Distribution and Drift of Atlantic Cod (*Gadus morhua*)
Eggs and Larvae in Greenland Offshore Waters

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Abstract

Catches of Atlantic cod (*Gadus morhua*) eggs and larvae from 45 national and international ichthyoplankton surveys conducted in Greenland offshore waters during the period 1950 to 1984 have been compiled and re-analysed. Southeast and Southwest Greenland were identified as important spawning areas from which eggs and early larvae drift towards the southern Davis Strait. Only a part of the larval population remained in the vicinity of favourable settling areas off West Greenland while a considerable part was obviously transported westward across the Davis Strait and thus did not contribute to the recruitment of the West Greenland cod stock. It is also shown that cod eggs and larvae occasionally drift from Southwest Iceland across the Denmark Strait to the East Greenland shelf from where a subsequent transport and immigration of juveniles to West Greenland waters can occur. Larval transport across the Denmark Strait appeared to be most crucial for short-term replenishment of the offshore stock of cod at East and West Greenland. In general, these results confirm the existing knowledge on the transport of cod fry in Greenland waters but they indicate a higher importance of Southeast and East Greenland waters as potential spawning and settling areas for the recruitment of West Greenland cod than reported in previous studies.

Key words: Atlantic cod, egg and larval distribution, egg and larval drift, Greenland, spawning location, spawning time

Introduction

The Atlantic cod (*Gadus morhua*) population in Greenland waters has shown large variations in abundance and distribution in the past decades. Prior to 1920 annual catches of cod were less than 100 tons and were restricted to inshore areas (Buch et al. 1994). Thereafter a large offshore fishery developed frequently yielding annual catches above 300 000 tons through the 1950s to 1960s (Horsted 2000). At the same time, the spawning stock biomass was gradually reduced and the catches declined dramatically in the late-1960s (Hansen and Buch 1986). In the 1970s and 1980s annual catches were generally poor and dependent on single strong year-classes, which gave rise to an intermediate fishery with catches of about 100 000 tons in 1988–89. Since then, Atlantic cod has disappeared from the offshore waters (Rätz 1999) and at present only a small inshore fishery takes place (Anon. 2002).

Tagging experiments have indicated that the Atlantic cod found offshore at West Greenland is a mixture of three components originating from spawning locations at East and West Greenland as well as at Iceland (Rasmussen 1959). In addition, relatively stationary populations of Atlantic cod exist in West Greenland inshore areas (Hansen 1949, Hovgård and Christensen 1990).

Migration of Atlantic cod from Greenland offshore waters back to the spawning ground at Iceland has been documented based on tagging experiments (Hovgård and Christensen 1990) and analytical assessments (Shepherd and Pope 1993; Schopka 1993, 1994).
The occurrence of strong year-classes at West Greenland is linked to egg and larval drift from Icelandic spawning grounds for which the conditions are more favourable in warm than in cold periods (Buch et al. 1994). A substantial increase in water temperature at West Greenland has been observed since the beginning of the 1990s (Buch et al. MS 2002). There are, however, no indications that any relevant advection of cod eggs and larvae from the Icelandic spawning areas has taken place recently as it could be expected from the actual temperature regime (Borovkov and Stein MS 2001; Rätz et al. 1999), and hence the offshore stock of Atlantic cod at West Greenland has not recovered yet (Anon. 2001).

The first studies on the distribution of Atlantic cod fry at West Greenland were conducted at the beginning of the 20th century (Jensen 1909a, 1909b, 1926). Since then, numerous ichthyoplankton surveys were carried out by Danish and Greenland Research Institutions, and also by other nations during the 1960s. An especially large amount of information on the occurrence of eggs and larvae in West and East Greenland waters was collected during the international NORWESTLANT project in 1963 (Anon. 1968). Except for a summary of the ichthyoplankton data collected prior to World War II given in Hansen (1949), the survey results have been published in a very fragmentary way.

