Reproduction of Faroe Plateau Cod: Spawning Grounds, Egg Advection and Larval Feeding

Nøringin hjá toskinum á landgrunninum: Gýtingarøki, eggspjaðing og føðin hjá larvunum

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Úrtak

Føroyski landgrunstoskurin gýtir serliga á tveimum økjum, ið liggja stutt innan fyri sjóvarfalsmótið, ið skilir landgrunssjógvin frá opna havinum. Eftir gýtingina reka rognkornini við sólini runt landgrunnin. Høvuðsgýtingin er í seinnu helvt av marsmánaði, og flestu toskalarvurnar byrja at eta í apríl. Um hetta mundið er nøringin av djóraæti ikki rættiliga byrjað á innaru landgrunsleiðunum, men á hellingini vestanfyri og norðanfyri reka *Calanus finmarchicus* frá árinum fyri inn á landgrunnin og byrja gýtingina longu í apríl. Kanningar frá apríl 1995 og 1999 vístu, at tað fyrsta, ið toskalarvurnar tóku, vóru serliga vatnloppuegg, ið eftir støddini verða mett at vera *C. finmarchicus* egg. Vatnloppu nauplius larvur høvdu bert lítlan týdning sum føði fyri hesar toskalarvur. Gýtingarøkini hjá toskinum eru nærindis leiðunum, har mest verður gýtt av *C. finmarchicus* eggum tíðliga á vári. Hetta ger, at toskarognkorn og –larvur og teirra høvuðsføði reka samstundis frá gýtingarleiðunum hjá toski. Tey reka við sólini eystureftir norðan fyri Føroyar og verða síðan spjadd runt landgrunnin. So hvørt sum toskalarvurnar vaksa, taka tær størri og størri føði. Kanningar í mai 1995 vístu, at tær ótu vatnloppu naupliur, ungar *C. finmarchicus* og ymisk sløg av landgrunsvatnloppum (serliga *Acartia* og *Temora*), ið vóru gýtt á landgrunninum sama várið.

Abstract

Faroe Plateau cod spawn mainly in two areas that lie close inside the tidal front that surrounds the Faroe Shelf. Eggs and larvae are advected in an anticyclonic direction around the Islands. Peak spawning is in the second half of March, and, thus, the majority of cod larvae start feeding in April. At this time, secondary production on the central shelf is still at a low level. However, over-wintered *Calanus finmarchicus*, which are advected from offshore onto the northern and western slope and shelf regions may spawn by April. Observations from April 1995 and 1999 showed that the first-feeding cod larvae fed mainly on copepod eggs, which, based on their sizes, are presumed to be mainly *C. finmarchicus* eggs. Copepod nauplii were only of minor importance. The spawning areas of Faroe Plateau cod are close to the areas with the highest average egg production of *C. finmarchicus* during early spring. This results in a coherent advection of cod eggs, larvae, and food from the spawning ground. They are advected clockwise, in an easterly direction, onto the northern shelf region and are then dispersed throughout the central shelf area. As the cod larvae grow, they switch over to larger prey. Food observations in late May 1995 showed mainly a mixture of copepod nauplii, young copepodites of *C. finmarchicus*, and various neritic copepod species (mainly *Acartia* and *Temora*), which were produced on the shelf during spring.

Introduction

The water on the Faroe Shelf (Fig. 1) is relatively well separated from the offshore environment by a persistent tidal front that surrounds all the islands. The tidal front is usually situated between the 100 and 150 m isobath (Gaard *et al.*, 1998; Gaard and Hansen, 2000). Due to extremely strong tidal currents, the water column over the shallow parts of the shelf is well mixed from the surface to the seabed. In addition to the tidal currents, a residual current flows anticyclonically on the shelf (Hansen, 1992; Simonsen, 1999; Hansen and Larsen, 1999). The renewal of the shelf water is highly variable and is, for example, affected by prolonged wind stress. The average flushing time of the central shelf water is estimated to be about three months (Gaard and Hansen, 2000).

The shelf water maintains its own neritic plankton ecosystem, which, with regard to the phytoplankton (Gaard, 1996; Gaard *et al.*, 1998) and zooplankton (Gaard, 1999) is, in most years, quite different from the surrounding oceanic environment. Zooplankton on the shelf is basically dominated by neritic species, of which *Acartia longiremis* and *Temora longicornis* are usually the most abundant copepod species during summer. During spring, barnacle larvae may also be quite abundant. The shelf ecosystem, however, is also affected by oceanic zooplankton. This influence is mainly by the copepod *Calanus finmarchicus,* which is advected onto the shelf in interannually, highly variable abundances (Gaard, 1999). This species is rarely found on the shelf during winter, but is advected

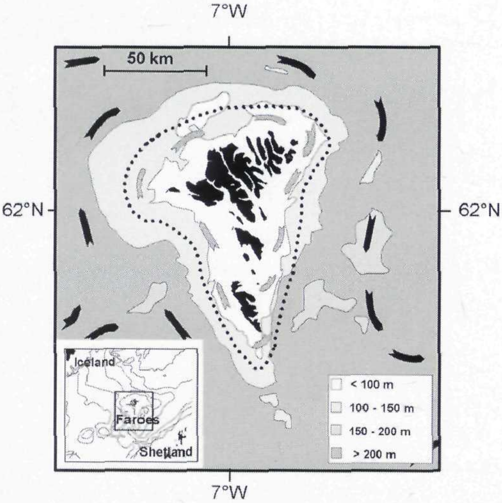


Fig. 1. *Bottom topography and main flow field around the Faroes. The dotted line indicates a typical position of the tidal front.*

Mynd 1. Botnskapið og høvuðsrákið rundan um Føroyar. Brotastrikan vísir, hvar sjóvarfalsfronturin vanliga kann vera.

onto the shelf during spring and summer (Gaard, 1999; Gaard and Hansen, 2000) and reproduces on the shelf (Gaard, 2000).

