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# A TENTATIVE METHOD TO ESTIMATE MORTALITY IN THE EGG AND EARLY FISH LARVAL STAGES, WITH SPECIAL REFERENCE TO COD *(Gadus morhua L.)*

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## ABSTRACT

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A tentative method to estimate egg and larval mortality is demonstrated. The material was sampled during the cod egg and larvae surveys in the Lofoten area in the years 1983 and 1984. Correct ageing of eggs and larvae, reliable estimation of the number of individuals in different age groups, and the spawning curve (number of eggs spawned per day) are the principal components in the method. To estimate the mortality, the number of eggs and larvae in different age groups (8–50 days after spawning) are compared with the estimated number of spawned eggs. A mean daily instantaneous mortality rate of 0.12 can explain the reduction in number of spawning products during the period of investigation both in 1983 and 1984. The course of the mortality curve is discussed in relation to starvation and predation.

## INTRODUCTION

Surveys of Northeast Arctic cod larvae have been carried out in the Lofoten area during the period 1979–86 (ELLERTSEN *et al.* in prep.) and cod egg surveys in the same area during the period 1983–85 to estimate the spawning stock of Northeast Arctic cod (SUNDBY and BRATLAND 1987). These surveys have provided material to estimate the mortality of the spawning products of the cod in the period 0–50 days after spawning for the years 1983 and 1984.

Little information exists on mortality rates of marine fish eggs and larvae, especially on cod (DAHLBERG 1979, HUNTER 1984). The data presented in the literature indicate that the mortality rates of pelagic fish eggs and larvae in general must be high and variable both between years and populations. The range of observed mortality rates is 7–67% per day. DAAN (1981) found a daily mortality rate of 22% for cod eggs in the North Sea. Thus, only 2% of the cod eggs spawned, hatched and produced larvae.

Predation and abiotic factors such such as wave action have been proposed as the main sources of mortality of pelagic fish and larvae with yolk sac. In older larvae, starvation and predation have been proposed as the main sources of mortality, and mesocosm investigations (ØIESTAD 1985) have shown that the ability to survive is enormous in predator-free productive systems.

Direct observations of the mortality of different egg and larval stages through the incubation and larval period may give some additional information on the importance of different regulating mechanisms.

Most authors believe that mortality in the early stages has significance for the strength of the year class, but there is a question about what is the most important recruitment regulating factor, starvation or predation. Much work has been done to evalute "the critical period concept" first put forward by HJORT (1914). The reviews by MAY (1974) and DAHLBERG (1979) failed to provide clear evidence of a critical period. But there is much evidence for the potential sensitivity of fish larvae to quantitative and qualitative alterations in the food supply (LASKER 1975, LAURENCE 1974, HOUDE 1975, YODER 1983, BAKUN and NELSON 1977, BAILEY 1981, FORTIER and LEGGETT 1984 and ELLERTSEN *et al.* in prep).

It is more difficult to find direct evidence of predation *in situ*, but it is a widely held belief that macroinvertebrates and planctonic-feeding fish consume large amounts of fish eggs and larvae (MAY 1974, HUNTER 1984, LAURENCE 1981, WARE 1975 and MØLLER 1979, 1980 and 1984). More direct evidence of predation has recently been found by MELLE (1985) and PURCELL (1984). A contradictory view is held by SISSENWINE (1984) who concludes that the recruitment of Georges Bank herring is most sensitive to the mortality in the period from five months to two years.

Other causes of great variations in recruitment may be long-term variations in the climate (KOSLOW 1984), or variable degrees of retention of the spawning products in areas where the survival of the progeny and the condition for their adopting the migration pattern of the stock they belong to are optimized (SINCLAIR and ILES 1985).

Thus the major cause or causes of recruitment variability is a question still to be answered. This paper will describe an attempt to estimate the mortality of the spawning products, and discuss the course of the mortality curves in relation to predation and starvation.