It is the objective of the present contribution to compile and analyse the considerable body of information on abundance and distribution of Atlantic cod eggs in Greenland offshore waters collected by various research institutes since 1950. This is done in order to evaluate possible links between the location of spawning and nursery areas and may further provide a basis for modelling the transport of cod eggs and larvae in the Northwest Atlantic.

Material and Methods

The major source of information used in the present study was derived from a series of plankton surveys carried out by the Greenland and Danish Research Institutes in the years 1950 to 1984. In addition, original data from the international NORWESTLANT surveys in 1963 were included in the analysis. Further information was extracted from ichthyoplankton surveys conducted by the former German Democratic Republic in the period 1961 to 1969.

The data from the different surveys were grouped into two main seasons, egg surveys in spring including samples taken from late-March to early-June and larval surveys in summer covering the period from late-May to early-August (Tables 1 and 2). Samples taken outside these periods were not considered in the present analysis. Maps of average egg and larval distributions combining survey results from different years were constructed by dividing the catch from a station by the corresponding annual mean catch. The relative catches were then mapped using ordinary point kriging (Chilès and Delfiner, 1999) with a spatial resolution of 2.5 nautical miles averaging the catches located at the same position for the considered decade, i.e. 1950-60, 1961-70, and 1971-80.

Surveys conducted by Denmark and Greenland

Danish and Greenland Research Institutes conducted comprehensive egg surveys only in the years 1968 to 1970 while in other years only few stations were sampled in spring (Table 1a). Larval surveys were carried out in summer in most of the years from 1950 to 1984 (Table 1b). The surveys initially covered West Greenland offshore waters between 58° and 70°N but were gradually reduced to shelf areas between 64° and 67°N in the later years.

Catches of cod eggs and larvae as well as corresponding station information have been compiled from the original field journals. The data have been thoroughly scrutinized and hauls with imprecise or unreliable information have been discarded. Over the several decades of surveys various changes in gear operation and rigging were made. It was therefore necessary to select comparable data and to adjust the catches to a common standard; a 30 min haul with a 2 m Stramin ring net towed obliquely from about 50 m depth to the surface as described below.

Towing speed and tow duration. Ship velocity was about 1.5 to 2 knots during the whole tow duration and the target towing time was 30 min. Hauls with shorter or longer towing times were adjusted accordingly, while no corrections for differences in towing speed were applied.

Gear size. Ring nets with diameters of 1 and 2 m both with a mesh size of 1 mm were used, and all catches were adjusted to a net opening diameter of 2 m. Calibration experiments with a flowmeter mounted in the net opening revealed that a standard haul with the 2 m Stramin ring net (30 min haul at 2 knots towing speed) equates to a filtered volume of water of about 6125 m³.
TABLE 1. Sampling dates for Stramin and Hensen net catches of cod eggs and larvae in West Greenland offshore waters 1950–84 (*: within the geographical limits shown in Fig. 4 and 6; GN: Greenland Institute of Natural Resources, GDR: former German Democratic Republic, INT: NORWESTLANT international surveys; see text for references; **: Day of year, weighted for number of samples in the case of combined surveys).

<table>
<thead>
<tr>
<th>Year</th>
<th>Source</th>
<th>Net type</th>
<th>Number of samples</th>
<th>Sampling period*</th>
<th>Survey midpoint**</th>
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TABLE 1. (Continued).

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<td>10 July</td>
<td>190</td>
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</table>

**Net material.** Stramin nets were used in the majority of the hauls, but in a few years during the late-1950s some hundreds of hauls were made with nylon netting. Comparative tows of which at least one of the two different nettings yielded non-zero catches revealed no significant difference for the eggs (28 stations) nor for the larvae (18 stations). Hence, the nylon net hauls were included in the analysis without any correction.

