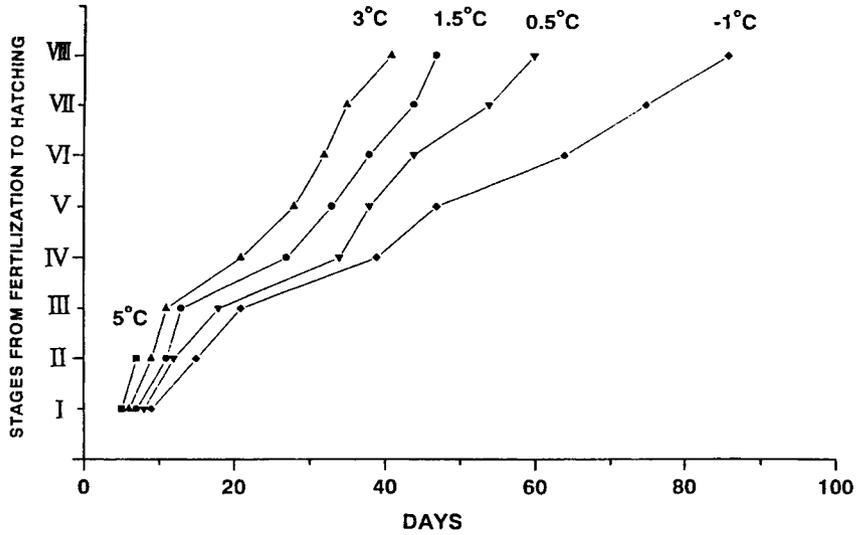


Fig.1. Course of embryonic development at five incubation temperatures in Arctic cod (*Boreogadus saida*).

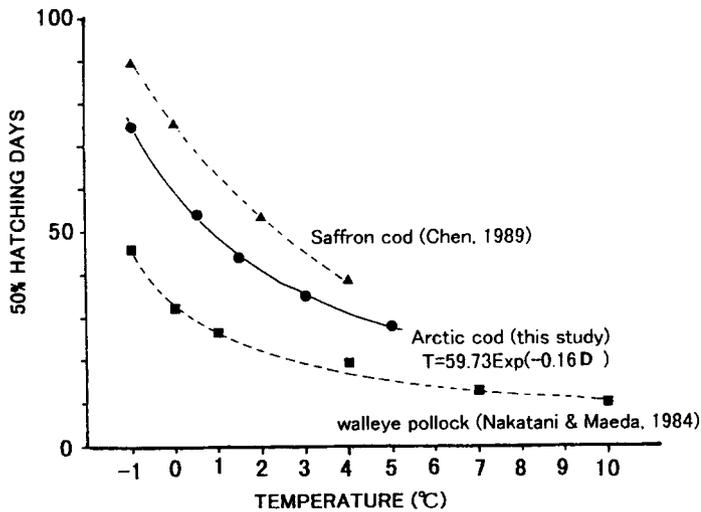


Fig.2. Relationship between number of days to 50% hatching and temperature for Arctic cod, walleye pollock (*Theragra chalcogramma*) and saffron cod (*Eleginus gracilis*).