C. finmarchicus overwinters in diapause, mainly in the cold waters of the Norwegian Sea at depths below about 500 m (Heath *et al.*, 2000a). During that time, large quantities of *C. finmarchicus* are transported by the deep overflow through the Faroe-Shetland Channel (Heath and Jónasdóttir, 1999) and further through the Faroe Bank Channel (Gaard and Hansen, 2000). During spring, it migrates towards the surface (Heath, 1999), and advection onto the Faroe Shelf is considered largely to originate from the Faroe Bank Channel (Gaard and Hansen, 2000). During early spring (the pre-bloom period); these copepods spawn mainly in the western and north-western shelf regions and the offspring are then advected clockwise and dispersed onto the central shelf. Later in spring, their spawning increases on the central shelf too (Gaard, 2000).

The shelf ecosystem is also inhabited by several fish stocks, which breed and grow within the ecosystem. One of these fish stocks is the Faroe Plateau cod. Its spawning takes place mainly from February to May (Joensen and Tåning, 1970). Peak spawning, however, occurs in the second half of March (Hansen *et al.*, 1990). The main spawning grounds are in two areas, one to the west and one to the north of the islands at bottom depths of about 80-150 m (Jákupsstovu and Reinert, 1994). These areas are close to the tidal front that separates the shelf water from the offshore environment. The relatively long renewal time of the shelf water is a prerequisite for retaining the cod eggs and larvae within the ecosystem. However, by spawning so close to the front, the risk for the eggs and larvae to drift out of the ecosystem may be considerable. Hansen *et al.* (1994) hypothesised that this risk would be especially high during periods with strong winds. As cod spawns in these areas despite this risk, there may be other benefits that, in the long term, compensate for the risk of drifting off the shelf.

In this study, we have examined the food-related spawning strategy of Faroe Plateau cod by comparing spawning localities and offspring advection with production and availability of preferred food items for cod larvae on the Faroe Shelf during spring.

Materials and Methods

The data presented in this paper originate from several research cruises with the R/V *Magnus Heinason* in Faroe Shelf waters and the surrounding area. Demersal spawning cod were collected during February-March 1995 and 1999; hydrographic data, cod eggs, and young cod larvae were collected in April 1995 and 1999; egg production rates of *Calanus finmarchicus* were measured in April 1997, 1998, and 1999; and larger cod larvae were collected in May 1995.

In order to avoid possible effects from diel vertical migration of the fish and plankton and to avoid possible diel differences in spawning activity of *C. finmarchicus*, all sampling was carried out during daytime, between 06:30 and 18:30.

Cod abundance, size and maturity

Demersal spawning cod were collected during the annual spring ground fish surveys. One hundred fixed stations, covering the area on the Faroe Plateau within the 500 m contour, were sampled annually, between 24 February and 21 March 1995, and between 26 February and 20 March 1999. The fishing gear was a box trawl (116 feet) with a mesh size of 40 mm in the cod end. The bridles had a length of 60 m at shallow stations and 120 m at deep stations. The doors were of Steinhamn Type No. 8. The trawling time was one hour and the distance covered was about three nautical miles.

Table 1. *Maturity stages 3-7 for Faroe Plateau cod.*
Talva 1. Búningarstig 3-7 hjá landgrunstoskinum.

Stage	Female gonads	Male gonads
3	The eggs are visible by eye and the roe fills about half the volume of the body cavity.	The testes fill about half of the body cavity.
4	The eggs are clearly visible by eye as white corns. The roe fills about two-thirds of the body cavity.	The testes fill about two-thirds of the body cavity.
5	The eggs are circular and many are transparent. The roe is full size.	Testes are full size. Pressure on the belly causes drops of sperm to come out of the sac.
6	Light pressure on the belly causes the eggs to come out.	Light pressure on the belly easily causes sperm to come out.
7	Post-spawning: the roe is nearly empty.	Post-spawning: the testes are nearly empty.

The catch of cod was separated into spawning cod (maturity stages 5 and 6, as shown in Table 1) and non-spawning cod (all other cod, which are not presented in the results). Stages 1 (immature) and 2 (mature gonad, length about half of the body cavity) were excluded since these fish were assumed not to spawn during the current season. First, a maturity-at-length key was calculated from about 600 cod in 1995 and 1,000 cod in 1999, which were investigated in detail (total length, round weight, sex, maturity, and age). Second, the length distribution of cod from each station (scaled to total catch of cod) was split into spawning cod and non-spawning cod using the maturity-at-length key. By using a length-weight key, the total weight of spawning cod was calculated from each station.

To investigate whether there were differences in peak spawning times between the two years, 1995 and 1999, the average maturity-stage determination was used. Since Faroe Plateau cod migrates to its spawning areas prior to spawning (Tåning, 1940), to get comparable results for the two years, it was necessary to use measurements from stations where both position and date were as similar as possible. Only one station (with big catches, located at the western spawning site) could be used.

In order to investigate possible differences in maturity distribution between the two years, the chi-square test statistic was used. Maturity stages 3 to 5 were pooled in order to fulfil the statistical assumption requiring expected frequencies above five. Despite a moderate violation of the assumptions (one expected frequency was 4.5), a p-value well below 0.05 suggests that the null hypothesis can be rejected without difficulties.