The estimates of egg and larval mortality are based upon the assumption that the whole area of distribution of the spawning products are covered during the egg and larval surveys. Three main spawning areas are found in the area: inside the Vestfjord, at Røst, and on the Moskenesbank. The spawning products from the Vestfjord are found in the near-shore coastal water masses and are retained in the area for a long period, while the spawning products from the outer areas are flushed out of the system in a short time.

Thus this investigation is based on the spawning products from the Vestfjord, approximately 50% of the total spawning of the Northeast Arctic cod in 1983 and 1984 (SUNDBY and BRATLAND 1987).

## MATERIALS AND METHODS

### *FIELD SAMPLING*

A total of eight surveys were conducted in 1983 and 1984. In both years three cod egg surveys were carried out in the period March–April to measure the cod egg production (SUNDBY and BRATLAND 1987). The cod egg survey tracks are shown in SUNDBY and BRATLAND (1987). In early May of both years a survey was conducted with two research vessels, "Johan Ruud" and "Eldjarn", to measure the distribution and abundance of first-feeding cod larvae. The cod larval survey tracks are shown in Fig. 1 and Fig. 2.

On each station of the cod egg surveys, nets with 0.5 $m^2$ opening were hauled from 75–0 m. During the cod larval surveys, the same nets were hauled from 50–0 m, covering the vertical distribution of eggs and larvae (SOLEMDAL and SUNDBY 1981, ELLERTSEN *et al.* 1977). The mesh size of the nets was 375 μm and the hauling velocity 0.5 m/s. On the stations, salinity and temperature data were collected by a CTD sonde.

### *SAMPLE PROSESSING*

The samples were sorted on board, and cod eggs and larvae were preserved in 4% formalin in 30% sea water. The whole egg sample or a subsample of 20 eggs, if the sizes of the sample was larger than 20, was classified according to 6 different substages, according to WESTERNHAGEN (1970) as modified by STRØMME (1977). All the cod larvae were staged according to FOSSUM (1986).

### *EGG AND LARVAE MORTALITY ESTIMATION*

The abundance, in numbers per square meter of surface, of eggs in stage 4+5 and stage 6 and larvae in stages 1–4, 5+6, 7+8 and 9 were plotted on maps. The duration of these egg and larval stages at the prevailing temperatures is shown in Table 1.

The duration of stage 9 is estimated to be about 14 days. The oldest larvae are to a certain extent able to avoid the nets. Thus a knife-edge selection curve with a threshold age of 42 days is used. This means that all the larvae with age under 43 days are caught, while all larvae over 42 days old avoid the nets.