**Haul method and sampling depth.** Since 1950 three different operational procedures were employed, step-wise settings with two or three different wire lengths and oblique hauls:

- Egg surveys in 1961–70: The net was towed for 15 min with 100 m wire followed by another 15 min with 50 m wire. These wire lengths correspond to sampling depth of 30 and 15 m, respectively (Hansen 1949).
- Larval surveys in 1950–62, 1964 and 1966: Two nets were operated simultaneously on the same wire with a distance of 100 m wire between. The wire lengths were 200, 150 and 125 m for the deeper net, and 100, 50 and 25 m for the shallow one. The towing time was 10 min for each of the three steps. The mean ratio of larval catches obtained with the shallow and the deep net being 1.05 was not statistically different from 1, and the catches from the two nets of the paired stepwise settings were averaged to match oblique hauls.
- Larval surveys in 1963 and 1968–84: Oblique hauls were made with a maximum wire length of 225 m, which corresponds to a maximum sampling depth of approximately 50 m.
TABLE 2. Sampling dates for Stramin and Hensen net catches and average number per tow of cod eggs and larvae off East Greenland and Iceland in spring and summer 1963 (*: geographical limits shown in Fig. 8 and 9, **: no Hensen net samples available in this period; average egg and larval catch refer to a 30 min standard tow with a 2 m Stramin ring net, -: conversion of Hensen net catches not possible).

<table>
<thead>
<tr>
<th>Area*</th>
<th>Net type</th>
<th>Number of samples</th>
<th>Sampling period</th>
<th>Average number of cod eggs</th>
<th>Average number of cod larvae</th>
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<td>22 April</td>
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<td>Hensen</td>
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<td>991.55</td>
</tr>
<tr>
<td></td>
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<td>31 May</td>
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**German Democratic Republic Surveys**

Results from ichthyoplankton surveys carried out by the former German Democratic Republic in West Greenland waters in April/May 1961, 1962, 1965, 1966 and 1969 and in June/July 1964 were used to supplement the existing data set (Table 1). Catches of cod eggs and larvae in numbers-per-haul were directly read from distribution charts given in the reports by Biester and Mahnke (1963), Mahnke (1967a, 1967b) and Ernst (1970) while the station positions were estimated from the figures after adequate magnification. A 2 m Stramin ring net was used in all of these surveys. The maximum wire length was 200 m and the net was towed obliquely from its maximum depth to surface for 30 min at a towing speed of about 2 knots except for 1964 in which the vessel speed was 4 knots due to technical reasons. Hence, the hauling procedure was more or less comparable but not identical to that used during the surveys conducted by Greenland.

However, the data were used in the analysis without any correction assuming that a possible bias due to methodological differences is small compared to other sources of error.

**NORWESTLANT surveys**

Catches of cod eggs and larvae from other countries than Denmark and Greenland were taken from the biological data report on the three international NORWESTLANT surveys conducted in 1963 (Anon., 1968). The original survey periods were 31 March to 9 May, 30 April to 30 June, and 30 June to 3 August. The survey area included West and East Greenland offshore waters as well as the western part of the spawning area of cod at Iceland. Samples from 30 min oblique tows with a 2 m Stramin ring net using a maximum wire length of 225 m and a towing speed of 2 knots were available for the majority of the survey area, but a significant part of Southeast Green-
land waters in spring was surveyed using a Hensen net (72 cm diameter, hauled vertically from a maximum depth of 100 m to surface) only (Table 2). However, results from 58 comparative tows with non-zero catches of cod eggs made it possible to convert Hensen net catches to the 2 m Stramin ring net standard based on a highly significant ($p<0.01$) log-log regression (Fig. 1) using the following equation:

$$
\log_{10}(\text{Stramin net catch of cod eggs}) = 1.3834 + 0.8275 \times \log_{10}(\text{Hensen net catch of cod eggs})
$$

A similar approach could not be used for cod larvae due to very low and infrequent catches obtained with the Hensen net.