Hydrography

Temperature and salinity were measured with a SeaBird CTD (model 911*plus*) at 50 stations at the central and northern shelf regions and slopes in 1995 during the period 10-14 April, and at 55 stations in 1999 during the period 22-27 April. The salinity was calibrated against water bottle samples, which were analysed on an Autosal (model 8400A) salinometer.

Calanus finmarchicus egg production

Egg production rates of *Calanus finmarchicus* were measured on three cruises: 25-29 April 1997 (50 stations), 17-25 April 1998 (73 stations), and 22-27 April 1999 (53 stations).

Live *Calanus finmarchicus* were collected with a WP2 net, equipped with a 1.1 litre plastic bottle at the cod end. Healthy females were transferred into 1.1 litre incubation chambers equipped with false bottoms (mesh size 400 µm) to separate eggs from females. They were incubated at the *in situ* temperature for 24 hours. Usually 10-12 females were incubated per station and two females were held in each incubation chamber. After incubation, the chamber content was filtered through a 30-µm mesh net and the eggs counted.

Zooplankton

In April 1995 and 1999, cod eggs, cod larvae, and *C. finmarchicus* females were collected for enumeration on the central and northern shelf regions and slopes during 10-14 April 1995 (50 stations), and 22-27 April 1999 (55 stations). In 1995, the samples were collected with a WP2 net on vertical hauls from a 50 m depth to the surface. The net had a mesh size of 200 µm and a towing speed of 0.3-0.5 m sec^{-1}. In April 1999, the samples were collected with a Bongo net (diameter: 0.6 m) with a mesh size of 200 µm. The net was slowly lowered down to approximately 50 m depth and hauled up again to the surface, while towing with a speed of about 2.5 knots. The volumes filtered by the net were measured with a Hydro Bios flow meter, which was mounted in the mouth of the net.

In May 1995, cod larvae were collected with a MIK net. The circular opening had a diameter of two metres. The mesh size was 1.5 mm in the net and 0.5 mm at the cod end. The net was lowered down to 10, 20, and 30 m depths while towing with a speed of about 2.5 knots. The volumes filtered by the net were measured with a Hydro Bios flow meter, which was mounted in the mouth of the net.

The zooplankton used for enumeration, cod larval length measurements, and food content investigation samples were preserved in 4% formaldehyde. In the laboratory, the larvae were identified and counted and their gut content was identified. The only cod eggs counted were those that were so well developed that the characteristic pigmentation pattern of cod embryos could be recognised inside the eggs. Thus, the cod egg enumeration only included those embryos in the latest developmental stages.

To see whether or not the mean cod larval length in April 1995 differed significantly from that in April 1999, a Welsch's approximate T-test for two samples with unequal variance was conducted.

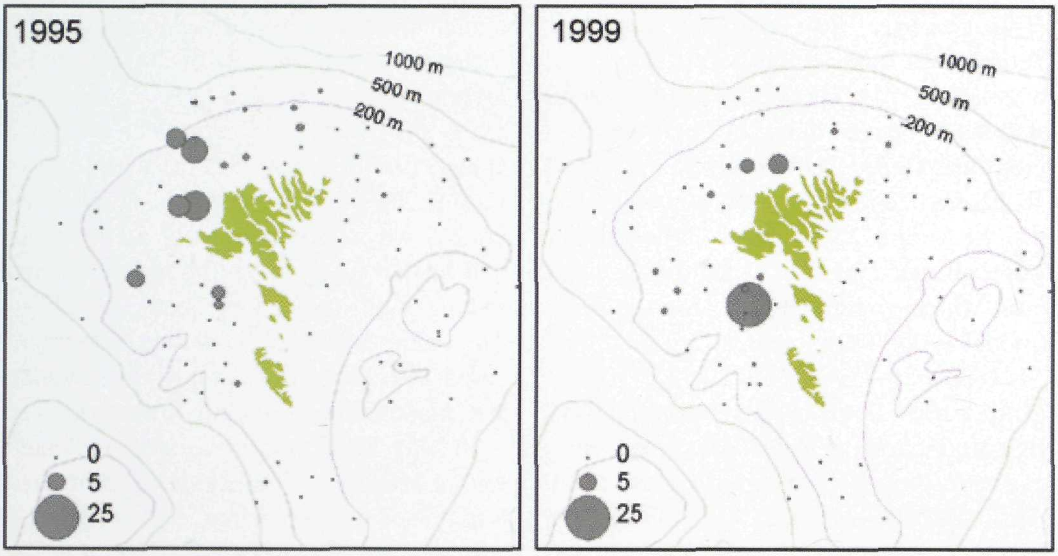


Fig. 2. Distribution of mature cod (tonnes per haul) on the Faroe Shelf during 24 February – 21 March 1995, and 26 February – 20 March 1999.

Mynd 2. Spjaðing av búnum toski (tons pr. tóv) á føroyska landgrunninum í tíðarskeiðinum 24. februar – 21. mars 1995 og 26. februar – 20. mars. 1999.