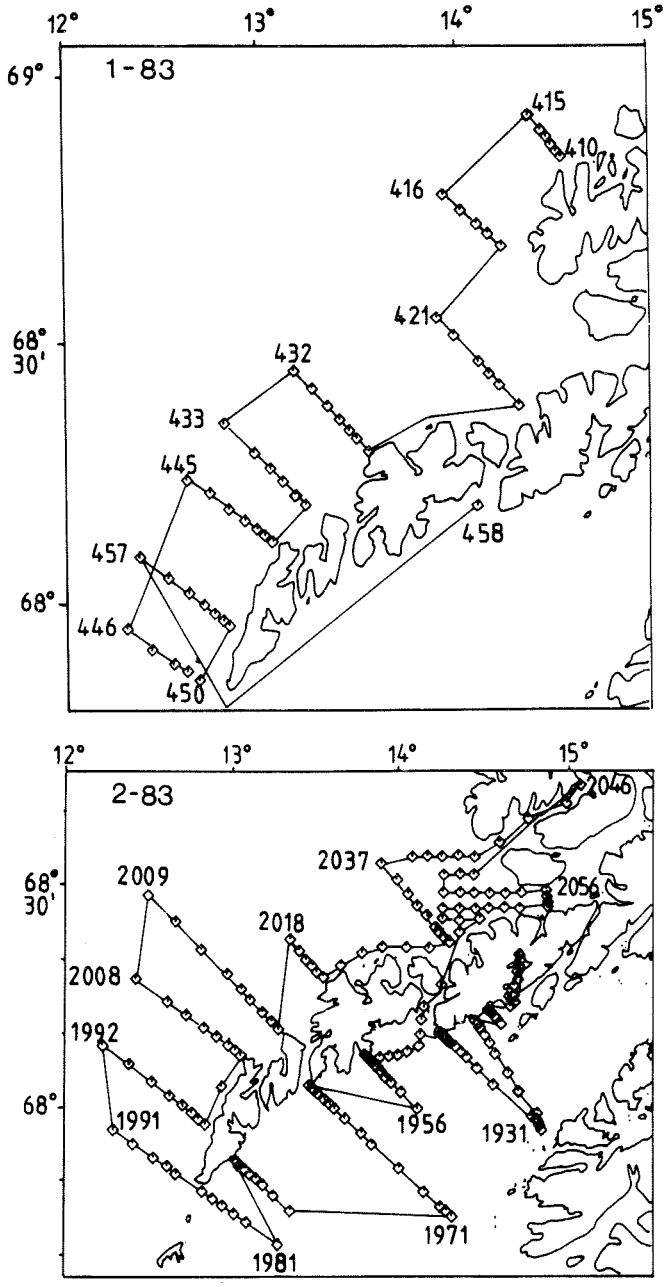


Fig. 1. The cod larval survey tracks in May 1983. 1–83 R/V "Eldjarn" 6–9 May 1983, 2–83 R/V "Johan Ruud" 6–9 May 1983.