**Results**

**Cod eggs and larvae at West Greenland**

Results from spring and summer surveys were available for 8 and 7 years, respectively, for the period 1961 to 1970 (Table 1). Average annual egg catches divided by the offshore spawning stock biomass (SSB) of cod at West Greenland (SSB as given in Hansen and Buch, 1986) in the corresponding year indicate a spawning period from mid-March to late-May (Fig. 2). Maximum egg abundance was found in late-April and almost no cod eggs occurred in June and July. Some cod larvae were observed during the spring surveys but much higher average catches were taken in June and July (Fig. 3).

![Fig. 1. Comparison of cod eggs catches obtained with 2 m Stramin ring net and Hensen net.](image1)

![Fig. 2. Timing of cod spawning at West Greenland 1961–70 (numbers at the symbols refer to years). Gaussian distribution fitted ($r^2 = 0.93$) to survey mean catch of cod eggs in NAFO Div. 1B–1F divided by spawning stock biomass (SSB) at West Greenland (offshore stock) of the corresponding year in relation to the survey midpoint (Table 1).](image2)

![Fig. 3. Mean monthly catch of cod larvae at West Greenland 1961–70 ($n$: number of hauls).](image3)

Annual distributions of cod eggs in spring are shown in Figure 4 summarizing the results from 12 surveys conducted the years 1961–63, 1965–66, and 1968–70 (Table 1a). Area coverage differed somewhat between the years and it is noteworthy that Southwest Greenland waters, i.e. NAFO Division 1F where the highest egg abundance was observed (e.g. two stations with 3 000 to 5 000 cod eggs per 30 min. tow in 1963), was covered only in two out of the 8 years. However, it appears that during the period considered here cod eggs occurred all along the West...
Greenland coast between about 59 to 67°N but with declining densities in the northern part and a pronounced maximum in egg abundance off Southwest Greenland (Fig. 5).
The distribution of cod larvae at West Greenland in summer is shown in Figure 6a–c by year using all of the information from a total of 33 national and international surveys conducted in the years 1950 to 1984 (Table 1b). A considerable proportion of the larvae was found far away from the coast in those years in which the surveys covered large parts of the Davis Strait and the area west of NAFO Divisions 1C and 1D. This was the case in 1957 in particular, and also notable in 1958, 1959, 1961, 1963 and 1964 (Fig. 6a,b). In the 1970s and 1980s, the area covered by the surveys was substantially reduced and high numbers of larvae were found occasionally at single stations in the vicinity of the fishing banks between 64 and 67°N (Fig. 6c).

The restricted survey coverage in many years does not allow firm conclusions about the dispersion of cod larvae over the entire Davis Strait area. It may however be noted that cod larvae were frequently found at the western border of the survey area and that on average the highest larval abundance was observed in the south-western or central part of the Davis Strait in the 1950s and 1960s, respectively (Fig. 7).

In the 1960s, for which both spring and summer survey data are available, the area of highest larval concentrations located in middle of the Davis Strait in June/July (Fig. 7) was about 350 naut. miles away from the centre of the egg distribution at Southwest Greenland in May/June (Fig. 5). According to the mean difference between the midpoints of the sampling periods of about two months (Table 1), this distance would correspond to an average transport of 6 naut. miles per day (12.5 cm/s).

**Cod eggs and larvae at East Greenland and Iceland**

Plankton samples covering the entire area from East Greenland to Iceland were available only for 1963. Cod eggs were found in high numbers widely distributed in Southeast and East Greenland waters (5 stations with 4 000 to 9 000 cod eggs per 30 min tow), were nearly absent in the Denmark Strait, and were most abundant in the coastal waters west from Iceland where the maximum catch (78 000 cod eggs per 30 min tow) was recorded in May/April (Fig. 8). Cod egg abundance was negligible in June/July in all regions (Table 2a).