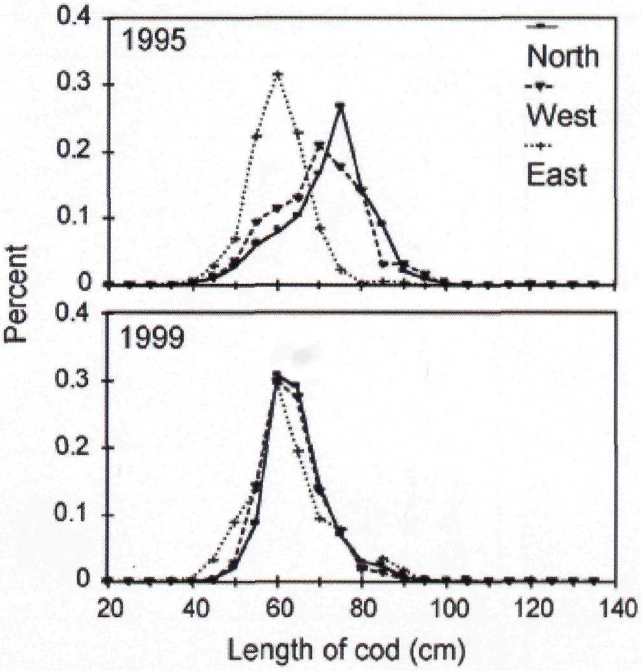
Results

Cod spawning

The spawning cod were concentrated in two areas, one in the western shelf region and one in the northern and north-western regions (Fig. 2). In the eastern and southern shelf regions, almost no mature cod were found. The cod were concentrated quite locally. The dots in Fig. 2 do not, therefore, necessarily show all the areas where mature cod were concentrated. Local areas with high concentrations may be missing. This may especially be the case at the northern spawning ground, which seems to cover a wider area than the western spawning ground.

The length of mature cod ranged mostly between 45 and 85 cm (Fig. 3; Table 2). In 1995, the few cod that were located in the eastern region were markedly smaller than the cod in the northern and western regions (the main spawning grounds). In 1999, however, no length difference was seen between the regions. Mature cod in the main spawning grounds were markedly larger in 1995 than in 1999 (Table 2).

The average maturity stage was quite similar in the two years (see Discussion). The variance (actually the maturity distribution) was, however, greater in 1995 compared to 1999 ($p<0.001$), when almost all mature fish had a maturity status of 6 (Table 3).



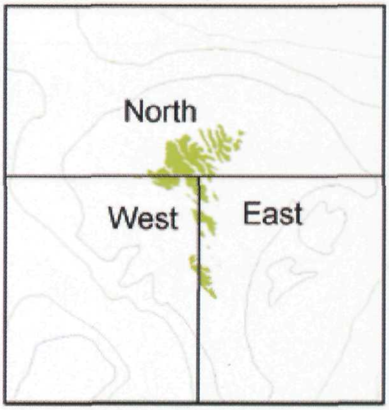


Fig. 3. Length distribution of mature cod in February – March 1995 and 1999.
Mynd 3. Longdarspjaðing av búnum toski í februar-mars 1995-1999.

Table 2. Mean length (cm) and standard deviation of mature cod during the spawning season in 1995 and 1999 in three main regions (Fig. 3) on the Faroe Shelf. The cod were caught between 24 February and 21 March in 1995, and 26 February and 20 March in 1999.
Talva 2. Miðallongdir (cm) og standardfrávik á búnum toski í gýtingartíðini í 1995 og 1999 í teimum trimum økjunum, sum víst eru á mynd 3. Toskurin varð fingin í tíðarskeiðunum 24. februar-21. mars 1995 og 26. februar-20. mars 1999.

	Mean length (cm)	St. dev.	Number examined
1995			
North	71.8	10.5	4,926
West	69.7	10.7	1,257
East	60.2	7.2	915
1999			
North	65.0	8.5	2,344
West	63.9	7.5	2,447
East	62.8	9.8	182

Hydrography in April 1995 and 1999

In mid-April 1995, the temperature on the shelf and slope was around 6.5°C. It ranged between 5.9°C and 7.2°C, with the lowest temperature at the shallowest stations and the highest temperature offshore, to the west of the Faroes. In late April 1999, the temperature hovered mostly at 7.0°C, ranging between 6.4 and 7.8°C. As a result of precipitation and shallow bottom depths, the shelf water has a slightly lower salinity than the surrounding oceanic water. An approximate position of the tidal front can be determined by this variance in the salinity gradient. The station grid covered a larger part of the shelf in 1999 than in 1995 and, therefore, the information about