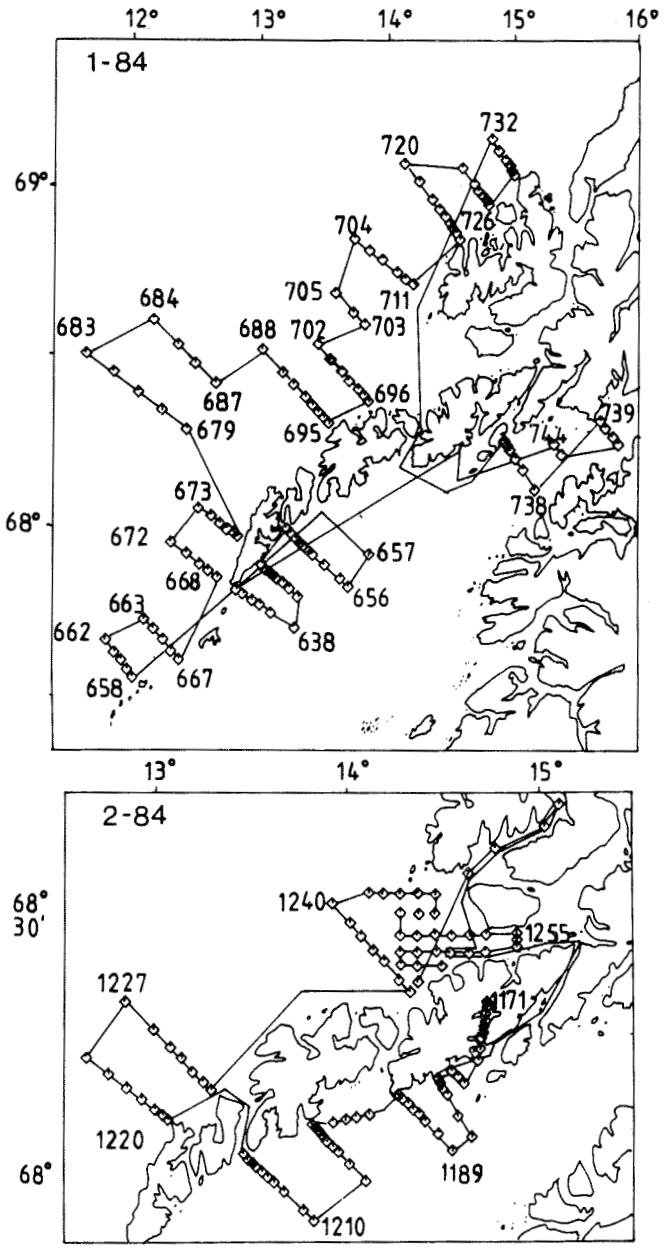


Fig. 2. The cod larval survey tracks in May 1984. 1–84 R/V "Eldjarn" 6–10 May 1984, 2–84 R/V "Johan Ruud" 6–10 May 1984.

Table 1. The duration of different egg and larval stages.

| Stage | Duration (days after spawning) |
|---|---|
| Egg stage 4–5 | 7–14 |
| Egg stage 6 | 15–19 |
| Larval stage 1–4 | 20–23 |
| Larval stage 5–6 | 24–27 |
| Larval stage 7–8 | 28–35 |
| Larval stage 9 | 36–50 |

Different stages are coalesced if the duration of the combined stages is shorter than one week, because of the relatively limited size of the larval material. The total number in each of these groups was calculated by an area-integrating method (SUNDBY and BRATLAND 1987). The area of investigation was divided into seven different subareas. Estimates of the total number in a certain group of spawning products within a subarea were calculated by the following method: Isolines between values of 1, 5, 10, 20 and 30 spawning products/$m^2$ of the surface were drawn. Then the area in square centimeters between the different isolines was calculated, adjusted according to the map correction factor (within the range 11–13 $km^2/cm^2$ in the area of investigation), and multiplied by the mean abundance of the specific spawning product between the two isolines. The total estimates within the subarea was the sum of spawning products between the different isolines, and the total estimate was the sum of the individual estimates from the different subareas.

The survival of the spawning products was calculated by a comparison of the estimated number of eggs spawned and the resulting number of spawning products 7–44 days later. (For example the number of stage 5–6 larvae aged 24–27 days post-spawning were compared with the estimated number of eggs spawned 24–27 days earlier). A spawning curve of eggs spawned per day for the area of investigation in 1983 and 1984 was calculated by SUNDBY and BRATLAND (1987). The estimates of spawned eggs are inferred from these curves, since the number of eggs spawned during a certain time period is the integral under the spawning curve.

No attempt is made to estimate the variance of the mortality because of the large errors involved in field sampling of eggs and larvae.

## RESULTS

The main spawing was concentrated in the last days of March and the first days of April, and 50% spawning occurred on 31 March for the period 1975–85 (ELLERTSEN *et al.* in prep.). During the peak spawning 200–300 $\times$ $10^9$ eggs were spawned per day in the Vestfjord.

Results of temperature and measurements are given in SUNDBY and BRATLAND (1987). The mean temperature in the mixed layers in March–April was 0.5 °C above the normal (last 30 years) in 1983 and at the normal in 1984.

In Fig. 3 the horizontal distribution of 8–15 day-old cod eggs is shown from the surveys 8–10 April and 6–9 May 1983. The number of cod eggs at this age was estimated to be $1100 \times 10^9$ on the first coverage and $149 \times 10^9$ on the second. The areas with the highest number of cod eggs changed from the central spawning areas in the Vestfjord to the outer side of the Lofoten islands from the first to the second coverage. This can be seen as an example of the westward movement of the spawning cod throughout the spawning season. The first coverage measured the abundance of eggs spawned during the peak of the spawning, and the last coverage the abundance of eggs spawned towards the end of the spawning period. The estimates of eggs spawned 8–15 days prior to the coverages, the orgin of the eggs within the age groups 8–15 days, were $3235 \times 10^9$ and $315 \times 10^9$, respectively. This means that the original number of eggs was reduced by 66 and 53% in the period from spawning to 12 days after spawning, and that the reduction is somewhat stronger for the eggs produced during the most intense spawning than towards the end of the spawning period.