Considerable numbers of cod larvae were found in the southwestern part of the Denmark Strait (6 stations with 10 to 90 cod larvae per 30 min tow) and in offshore waters west from Iceland (3 stations with 10 to 20 cod larvae per 30 min tow) in June/July, but not in the other regions during this period (Fig. 9). Cod larvae were almost totally absent in the entire survey area in April/May (Table 2b).

The distance between the centre of the larval distribution in the southern Denmark Strait observed in June/July (Fig. 9) and the area of highest egg concentration off Southwest Iceland in April/May (Fig. 8) was about 150 naut. miles. This would be equal to an average drift of 2.5 naut. miles per day (5.4 cm/s) taking a difference of two months between the sampling dates into account (Table 2).

**Discussion**

It is very difficult, at all if possible, to distinguish the larvae of Atlantic cod (*Gadus morhua*) from that
Fig. 6a. Distribution of cod larvae in West Greenland offshore waters 1950 to 1959. Larvae numbers refer to 30 min haul with 2 m Stramin ring net. Sampling period: late-May to early-August (see Table 1b for details; 1951 no data).
Fig. 6b. Distribution of cod larvae in West Greenland offshore waters 1960 to 1971. Larvae numbers refer to 30 min haul with 2 m Stramin ring net. Sampling period: late-May to early-August (see Table 1b for details; 1962, 1965 and 1967 no data).
Fig. 6c. Distribution of cod larvae in West Greenland offshore waters 1972 to 1984. Larvae numbers refer to 30 min haul with 2 m Stramin ring net. Sampling period: late-May to early-August (see Table 1b for details.)
of Greenland cod (*Gadus ogac*) (Andersen *et al.* 1994) and this was not attempted in the sample analysis. Greenland cod is common in inshore areas all along the West Greenland coast from about 60° to 73°N but is absent in East Greenland. For the larvae found offshore it can be assumed that they are predominantly Atlantic cod because Greenland cod is only found in the fjords and coastal areas. Furthermore, Greenland cod spawn earlier (February to March) than Atlantic cod (March to April) and has demersal eggs, which are not transported to the open sea by the currents (Hansen 1949).

Direct observations on spawning of Atlantic cod at West Greenland are scarce. Jonsson (1959) found that 50% of the mature fish were spawning and 38% had finished spawning in the end of April, and Bratberg (1965) noted that 40% of cod caught in the middle of April had not yet finished spawning. In 1961 and 1966 spawning was at its peak by the end of March and the beginning of April (Meyer, 1963, 1967), and a high proportion of spawning cod were observed in March 1967 during a Union of Soviet Socialist Republic survey (Konstantinov and Noskow 1968). However, information on cod maturity from a Portuguese survey in 1968 revealed that spawning was nearly completed by June except for a small fraction of males, which were in running condition (Diaz 1969), and Serebryakov (1967) also reported spawning as late as June. Spawning locations were observed at the offshore slope of Fyllas Bank (64°N) in 120 m depth at a temperature of 1.5°C (Jonsson 1959), but more frequently west of the various fishing banks further south below 350 m depth in the warmer Atlantic water (Meyer 1963, 1967; Meyer and Lenz 1972; Konstantinov and Noskow 1968).

At East Greenland, spawning cod were observed from March to June (Meyer 1958, 1962, 1963; Jonsson 1959, 1961, 1975; Serebryakov 1967) along the offshore slope of the shelf from about 62° to 66°N. Spawning depth ranged from 170 to 400 m (Jonsson 1959; Meyer 1963) at which temperatures were between 3.2°C and 5.2°C (Jonsson 1959, 1961). The results from the ichthyoplankton surveys presented in this study confirm the observations on the timing of cod spawning at West and East Greenland from the studies cited above.

Cod egg abundance data from the NORWEST-LANT surveys in 1963 including both Stramin and Hensen net samples emphasize a high importance of the spawning area at East Greenland. This was not recognized by Hansen (1968) who considered only the
Stramin net samples but is in accordance with the findings of Serebryakov (1967) who analysed Hensen net samples and reported that there were substantially more cod eggs off East Greenland than off West Greenland.