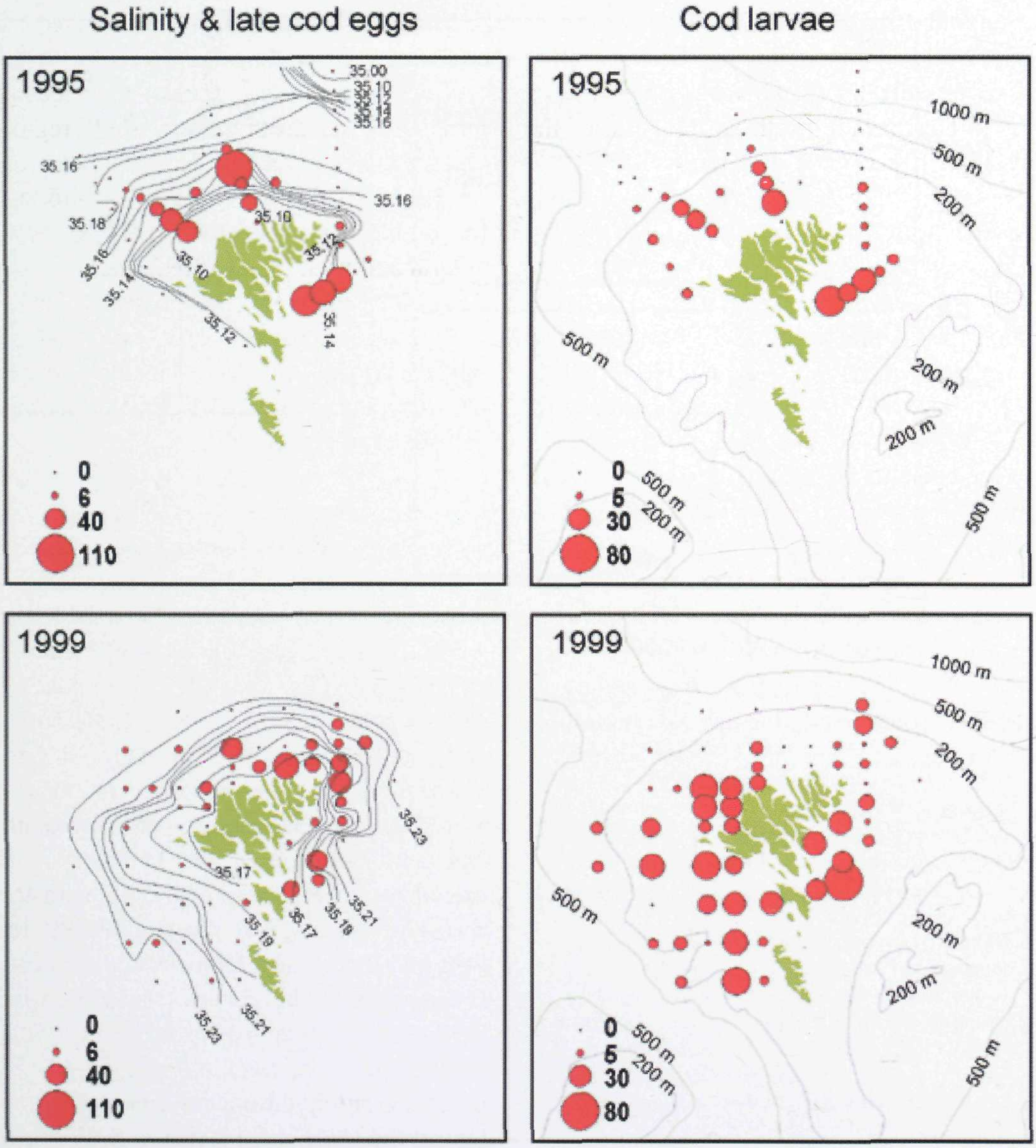


Fig. 4. Salinity at 50 m depth and abundance of late cod eggs (see text) and early cod larvae (number m^{-2}) in the upper 50 m of the water column on and around the Faroe Shelf during 10 – 14 April 1995, and 22 – 27 April 1999.
Mynd 4. Saltinnihald á 50 m dýpi og nøgdir av toskarognkornum, ið eru komin nær kleking (tí tekst) og ungar toskalarvur (tal m^{-2}) í ovastu 50 metrunum av sjónum, á og rundan um føroyska landgrunnin í tíðarskeiðinum 10.-14. apríl 1995 og 22.-27. apríl 1999.

horizontal salinity distribution is better in 1999 than in 1995 (Fig. 4). The isohaline figures indicate that the tidal front was closer to land on the north-eastern part of the shelf than on the western part in 1999.

Distribution and abundance of cod eggs and larvae in April

From the spawning grounds, cod eggs are advected with the residual currents in a clockwise direction. In mid-April 1995, most eggs (the latest stages) and larvae that were located to the north of the Islands were close to the salinity gradients that indicate the position of the tidal front (Fig. 4). However, while drifting eastwards in the northern region and southwards in the northeastern shelf region, most larvae were gradually advected into shallower areas. While drifting, the eggs develop and hatch and the larvae start feeding soon after hatching.

***Table 3.** Maturity distribution of mature cod in the western spawning site on 17 March in 1995 and 1999.*
Talva 3. Búningarstig á búnum toski á vestara gýtingarøkinum hin 17. mars 1995 og 1999.

Maturity stage	1995	1999
3	0	0
4	1	2
5	7	2
6	31	56
7	10	0
Average	6.0	5.9
St. dev.	0.7	0.4
N	49	60

In 1999, the samplings were carried out two weeks later than they were in 1995. Now the eggs (latest stages) were located mainly in the north-eastern shelf region. On the other hand, the larvae were more evenly distributed than the eggs, although the highest abundance was located in the central and western shelf regions.

In both years, very few eggs and larvae were found offshore. This indicates that the loss of eggs and larvae from the ecosystem may have been small during these two periods of observations.

Cod larval sizes in April 1995 and 1999

Even though the cod larvae in April 1995 were sampled about 12 days earlier relative to April 1999, the mean length of the larvae was significantly larger in 1995 than in 1999 ($P \cong 0$). The mean length ± standard deviation in April 1995 was 5.4±0.7 mm, and in 1999 it was 4.3±0.7 mm. In April 1995, the larval length distribution was quite large, however, there were two abundance peaks, one around 5.0-5.5 mm and one about 6-7 mm. No larvae were smaller than 4.0 mm (Fig. 5). In April 1999, the length distribution had only one peak, around 4 mm, and the smallest larvae were 3 mm.

Food content in the cod larvae

In April of both years, almost 50% of the first feeding larvae had an empty gut (Table 4). Green gut and small, unidentified particles, about 30 μm in diameter, occurred frequently. In addition, copepod eggs were by far the most important prey items, while copepod larvae were only of minor impor-