In 1984, samples of cod eggs in the same age group, 8–15 days old, were examined from a survey carried out in the period 2–7 April. Their horizontal distribution is given in Fig. 4. Most of the eggs were found inside the Vestfjord. The total number of eggs in this age group was estimated to be $463 \times 10^9$. They originated from $1593 \times 10^9$ eggs spawned 8–15 days earlier, a reduction of 71%.

In Fig. 5, the horizontal distribution of eggs near hatching, aged 15–20 days, is shown. The eggs are from the survey carried out in the period 6–9 May 1983. Most of the eggs were found inside the Vestfjord over the spawning grounds of the cod, but some eggs were also found on the outer side of Lofoten and in the Vesterålsfjord. The total number of eggs near hatching found during this period is estimated to be $54 \times 10^9$. The estimate of the original number of eggs spawned 15–20 days earlier is $340 \times 10^9$. Thus a reduction of 84% in numbers of eggs in this period can be calculated. Comparable data are not available for 1984.

The following results are all from the larval surveys in 1983 and 1984. The cod larval material consisted of 2260 and 2156 larvae in 1983 and 1984, respectively. The same pattern of larval distribution was seen both years. Most of the larvae were found inside the Vestfjord. However, the center of distribution moved slightly westward in 1984 compared to 1983, and more of the oldest larvae were found on the outer side of the Lofoten Islands, especially in the Vesterålsfjord in 1983.

