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Aspects of Reproduction and Larval Biology of Arctic Cod (*Boreogadus saida*)

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ABSTRACT. Arctic cod (*Boreogadus saida*) were captured from Resolute Bay, Northwest Territories, shipped to Vancouver and reared in holding tanks for up to three years. Spawning and development of larvae were monitored in two separate years. Fish that were in the laboratory for less than one year spawned during the normal spawning period for wild fish, January to February. The timing of spawning was altered by water temperature and light regime. Elevated water temperature caused spawning to occur earlier, and increased mortality and rate of deformity in larvae. The absence of "light" and "dark" seasons may have caused spawning to deviate from the predicted time in successive years. Larvae hatched at 87–91˚C·days. The newly hatched planktonic larvae were 5–6 mm long (total length), non-pigmented, and had poor swimming ability, likely because of the large yolk sac (1.5 mm in length). Even though swimming ability remained poor for the entire rearing time (up to 100 days), it improved as the yolk dissipated. Yolk nutrition lasted 20 to 40 days after hatching. Healthy larvae remained within the top 15 cm of the water column, and fed on brine shrimp and barnacle nauplii, and oyster trochophores. Growth rate under laboratory conditions was similar to those for fish sampled from the field. Fish that were not near the surface did not grow.

Key words: Arctic cod, larvae, spawning, temperature, behaviour, growth

RÉSUMÉ. On a capturé des morues polaires (*Boreogadus saida*) dans la baie Resolute (Territoires du Nord-Ouest), pour les expédier à Vancouver et les garder dans des bassins d'élevage pendant une durée allant jusqu'à trois ans. On a surveillé la fraie et le développement des larves au cours de deux années distinctes. Les poissons qui étaient dans le laboratoire depuis moins d'un an frayaient pendant la période normale de fraie des poissons sauvages, soit de janvier à février. L'époque de la fraie était affectée par la température de l'eau et le régime d'éclairement. Une élévation de la température de l'eau provoquait une arrivée hâtive de la fraie, ainsi qu'une augmentation de la mortalité et du taux de malformation des larves. L'absence de saisons «éclairées» et «sombres» peut avoir entraîné une déviation, au cours des années, du moment de la fraie par rapport au moment prédit. L'éclosion des larves se produisait au bout de 87 à 91˚C·jours. Les larves planctoniques nouvellement écloses mesuraient de 5 à 6 mm de longueur (totale), n'étaient pas colorées et ne pouvaient pas bien nager, probablement à cause du grand sac vitellin (1,5 mm de longueur). Bien que leur capacité de nage restât médiocre pendant toute la durée de l'élevage (jusqu'à 100 jours), elle s'améliorait à mesure que le sac vitellin se résorbait. L'alimentation à partir du sac vitellin durait de 20 à 40 jours après l'éclosion. Les larves saines restaient dans les 15 cm supérieurs de la colonne d'eau et se nourrissaient de nauplius d'artémias et d'anatifes, et de trochophores d'huîtres. Le taux de croissance dans les conditions de laboratoire était semblable à celui des poissons prélevés sur le terrain. Les poissons qui ne restaient pas près de la surface ne grandissaient pas.

Mots clés: morue polaire, larve, fraie, température, comportement, croissance

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INTRODUCTION

The Arctic cod (*Boreogadus saida* Lepechin, 1774), is a prominent species in the Arctic marine food web (Bradstreet, 1982; Bradstreet and Cross, 1982; Craig et al., 1982; Bradstreet et al., 1986; Hobson and Welch, 1992; Welch et al., 1992). Despite its central ecological importance, little information exists on its reproductive and larval biology in the North American Arctic (Sekerak, 1982).

This species spawns under sea ice during winter (Craig et al., 1982; Sameoto, 1984; Bradstreet et al., 1986), making it difficult to study this aspect of its life history in the field. In the North American Arctic one spawning area has been identified in the Beaufort Sea (Craig et al., 1982). Largely because the Arctic cod lacks significance as a commercial species in North America, little is know about its biology, including why it might form massive schools (Crawford and Jorgenson, 1993; Welch et al., 1993). In the central Arctic (vicinity of Cornwallis Island, Northwest Territories), and the eastern region (south Baffin Island and Labrador), information exists on habitat use during ice-free times, stomach contents, sex ratio, growth rate (derived from the age-to-length relationships of 1+ years to adult-sized fish), distribution and the temperature at which fish are most frequently caught (Bain and Sekerak, 1978; Lear, 1979; Wells, 1980; Bradstreet, 1982; Bradstreet and Cross, 1982; Sekerak, 1982; Moulton and Tarbox, 1987).