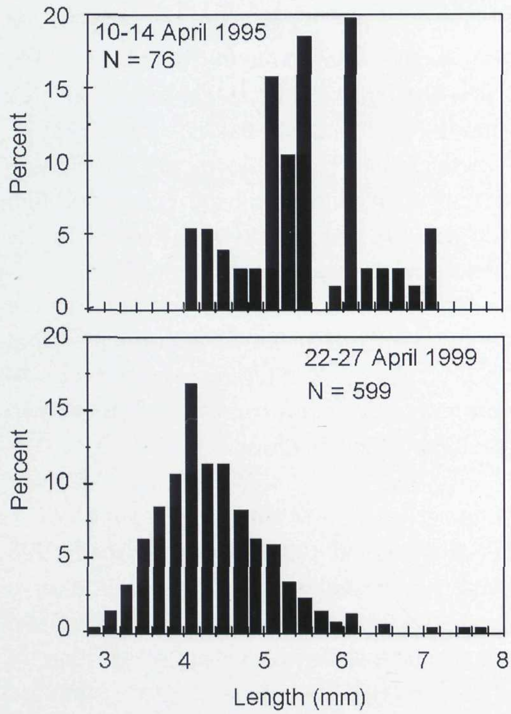


Fig. 5. Length distribution of cod larvae during 10-14 April 1995 and 22-27 April 1999.
Mynd 5. Longdarspjaðing av toskalarvum í tíðarskeiðinum 10.-14. apríl 1995 og 22.-27. apríl 1999.

tance. In April 1995, about 13%, and, in 1999, about 26% of the cod larvae had copepod eggs in their gut. Copepod nauplii were, on the other hand, not found in the cod larvae in 1995 and were found in only 4% of the larvae in 1999. Other zooplankton (*e.g.* Cirripedia nauplii, *Podon sp.* (Cladocera), and small copepodite stages) were only rarely found. The mean gut content of these prey items per larvae in April 1999 was 0.37 copepod eggs, 0.06 copepod nauplii, and 0.01 other zooplankton.

Most of the copepod eggs (~ 80-90%) found in the gut of the cod larvae were about 130-140μm in diameter and most likely were *Calanus finmarchicus* eggs. The rest of the eggs were smaller in size and most likely belonged to the neritic copepod species that occurred in the water. These were mainly *Acartia* and *Temora*. Thus, the first feeding cod larvae on the Faroe Shelf seem to have predated mainly on *C. finmarchicus* eggs during April 1995 and 1999.

In late May 1995, the gut content had changed considerably. Copepod eggs were only rarely found, and, instead, cod larvae preferred larger prey (Table 5). Copepod nauplii were commonly found, but the most frequently found food items were small and medium-sized copepodites, mainly within the size range of 0.6 to 1 mm. In 11% of these cod larvae, the gut was either empty or the content so well digested that the food could not be identified.

***Table 4.** Frequency of prey groups in the gut of cod larvae in April of 1995 and 1999.*
Talva 4. Títtleiki av ymiskari føði hjá toskalarvum í apríl 1995 og 1999.

Date	10-14 April 1995	22-27 April 1999
Copepod eggs	12.7%	26.7%
Copepod nauplii	0.0%	4.0%
Other zooplankton	0.0%	1.2%
Phytoplankton a.o. unidentified	39.7%	21.8%
Empty gut	47.6%	46.4%
Number of larvae	63	524

Table 5. Mean relative numbers of prey groups in cod larvae on the Faroe Shelf during 29-30 May 1995. Mean larval length and standard deviation was 12.2 ± 2.4 mm. N = 60

Talva 5. Miðal lutfalsligar nøgdir av ymiskari føði hjá toskalarvum á landgrunninum 29.-30. mai 1995. Miðalstøddin og standardfrávik á larvunum var 12,2 ± 2,4 mm. N = 60.

Prey group	Relative numbers (%)
Copepod eggs	3.2
Copepod nauplii	14.9
Calanus (CI-CIII)	21.3
Acartia	29.8
Temora	11.7
Other copepods	18.1
Other	1.0

Egg production of Calanus finmarchicus

The mean egg production of *C. finmarchicus* on the Faroe Shelf and slope in late April 1997, 1998, and 1999 was highly variable horizontally. It was highest in the western and north-western shelf and slope regions, with a mean production per stratum of 150-200 eggs m^{-3} day^{-1} (Fig. 6). It was markedly lower in the eastern and southern regions (50-100 eggs m^{-3} day^{-1}), and lowest in the central shelf region (<25 eggs m^{-3} day^{-1}).

Discussion

The two spawning grounds that were identified in spring of 1995 and 1999 (Fig. 2) are, to a large extent, identical to what has been reported earlier (e.g. Joensen, 1954; Joensen and Tåning, 1970; Jákupsstovu and Reinert, 1994). Cod spawn in two main areas, one western and one northern. The northern spawning ground seems to cover a much larger area than the western one. As mentioned earlier, Fig. 2 does not necessarily show all the high concentrations of spawning cod, as there may have been high concentrations between the sampling stations. However, the maps clearly show the positions of the main

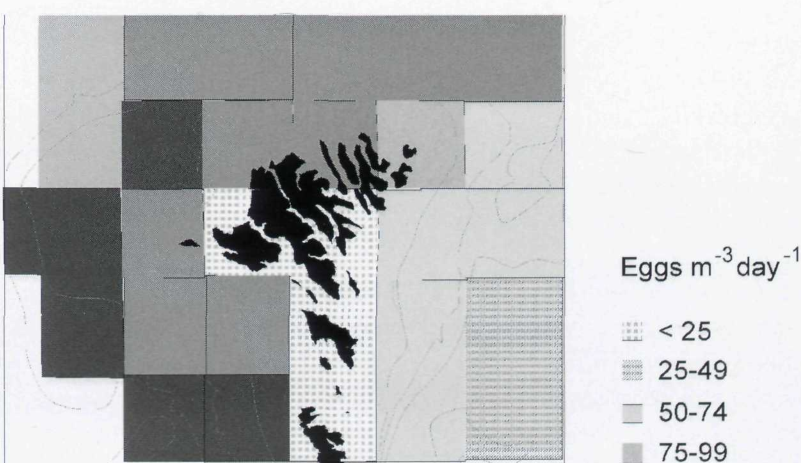


Fig. 6. Mean egg production of Calanus finmarchicus in the upper 50 m of the water column, per stratum, on and around the Faroe Shelf, 17-29 April 1997-1999.