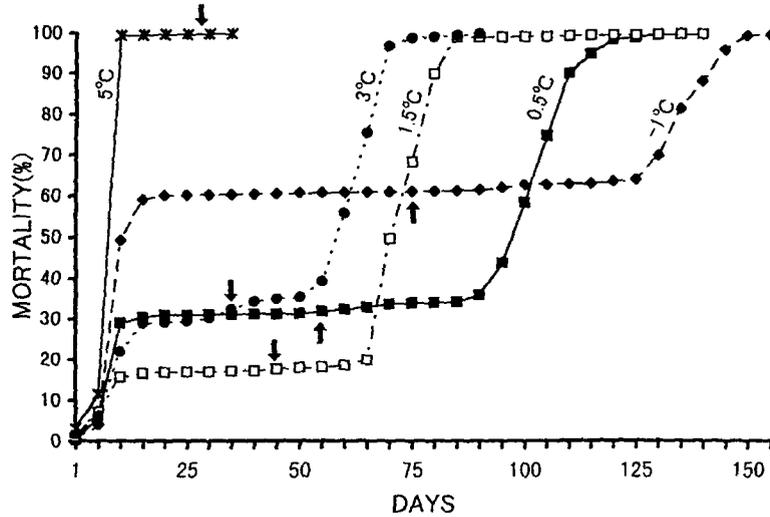


Fig.3. Arctic cod eggs and larval mortality rates at temperatures between -1 and 5°C. Arrow indicates 50% hatching day.

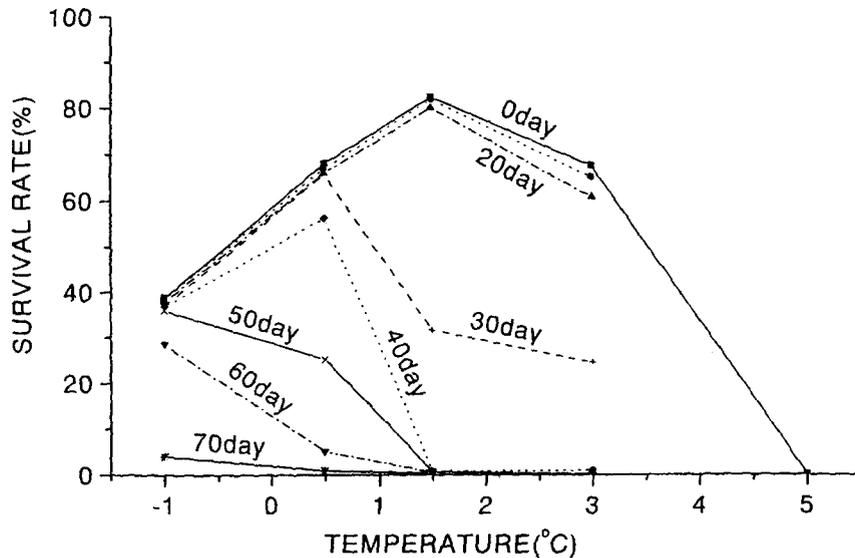


Fig.4. Survival rates at 10-day intervals of Arctic cod larvae from the 50% hatching date to 70 days post-hatching at temperatures between -1 and 5°C.

The number of days from fertilization to 50% hatching was 54 at 12.9 psu, 51 at 22.5 psu, and 44-45 at 32.1 to 51.6 psu. Organogenesis and hatching at 12.9 and 22.5 psu occurred

about 7-10 days later than at 32.1 to 51.6 psu.

Survival rates of unfed Arctic cod larvae from the 50% hatching date were adjusted to 100% at each salinity unit for examining the salinity tolerance of larvae after hatching (Fig.6). Survival rates at 20 days after 50% hatching were >95% at salinities between 22.5 and 40.8 psu. The survival rate at 12.9 psu was over 60% at 20 days after 50% hatching, but was extremely low at 51.6 psu after hatching.

Discussion

In the present study, we succeeded in long-distance transport by ship from the northern Bering Sea to Japan and long-term maintenance of Arctic cod for up to 4 years, which allowed us to perform captive experiments to study reproduction, and the development and survival of eggs and larvae. Graham and Hop (1995) successfully reared Arctic cod for up to three years, during which they monitored the spawning and development of larvae. They noted that Arctic cod maintained in the laboratory for less than one year spawned during the same period (January and February) as fish in the wild. Spawning in the sea occurs from late December to late March, with a peak occurring in January-February (Rass, 1968; Craig et al., 1981; Hop et al., 1995). Spawning in our laboratory occurred during the same time as spawning in the sea, despite the different light regimes in the wild and in this experiment. The normal maturation cycle of Arctic cod continues even under captive conditions, because most fish spawned on time after 7 months, except for a female that was collected in 1992 and spawned on 1 March of 1994.