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Because Arctic cod cannot be studied under sea ice, laboratory research is essential, and has provided insight into oxygen requirements during fasting and feeding conditions (Steffensen et al., 1994; Hop and Graham, in press). The energetics of reproduction have also been investigated (Hop et al., in press [a]). This emerging understanding of the energy requirements of this species provides information useful to researchers who attempt to model Arctic food webs (e.g., Welch et al., 1992; Hop, 1994; Sakshaug et al., 1994).

Studies on reproductive biology and larval biology of Arctic cod have been conducted in the Russian Arctic. Rass (1968) has provided information about the timing of spawning within clearly identified regions. Laboratory studies of fertilization, egg incubation, and larval rearing were conducted by Aronovich et al. (1975) and Altukhov (1981).

Aspects of reproductive and larval biology of the Arctic cod were studied at the Vancouver Aquarium's arctic marine holding facility for fish and invertebrates (Graham and Wong, 1992). The objective was to study adult cod during captive spawning under arctic-like conditions in the laboratory, and to describe hatching and larval development.

MATERIALS AND METHODS

Arctic cod were captured in August of 1990 (n = 30) and 1991 (n = 30) by trap net from Resolute Bay, Cornwallis Island, Northwest Territories, and held in flowing seawater before transport to the laboratory in Vancouver. Larger specimens were selected from trap-net catches to maximize gamete production. Only fish in excellent condition within one month of capture were selected for transport south. To maintain proper water conditions during transport, a specific packing procedure was followed. Up to five fish (< 250 g total wet mass) were put into polyethylene bags with 5 L of ambient seawater and 15 L of oxygen, then sealed with elastic bands before being placed into an insulated container (e.g., a double-walled ice chest). Ice was packed on the floor of the shipping container and between bags. Transport time was approximately 24 h from the time of packing to the time of unpacking, during which water temperature increased from 0˚ to 2˚C, with no deleterious effect upon the fish.

Arctic cod adapted well to laboratory conditions, and fed readily on frozen food. Once in Vancouver, fish were kept at 1˚ ± 1˚C in an 800 L fibreglass tank as part of a closed system of water filtration (Graham and Wong, 1992). Fluorescent lighting was controlled to approximate the light/dark cycle for Vancouver. Fish were fed frozen euphausiids (*Euphausia pacifica* and *E. superba*), three to five times per week. Adult Arctic cod would also eat cut herring (*Clupea pallasi*), squid (*Loligo* sp.) and the geoduck clam (*Panopea generosa*), if offered.

Both year catches of cod spawned after five to six months in captivity. Fish were stripped of eggs when gametes were released by applying gentle pressure on the abdomen. Eggs were put into a chilled, sterilized stainless steel bowl with enough seawater to just cover them. Sperm from one fish (~5 mL) was mixed with the eggs from one or more females. Gametes were kept in the bowl for 10–15 minutes at 1˚C before being immersed in a 20 L floating container. The bottom and two side portions of the container were fitted with nytex screen (~500 μm) to allow passive water flow from the holding tank.

Brine shrimp nauplii (*Artemia salina*), unable to swim in the cold water, fell through the bottom screen rapidly. A gentle, upwelling current was piped into the floating container to facilitate the suspension of the live food. The current extended the time nauplii remained in the water column to 30 to 60 minutes.

Larval morphometrics were determined with a dissecting microscope (magnified 25 ×). Total length and notochord length were measured from the snout to the tip of the tail, and the posterior end of the notochord, respectively. Head diameter was the distance from the snout to the posterior edge of the operculum. Yolk sac length and depth were the largest anterior-posterior and dorso-ventral distances, respectively.

RESULTS

Spawning

Fish appeared gravid in mid December, about one month prior to spawning. It was impossible to distinguish male and female fish by exterior appearance. Following dissection, most fish in the present experiments were found to be females; the sex ratio of two samples from two separate years was one male to nine females in each case.

Under conditions of unconstrained feeding, zero predation, and stable physical environment, three females and one male provided viable gametes on two successive years. Eggs and sperm were taken each year as outlined above, and larvae were reared at least to hatching, confirming that iteroparity was possible.

When handled for egg collection, ripe fish began to release eggs immediately. Whether or not fish continued spawning on their own, hand stripping at the termination of abdominal contractions produced few eggs. Few or no eggs were found after dissection. Females became visibly smaller following egg release. Eggs released naturally or stripped produced viable young, indicating that the entire egg mass was developed to the same degree at the time of spawning. No fish died in the laboratory as a result of spawning. Although gametes filled most of the abdominal cavity, fish continued feeding to the day of spawning. Resumption of feeding after complete spawning occurred within zero to seven days.