Mynd 6. Miðal gýting hjá *Calanus finmarchicus* í ovastu 50 metrunum av sjónum, pr. punt, á og rundan um føroyska landgrunnin í tíðarskeiðinum 17.-29. apríl 1997-1999.

spawning grounds. Inside these spawning grounds (mainly the northern one), the positions of the densest concentrations of spawning cod may also vary interannually.

The peak spawning time in the western spawning area occurred at the same time of year in 1995 and 1999 (Table 3). Even though the material is based on data from only one station, the large cod catches and the high maturity status each year indicate that the results are representative for the whole western spawning area. The material for the northern spawning area did not allow direct comparison in time and location, but indicates, nevertheless, that the peak spawning time could be somewhat later in 1995 (two stations having average maturity of 5.0 on March 5) compared to 1999 (5.7 and 5.9 on 13 March at the same stations). These stations had good cod catches (between 900 and 6.100 kg) and were located just north of the second largest island and north of the northernmost island, respectively (Fig. 2).

The *in situ* temperature on the Faroe Shelf in April 1995 and 1999 (mainly between 6.5 and 7.0°C) is typical for that time of the year (Smed, 1952; Hansen, 2000; Heath *et al.*, 2000b). At this temperature, the duration from spawning to hatching for cod eggs has been estimated to be about 12-14 days (Iversen and Danielsen, 1984). The average, residual anticyclonic current at the spawning grounds is about 5-10 cm sec^{-1}, corresponding to about 4-9 km day^{-1} (Hansen, 1992; Hansen and Larsen, 1999). Hence, the cod eggs can be expected to drift about 50-100 km clockwise from the spawning areas before they hatch. Thus, eggs that are spawned in the western cod spawning area can be expected to hatch in the northern shelf region, while eggs that are spawned in the northern spawning grounds can be expected to hatch in the north-eastern and eastern shelf regions (Figs. 2 and 4).

Since only those cod eggs that were so well developed that the characteristic pigment pattern for cod larvae could be recognised in the embryos were counted, the eggs in Fig. 4 are estimated to represent only the last one or two days prior to hatching. Hence, the cod eggs in Fig. 4 most likely have been transported about 50-100 km anticyclonically from their spawning grounds. The distribution of these eggs in mid-April 1995 showed one abundance maximum in the north-western and northern shelf regions and another on the eastern shelf region. The question arises as to whether or not the two patches originate from the western and northern cod spawning grounds, respectively. In the north-western shelf region, cod eggs were distributed quite close to the salinity gradient border. This could make the eggs quite vulnerable to drifting off the shelf during periods of south-westerly storms, which are quite common in the area. Further east, they were advected closer to land. Unfortunately, no samples were collected in the southern part of the shelf that year, and, therefore, the distribution information in Fig. 4 does not show a complete picture.

In late April 1999, the larvae were largely concentrated in the central and western shelf areas. These larvae (and eggs) may have been transported in an almost complete circle around the archipelago prior to the samplings.

Despite the fact that the samplings were carried out almost two weeks earlier in 1995 than in 1999, most larvae were markedly larger in 1995 than in 1999. The use of different sampling gears in each of the years (WP2 net in 1995 and Bongo net in 1999) may have caused some differences in selectivity of the cod larvae. The mesh sizes of the two nets were the same (200 µm), but the Bongo net was towed approximately four times faster than the WP2 net, which would result in a higher selectivity of the largest larvae in the Bongo net. Since cod larvae collected with the WP2 net (1995) were larger than larvae collected with the Bongo net (1999), the size difference of the cod larvae that were observed between the two years must be assumed to have been real and not due to the different nets used.

The maturity-stage distribution of the spawning cod indicates that peak spawning during these two years occurred at about the same time (in the western area), or possibly a little later in 1995 than in 1999 (in the northern area). The water temperature was almost the same in both years (or even a little higher in 1999 than in 1995), and the gut content was not much different as well, with the same frequency of empty gut in both years (Table 4). Different growth rates, therefore, can hardly explain the size difference between the years. One could ask whether mortality of the larvae was higher in 1999 than in 1995, but this does not explain the lack of the smallest larvae in 1999 compared to 1995, especially when considering the fact that yolk sac larvae and young larval stages (Fossum, 1986) were commonly found in both years. One could speculate also as to whether or not the size of the cod eggs might have been different these two years. If so, then hatching larvae collected in 1999 would have been smaller than those collected in 1995.

Despite a large number of studies, there is still a general lack of information (and some contradictions too) about the factors that may affect cod egg size. Available information, however, indicates that egg size may be affected by a combination of several factors, including female size (or age), condition, spawning stage, and sea temperature. Based on the available information, it is not possible to determine which factors may have affected the observed size difference these two years, although some factors are more likely than others. Pepin *et al.* (1997) reported an increased length at hatch with increasing temperature. However, since the *in situ* temperature was about 0.5°C lower in the year with the larger larvae (1995,) this cannot explain the difference in larval lengths between the years. Other studies demonstrated that large cod females generally produce larger eggs than small females (Kjesbu *et al.*, 1996; Marteinsdóttir and Steinarsson, 1998). The spawning cod in 1995 was about six cm larger than in 1999 (Fig. 3; Table 2). This may have affected egg sizes, but this factor alone does not seem to be enough to explain the larval size difference between the two years. Another possible explanation is that the sampling in 1999 was carried out almost two weeks later than in 1995. Cod eggs are reported to decrease in size as the spawning season advances (Kjesbu *et al.* 1992; 1996; Chambers and Waiwood, 1996; Bleil and Oeberst, 1998; Marteinsdóttir and Steinarsson, 1998; Trippel, 1998). The eggs in 1995 were spawned during the peak spawning period, while the eggs and larvae sampled in 1999 were spawned quite late in the spawning period. We may thus speculate whether or not the difference in larval lengths these two years may have been due to the combined effect of these two parameters (female size and spawning stage).