It has been suggested that Arctic cod is semelparous (Nikol'skii, 1954; Cohen et al., 1990). However, Graham and Hop (1995) reported that captive Arctic cod resumed feeding 0-7 days after spawning, and concluded that Arctic cod are iteroparous, at least under laboratory conditions, despite the large amount of energy that is allocated to reproduction (Hop et al., 1995). In the present study, most spawned females and males gradually stopped feeding, weakened and died within several months after spawning, but a few spent females and males resumed feeding after spawning, and survived to spawn again one year later.

It has been suggested that post-spawning survival in Arctic cod is enhanced by several factors, including low respiration energy costs (Hop and Graham, 1995; Hop et al., 1997b) and their ability to resume feeding immediately after spawning (Graham and Hop, 1995). However, the chance of surviving to the next spawning season may be rather low because of high predation rates on this species during the post-spawning season (Welch et al., 1992; Welch et al., 1993). The reproductive strategy of Arctic cod, therefore, seems to involve a delicate balance between reproductive costs and survival after spawning (Hop et al., 1995), which strongly depends on food availability during post-winter.

Sakurai and Hattori (1996) compared the reproductive characteristics among Atlantic and Pacific gadid species, not including Arctic cod. These fishes can be grouped into two types, based on their reproductive characteristics and the nature of spawned eggs.

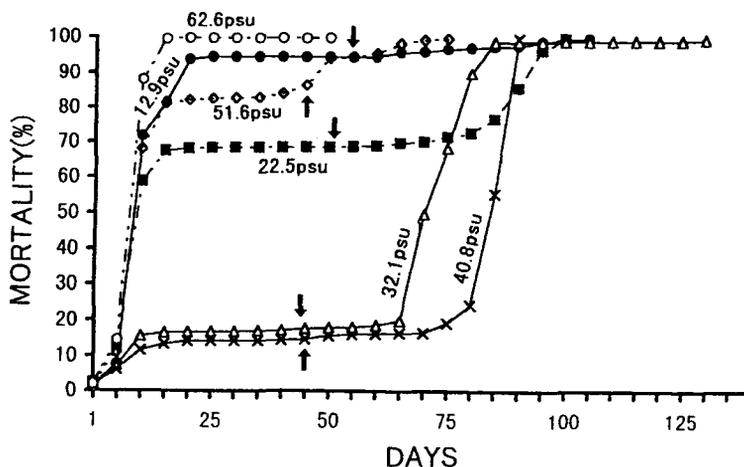


Fig.5. Arctic cod eggs and larval mortality rates at salinities between 12.9 and 62.6 psu at 1.5°C. Arrows indicate 50% hatching.

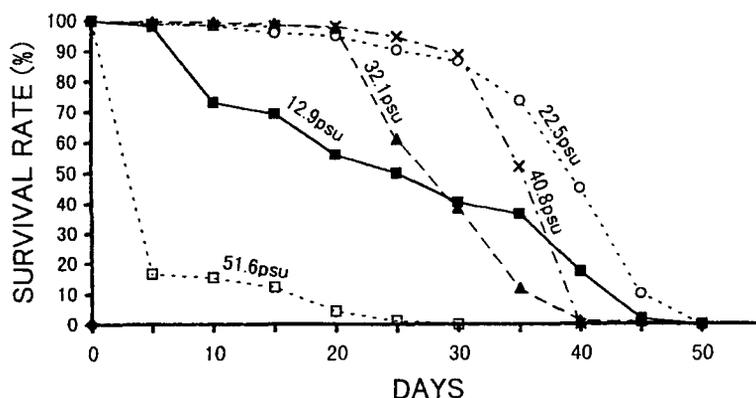


Fig.6. Survival rates of Arctic cod larvae from 50% hatching date at salinities between 12.9 and 51.6 psu. Survival rates of larvae at 50% hatching were adjusted to 100% for examining the salinity tolerance of larvae after hatching.