Light /dark exposure seemed important for the timing of spawning. All adult fish were brought to Vancouver in August, and spawned five to six months later. The reproductive condition was observed, but not quantified, for two more years with the 1990 group of fish. In the second spawning year in captivity, the spawning time extended from December to April. In the third year, no distinct spawning period was evident; some fish spawned in mid-summer.

Eggs, Hatching and Larvae

After fertilization the transparent eggs floated at or near the surface (<10 cm). Eggs that sank to the bottom of the container always failed to hatch. Fertilized eggs were incubated from two separate groups of fish: ~25,000 eggs each year. The eggs from 1991 were reared under stable physical conditions, and the temperature·time index for hatching was quantified for this season. In 1991 the mean water temperature was 1.5 ˚C, and eggs began to hatch after 58 d (87.0˚C·d); all eggs had finished hatching within one week.

The eggs from 1992 were induced to hatch by acute temperature increase. The acute temperature increase was uncontrolled. Results from that year revealed the importance of temperature to incubation time and larval development. In the 1992 group, water was 2.0˚C for 43 days, then rose to 9.0˚C over a 24 h period; this makes a total of 44 days, or 91.5˚C·d using 5.5˚C as an average for the one day of changing water temperature. The 1992 fish were returned gradually to 2˚C during the next two days.

In the 1991 group few mortalities and no deformities were seen at hatching, whereas the 1992 group had massive mortality. Larvae sampled randomly from the 1992 group often had spinal scoliosis and protrusion of the lower jaw, causing misalignment.

Upon hatching, the fish had a yolk sac large enough to impede swimming ability, so that short swimming bursts carried the fish in small circles (2 cm radius). After absorption of yolk sacs, larvae were able to make 4–8 cm linear swimming bursts. The range of time for yolk nutrition after hatching was 20 to 40 days.

Food was introduced to the larvae while yolk was still abundant, and they attempted to feed within a day of hatching. Feeding was cumbersome as fish swam with large yolk sacs. Larvae seemed to eat after colliding with food organisms, and ingested *Artemia* nauplii (850 μm), barnacle nauplii (500–700 μm), and oyster trochophore larvae (50 μm), as well as air bubbles and *Artemia* cysts (250μm).

Larval Growth

Larvae stayed near the surface, although their swimming ability and the upwelling current in the container expanded the depth range to 15 cm. Larvae that sank to the bottom of the container failed to grow and eventually died. Larvae sampled from the bottom of the container did not grow within two weeks after yolk absorbtion (Fig. 1), indicating a possible lack of feeding. At 93 days, surface-dwelling cod tended to be larger than those on the bottom of the container (p = 0.074) and after 95 days were significantly larger (p = 0.001, Student's t-test). This difference was due to growth of surface larvae at 0.068 mm·d^{-1}. Fish from the 1991 group grew at a similar rate (0.061 mm·d^{-1}) to the 1992 group (Fig. 1), but were larger at any given age. The 1992 larvae hatched at a smaller length (5 mm versus 6 mm), and had yolk present for up to 40 days after hatching; fish from the stable temperature 1991 group had no yolk at 20 days after hatching.

Morphometrics were investigated during and after the period of yolk nutrition (Table 1). Growth was best expressed by total length and notochord length, and secondarily by snout to anus length (Fig. 1, Table 1). Head length and eye diameter underwent minor increases during this time period. The two yolk sac dimensions gave little indication of growth. Although there are no field data with which to compare most of these measures, the rate of increase in total length was comparable to that of wild fish (Fig. 1).

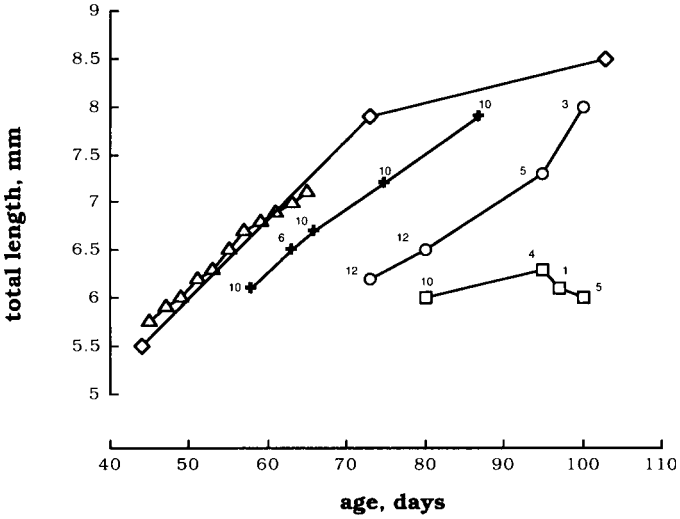

FIG. 1. Growth of Arctic cod larvae reared in the laboratory. ○ = planktonic (1992); + = planktonic (1991), feeding animals; and □ = bottom (1992), non-feeding animals. From wild caught fish, ◇ = Baranenkova et al., 1966; △ = Aronovich et al., 1975. Values for laboratory reared larvae are means ± SE. The number of animals sampled is indicated above each symbol for the present study.