During June/July cod larvae were predominantly found between 63 and 67°N at West Greenland, which is about 350 to 600 nautical miles away from the spawning areas at Southwest and Southeast Greenland as identified by the egg distribution in May/April. Such a drift pattern is in agreement with the direction of the currents around South Greenland and would require an average transport of about 6 to 10 nautical miles per day (12.5 to 21.4 cm/s) assuming that the distance is covered within two months (Fig. 10). Current data compiled by Serebryakov (1967) revealed mean velocities of 30 cm/s in the area between 67°N at East Greenland and 64°N at West Greenland and 10 cm/s at West Greenland between 64 and 67°N, which are sufficient to explain the difference between the egg and the larval distribution presented in this study. A considerable proportion of cod larvae found in the south-western part of the Davis Strait, as observed in a couple of years in the 1950’s and 1960’s, was likely transported further towards the coast of Labrador based on the current regime in this region (Serebryakov 1967; Dickson and Brander 1993) and must be considered as lost to the recruitment of cod at West Greenland (Fig. 10).

At Iceland, cod spawn off the southwest coast from the end of March to the beginning of May with a peak usually at the end of April (Jonsson 1982). Spawning takes place at a depth below 35 m where temperatures are rarely below 6°C. The eggs and larvae drift from the spawning area by clockwise currents to the northwest, north, and the northeast coast.
Fig. 9. Distribution of cod larvae off East Greenland and Island in June/July 1963 (see Table 2b for details). Larvae numbers refer to 30 min haul with 2 m Stramin ring net.

of Iceland and in some years a considerable fraction may also drift across the Denmark Strait to East Greenland waters (Astthorsson et al. 1994).

Tåning (1943) originally were described the drift of cod larvae from Southwest Iceland to East Greenland, and cod larvae were observed during the June/July 1963 NORWESTLANT surveys in the southern Denmark Strait as described in this study. Herman and Thomsen (1946) reported a mean velocity of the currents in that region of 20 cm/s, which would result in a transport over a distance of 300 nautical miles from the Denmark Strait to the East Greenland coast within one month (Fig. 10).

Icelandic and East Greenland waters have been covered by pelagic trawl surveys carried out by Iceland annually since 1970 in August/September. In some years, notably 1973 and 1984, high numbers of 0-group cod were found southwest from the Denmark Strait (Astthorsson et al. 1994). Settling areas of 0-group cod at Greenland are not precisely known. For year-classes that are indicated to be mainly of Icelandic origin, e.g. that of 1984, it appears reasonable to assume that settling occurred at East Greenland and the southernmost part of West Greenland because haddock, which is rare at Greenland but spawns in Icelandic waters, also settled in these areas (Hovgård and Messtorff MS 1987). However, nursery areas of Atlantic cod at Greenland can have a wider extension than the primary settling areas as the 1984 year-class was abundant and widely distributed from East Greenland to about 64°30’N at West Greenland at age 3 (Anon. 1990), which implies a subsequent transport and migration of the early juveniles.

The distribution patterns of cod fry in Greenland waters presented in this study can serve as a basis for
simulations using hydrodynamic models, which may provide a more realistic and detail view of transport processes than a comparison of the observed egg and larval distributions linked to a generalized current regime can do. In the recent years, temperature conditions have been favourable at East and Southwest Greenland (Borovkov and Stein MS 2001, Buch et al. MS 2002) and spawning stock biomass of Icelandic cod as well as 0-group abundance in Icelandic waters has been at or even above the levels reported for the 1980s, but cod have not been observed in Greenland waters in considerable numbers yet (Anon. 2002). Although changes in survival related to other factors than temperature might be at play, larval drift across the Denmark Strait appears to be crucial for a short-term recovery of the cod stock in Greenland offshore waters, and model simulations using actual wind fields encountered during the egg and larval period may help to explain why this has obviously not taken place in recent years.

References