A large number of studies show size-dependent food selectivity by cod larvae, where first-feeding larvae select small-sized prey (mainly copepod eggs and nauplii), gradually switching over to larger prey as they grow (e.g. Thorisson, 1989; Kane, 1984; Otterå, 1993; McLaren and Avendaño, 1995). The present study provides similar results. A great number of first-feeding larvae had phytoplankton in their guts in April. This is a common finding in small larvae (Nordeng and Bratland, 1971; Ellertsen *et al.*, 1980). Among the zooplankton prey group, copepod eggs (presumably *Calanus finmarchicus* eggs) were by far the most important food item for first-feeding cod larvae. This finding was also seen in the above-mentioned studies, but in those studies the number of eggs was markedly lower in proportion to nauplii than in the present study (Table 4). As the larvae grew, they switched over to larger prey. In May 1995, cod larvae selected mainly small and medium-sized copepodites and copepod nauplii (Table 5). This increase in the size of selected prey items continues as the larvae and pelagic juveniles on the Faroe Shelf grow during summer (Gaard and Reinert, 2000).

Since *C. finmarchicus* eggs seem to be a key food source for the first-feeding cod larvae during early spring, knowledge about the egg production of *C. finmarchicus* during the early spring is important in order to understand feeding conditions for first-feeding cod larvae on the Faroe Shelf. The fecundity of copepods is generally considered to be food limited (Diel and Tande, 1992; Kiørboe *et al.*, 1990; Kiørboe and Nielsen, 1994; Hirche, 1996; Niehoff *et al.*, 1999). On the Faroe Shelf, the spring bloom develops during May in most years (Gaard, 1996; Gaard *et al.*, 1998; Gaard, 1999). However, the lag phase on the shelf may be quite long. During this pre-bloom period (in April), the phytoplankton biomass is clearly higher on the shelf than offshore in most years (Gaard, 1994; 2000). During spring, copepod production on the central shelf, for the most part, increases simultaneously with the increase in phytoplankton (Gaard, 1999; 2000). However, overwintered *C. finmarchicus* that are advected onto the shelf slope start to reproduce on the western and north-western shelf and slope regions during the pre-bloom period in most years. Offspring from this reproduction appear to be advected clockwise in an easterly direction in the northern shelf region, and, subsequently, are dispersed throughout the central shelf area. This happens in most years prior to the increase in copepod reproduction in the central shelf region (Gaard, 1999; 2000).

Hence, in most years, significant egg production of *C. finmarchicus* occurs during early spring in the western and north-western shelf regions, which is markedly earlier than in the central shelf region.

Faroe Plateau cod seem to select their spawning grounds close to the main spawning areas of *C. finmarchicus*. At the time of year when most first-feeding cod larvae occur on the Faroe Shelf (April), reproduction of most of the neritic copepods is still at a low level (Gaard, 1999). However, overwintered *C. finmarchicus* that have ascended from diapause in deep water (Heath and Jónasdóttir, 1999; Gaard and Hansen, 2000) may have some significant spawning at this early time of the year. This spawning is mainly in the western and north-western shelf areas (Fig. 6; Gaard, 2000), which are also the areas that are assumed to be a major inflow area of *C. finmarchicus* onto the shelf during spring (Gaard and Hansen, 2000). Thus, taking into account the low reproduction of neritic copepods on the shelf at this early time of the year (Gaard, 1999), spawning of the overwintered *C. finmarchicus* would, in most years, be the most reliable food source for cod larvae. By spawning in these areas, cod ensure that their eggs drift together with spawning *C. finmarchicus* clockwise, first to the west and north of the islands, and then disperse onto the central shelf area. This hypothesis is supported by the gut contents (Table 4), where copepod eggs (presumably mainly *C. finmarchicus* eggs) were the most important food items for first-feeding cod larvae.

By spawning in areas close to the tidal front, cod expose their eggs to considerable risk of drifting off the shelf. The dominant wind force in the area is from the south-west (Gaard and Hansen, 2000). During stormy periods, the risk of drifting off the shelf to the north of the Faroes may be considerable for cod eggs (Hansen *et al.* 1994). Because the cod spawn in these areas, despite this risk, the food-related benefits may, in the long run, outweigh the possibility of drifting off the shelf.

In late spring, when cod larvae select larger prey (mainly small copepodite stages), they are dispersed inside the shelf region and can prey on the neritic species, which by that time in most years have started their reproduction.

Based on what is presented above, good feeding conditions for Faroe Plateau cod larvae would require a high level of reproduction of *C. finmarchicus* close to cod spawning grounds during the early spring, and then high copepod reproduction on the shelf during late spring and summer. Some advection of overwintered *C. finmarchicus*, together with some pre-bloom egg production of *C. finmarchicus* close to the cod spawning grounds, therefore, seem to be the prerequisites for successful feeding conditions for first-feeding larvae. On the other hand, Gaard *et al.* (1998) suggests that too high an advection of overwintered *C. finmarchicus* onto the shelf during early spring most likely would have an inhibitory effect on phytoplankton production on the Faroe Shelf. This could potentially negatively affect copepod fecundity on the shelf during spring. If this holds true, the best feeding conditions for Faroe Plateau cod larvae will be in years with moderate advection of overwintered *C. finmarchicus* onto the shelf.

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