TABLE 1. Morphometrics of Arctic cod reared in the laboratory under stable temperature conditions (fish in the 1991 group). External feeding began after about 70 days, and no yolk remained after 77 days. Values are means and in mm ± SE.

Age (days)	Total length	Notochord length	Head length	Snout-anus	Eye diameter	Yolk width	Yolk depth
59 n = 10	6.1 ± .07	5.9 ± .07	0.8 ± .01	2.2 ± .01	0.4 ± .00	1.5 ± .04	0.5 ± .03
63 n = 6	6.5 ± .09	6.3 ± .10	0.9 ± .04	2.3 ± .03	0.4 ± .00	1.6 ± .03	0.6 ± .06
66 n = 10	6.7 ± .08	6.4 ± .06	0.9 ± .00	2.4 ± .02	0.4 ± .00	1.6 ± .02	0.5 ± .02
74 n = 11[1]	7.2 ± .11	7.0 ± .09	1.1 ± .03	2.6 ± .05	0.6 ± .01	1.8 ± .03	0.6 ± .01
86 n = 10	7.9 ± .05	7.7 ± .05	1.1 ± .01	2.9 ± .01	0.5 ± .00		

[1] Only 10 samples were measured for total length.

DISCUSSION

Arctic cod eggs are large compared to those of other gadids, ranging in size from 1.5 mm to 1.9 mm in diameter (Andriyashev, 1954; Matarese et al., 1989). Eggs from the present study compared well with these data (diameter 1.65 mm ± 0.1 mm, mean ± SE, with n = 11 gonads and 20 eggs measured from each sample). The eggs are unpigmented, transparent, and buoyant, remaining at the surface. The temperature·time index for hatching in the present study, 87–91.5˚C·days, was within the broad range describing Arctic cod in the Russian Arctic (Rass, 1968; 45 to 90 days in the Barents Sea, at ~1˚C), but different from the laboratory findings of Aronovich et al. (1975; 39–52.5˚C·days, at 1.5˚C).

The time of spawning changed with each successive year that fish were held in Vancouver, in that the "season" broadened. Because both temperature and salinity in the holding facility approximated ambient summer arctic conditions, it was concluded that the arctic light/dark cycle, a part of the physical environment that was not provided, may be important to the proper timing of the onset of spawning.

Fish in the laboratory fed regularly until spawning and resumed feeding soon after spawning. Craig et al. (1982:398) reported that gravid fish from the Beaufort had "advanced gonadal development and full stomachs" in November, 1–2 months before spawning. Field samples from Russian waters also indicated that fish will feed before and after spawning, the frequency of stomachs containing food after spawning being 66.7% (Altukhov, 1981).

Sekerak (1982) commented that the life history of Arctic cod from the North American Arctic could be pieced together on the basis of European and Russian studies, a more thorough body of research to date. Rass (1968) outlined the spawning time to be December to March for fishes in the Barents Sea, similar to the present Arctic cod from Resolute Bay (even though the light/dark regime did not simulate arctic conditions). Craig et al. (1982) proposed a spawning period for Arctic cod in the Beaufort Sea between November and February, largely overlapping that for the Russian Arctic.

Acute temperature increase, from 2˚ to 9˚C over a 24 h period, stimulated spawning three to five weeks earlier than if no temperature change had occurred, and did not cause mortality among adults. This reflects the great difference in temperature tolerance between adult and larval Arctic cod; larvae had a high mortality rate after a similar temperature change. Temperature was also important to embryonic development. Because of the small number of accumulated thermal units (˚C·d) before hatching, low water temperature is a critical feature of successful early life, especially considering that the timing of Arctic cod spawning and subsequent hatching has likely evolved to provide a favourable feeding environment for larvae (Ponomerenko, 1967), such as the enhanced secondary production associated with the early spring plankton bloom in the marginal ice-zone.