The abundance and distribution of stage 1–4 larvae 20–23 days after spawn-

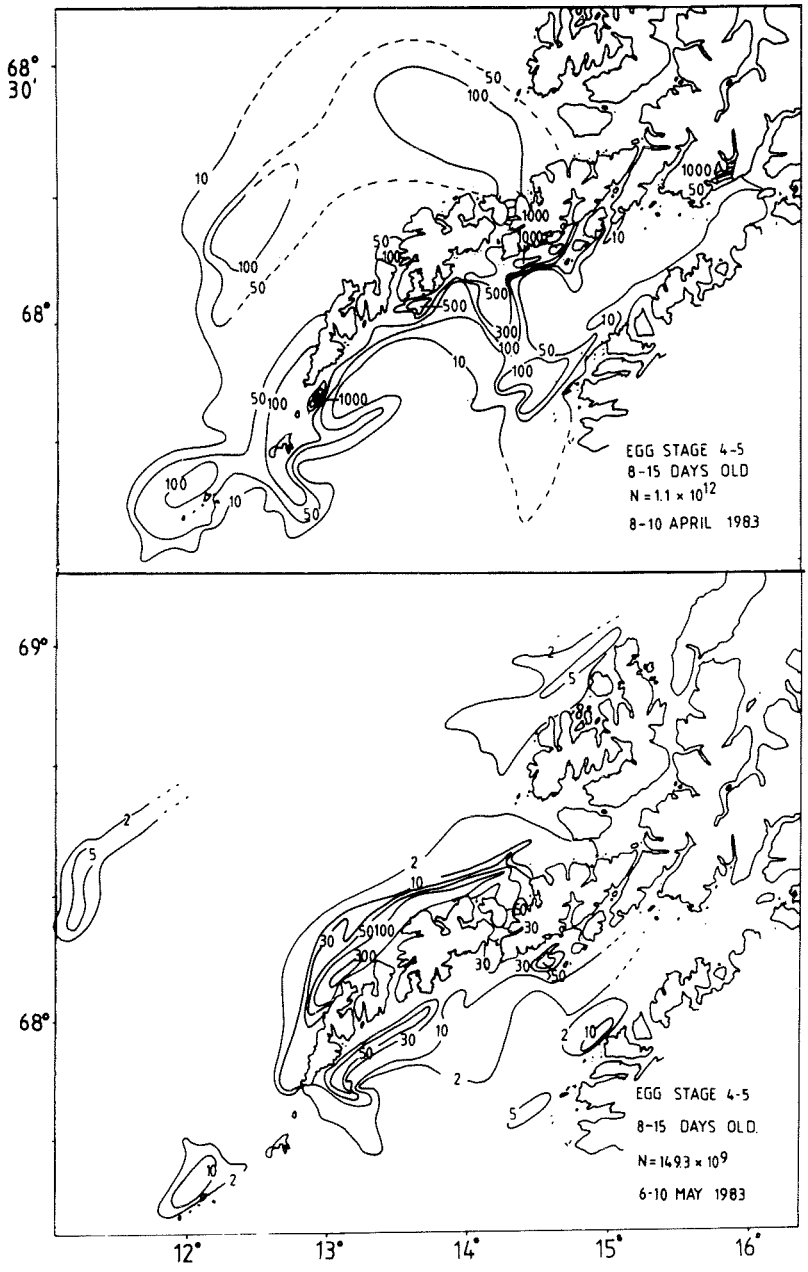


Fig. 3. The horizontal distribution of 8–15 day-old cod eggs.

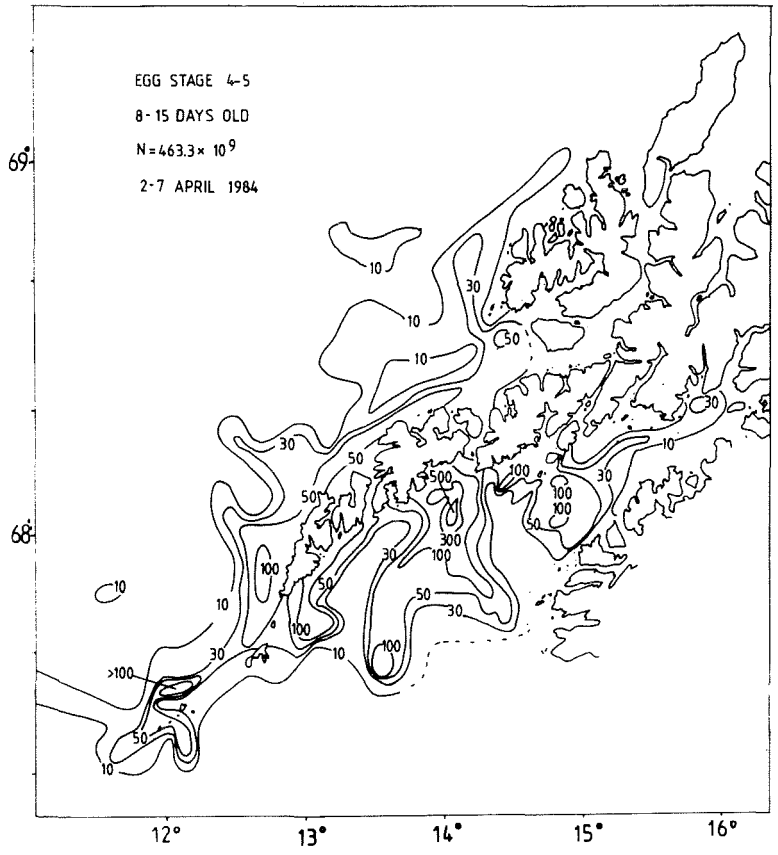


Fig. 4. The horizontal distribution of 8–15 day-old cod eggs from a coverage carried out 2–7 April 1984.

ing in 1983 and 1984 is shown in Fig. 6. The total number in these stages within the area of investigation is estimated to $18 \times 10^9$ at the mean date of the coverage in 1983. The estimate of the total number of eggs spawned 20–23 days earlier is $400 \times 10^9$, thus the number of spawning products is reduced by 95.5% over this time period. The data for 1984 give a reduction from $403 \times 10^9$ to $24 \times 10^9$, or 94.1%.