The first type includes Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and walleye pollock; all are multiple spawners that spawn pelagic eggs at intervals of a few days in a spawning season (Hawkins et al., 1967; Nakatani and Maeda, 1984, Kjesbu, 1989; Sakurai, 1989). The second type includes Pacific cod (*Gadus macrocephalus*) and saffron cod; all of which lay slightly adhesive demersal eggs that settle on the sea bottom and they

release most of their ripe eggs in a single spawning (Nishiyama et al., 1986; Chen, 1989; Park et al., 1994; Sakurai and Hattori, 1996). In the present study, however, Arctic cod released most of their non-adhesive and pelagic eggs in a single spawning. Their eggs are among the largest of gadid eggs, measuring 1.5-1.7 mm in diameter (Hop et al., 1995; this study). Arctic cod have a smaller maximum size and shorter life span (Craig et al., 1982) than boreal gadid species. In the circumpolar arctic, spawning of Arctic cod is believed to occur in winter below the under-surface of the ice, and the development of eggs begins under the ice-cover and ends under the open sea-surface free of the thawed ice (Rass, 1968).

Floating developing eggs of Arctic cod have been collected at 0°C-1.8°C in the Barents Sea (Rass, 1968), and at 1.5-6°C and 18.9 to 27.7 psu (salinity) in the White Sea (Altukhov, 1981). The present study demonstrates that normal embryonic development through hatching occurred at temperatures between -1 and 3°C, with highest survival rates (> 65%) occurring between 0.5°C and 3°C. The hatching rate was lower (39%) at -1°C, which is the approximate temperature of water under the ice cover (Drolet et al., 1991). We also found that normal embryonic development occurred over a salinity range of 12.9-51.6 psu at 1.5°C, with highest survival rates (>70%) occurring at 32.1 and 40.80 psu. At salinities below 32.1 psu, hatching occurred at 22.5 and 12.9 psu, but the hatching rate was lower (31%) at 22.5 psu, and extremely low (6%) at 12.9 psu. Furthermore, hatching at 12.9 and 22.5 psu occurred about 7-10 days later than at 32.1 to 51.6 psu. In the present study, the optimum temperatures and salinities for embryonic development to hatching were concluded to be 0-3°C and 30-33 psu. The optimum temperature and salinity ranges for normal embryonic development will delimit the timing and location of spawning and the distribution of eggs.

In the present study, the relationship between temperature and the number of days to 50% hatching could be expressed as an exponential function. The number of days from fertilization to hatching were estimated to be 75 at -1°C, 60 at 0°C, 50 at 1°C, 42 at 2°C, and 35 at 3°C. The incubation period for Arctic cod eggs has been estimated to be 77-79 days at -1.5°C (Altukhov, 1981), 35 days at a mean monthly temperature of 1.5°C (Aronovich et al., 1974), and 43-44 days at 2°C (Graham and Hop, 1995). These incubation periods at different temperatures are similar to our results, with the differences probably due to egg size and accuracy of temperature measurement at each incubation. Environmental conditions under the ice through embryonic development of Arctic cod will be stable, with temperatures below 0°C and waters slightly saline before the ice-melt. Thus, the duration from spawning to hatching is estimated to be about 2 months.

Drolet et al. (1991) reported that pelagic larvae of Arctic cod hatch several weeks before the ice break-up in Hudson Bay. Further, the surface layer in the Arctic Ocean during the spring is cold (<0°C) and the salinity is low, because of ice-melt and river outflow (Drolet et al., 1991; Pondon and Fortier, 1992; Gilbert et al., 1992). Aronovich et al. (1975) reported that the critical period for Arctic cod larvae occurs 20 days after hatching, which is

the yolk-absorption stage. Doroshev and Anorovich (1974) showed that Arctic cod larvae can tolerate reduced salinities of 10-15 psu over a period of 5 days after hatching. The present study showed that hatching larvae had high survival at temperatures below 0.5°C and at a wide range of salinities from 12.9 to 40.8 psu through the critical period. This suggests that the early life stages can tolerate the fluctuating cold temperatures and low salinities that occur during the ice-melt in marginal ice zones.

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