Arctic cod have been found in water temperatures ranging from -1.5˚C to 13.5˚C (Moskalenko, 1964; Hognestad, 1968; Ponomarenko, 1968; Rass, 1968; Lear, 1979; Craig et al., 1982; Sameoto, 1984; Falk-Petersen et al., 1986; Monstad and Gjøsæter, 1987; Moulton and Tarbox, 1987). Arctic cod in the central Arctic of North America have a limited range of temperature exposure. For example, in Resolute Bay annual temperature varied between -1.8˚ and 1.0˚C, a relatively stable thermal condition (Hop and Graham, in press). However, in the northwest Atlantic or western portions of the North American Arctic this species has been found associated with temperatures of 4–7˚C (Lear, 1979) and 13.5˚C (Craig et al., 1982). Adult fish tend to avoid high temperatures (Ponomarenko, 1968; Lear, 1979; Monstad and Gjøsæter, 1987), although they do make excursions into warmer waters, often along the transition area of water masses, presumably to feed on concentrated prey items (Craig et al., 1982; Moulton and Tarbox, 1987). In the European and Russian Arctic, larval development can occur in warmer water near the surface (2–7˚C; Rass, 1968; Falk-Petersen et al., 1986), although in the Canadian high Arctic larvae must develop in colder water (< 3˚C).

In the laboratory, thriving larvae were always at or near the surface, consistent with field observations (Ponomarenko, 1967). Just after hatching there is no response to different light levels (Aronovich et al., 1975). Eventually young-of-the-year Arctic cod develop a negative phototaxis. Quast (1974) noted distribution patterns in young-of-the-year Arctic cod that indicated negative phototaxis. In the wild, water currents would probably broaden the depth distribution of larvae. In the Lancaster Sound area larvae were concentrated in the upper 10–20 m from June to mid-August, although densities were low near the immediate surface (Sekerak, 1982). Baranenkova et al. (1966) found that Arctic cod larvae in the Barents Sea remained in the water column until August. In September a large number of the larvae appeared in bottom trawls, indicating that settling had occurred.

In the present study food availability was affected by the mobility of *Artemia* nauplii since they dropped from the water column rapidly. To successfully rear these fish in captivity, it will be necessary to ensure that suitable food is available at all times. This will require live items that can withstand low water temperature or, as a substitute, specialized micro-pelletized food. In the wild, larval Arctic cod of 6–12 mm size from the Barents Sea utilize copepod nauplii as a main food item, but they also eat copepod eggs and copepodites (Ponomarenko, 1967). When observed under the microscope, Arctic cod in the present study always had *Artemia* cysts in their digestive tracts, but also ate nauplii. This feeding pattern was related to the availability of the cysts which floated near the surface, such that stomach contents reflected food availability, indicating that larvae did not feed selectively. Ponomarenko (1967) found that Arctic cod larvae appeared in areas with the highest concentrations of copepod eggs, and that the hatching of cod larvae was timed closely with the development of *Pseudocalanus* sp. generations in the Barents and Kara Seas. A large yolk sac at hatching, the resultant clumsy swimming performance and the need to feed immediately after hatching (Aronovich et al., 1975) point to the importance of larval Arctic cod being near an abundant food source early in their life.

The sex ratio in samples of wild fish generally indicates a majority of females, a higher proportion of the large fish being female (Lear, 1979; Craig et al., 1982; Hop et al., in press [b]). The selection of larger fish for transport to Vancouver likely resulted in the abundance of females in the present study: few of the fish were male. Therefore, if the purpose is to have a breeding program, it is advisable to transport larger numbers of smaller Arctic cod, or various sizes. That will not maximize the number of eggs produced, but will ensure sufficient numbers of both males and females. The sex ratio of our experimental fish (90% female), showed a greater surplus of females than did previous studies. Craig et al. (1982) found the sex ratio of the Arctic cod population in the western Arctic to range from 66% to 80% female (except for one winter sample which was 35% female). Lear (1979) reported eastern Arctic catches with 75% females for fish larger than 25 cm: 9–25 cm long fish had an equal number of males and females.

Further laboratory studies are necessary to more closely understand the biology of wild Arctic cod. These preliminary findings indicate the likely success of rearing Arctic cod to the point of eating live food items, and thus providing access to a fragile life stage for testing with environmental toxicants (e.g., Hargrave et al., 1992). Our observation that light regime may be influential as a cue to spawning should be studied under controlled experimental conditions. Finally, temperature seems to be an important influence in the development of this species, which has a remarkable tolerance range (from -1.8˚C to 13.5˚C). More detailed study should quantify the effects of small temperature alterations (i.e., increment changes of 0.5˚C) on the development and growth rate of larval and juvenile Arctic cod.

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