The abundance and distribution of first-feeding yolk sac-larvae stage 5–6, of age 24–27 days after spawning, is shown in Fig. 7. The total number of these larvae was $14 \times 10^9$ in 1983. An estimate of the total number of eggs spawned 24–27 days earlier, $620 \times 10^9$, gave a reduction of 97.7%. The coverage in 1984, shown in the same figure, gave the following results: $22 \times 10^9$ larvae belonged to stage 5–6, and these orginated from $482 \times 10^9$ eggs, hence a reduction of 95.5%.

The horizontal distribution of post-yolk sac first-feeding larvae, stage 7–8,

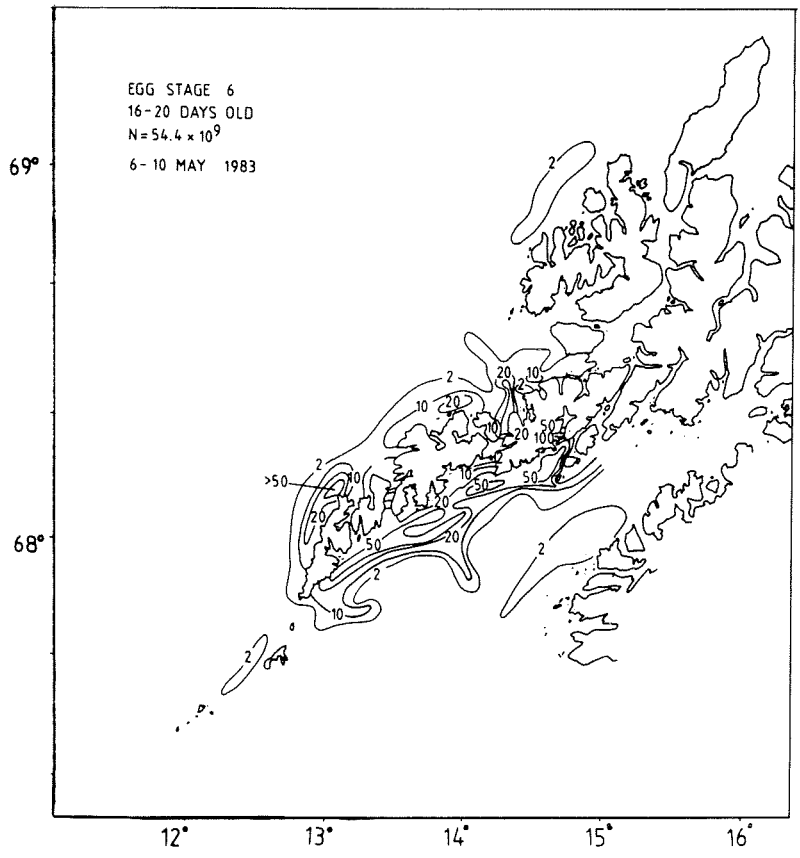


Fig. 5. The horizontal distribution of cod eggs near hatching, from a coverage carried out 6–9 May 1983.

is shown in Fig. 8. In 1983, $23 \times 10^9$ larvae were found, orginating from $2600 \times 10^9$ eggs, a reduction of 99.1%. In 1984, $28 \times 10^9$ larvae were found in these stages. The original number of spawned eggs was $1524 \times 10^9$, hence a reduction of 98.2%.

The horizontal distribution of the oldest larvae, stage 9, 36–50 days after hatching, is given in Fig. 9. The estimated number in this stage was $10 \times 10^9$ in 1983 and $6 \times 10^9$ in 1984, originating from $2940 \times 10^9$ and $1632 \times 10^9$ eggs, respectively. A reduction of 99.7% was observed both years.

In Table 2 the estimated numbers in all of the different age groups of eggs and larvae are given, together with the estimated number of eggs they orginated from, the reduction in number (%), and the daily instantaneous mortality rate (z).

Both this table and Fig. 10, showing the mortality of the spawning products from spawning to 50 days after spawning on a logarithmic scale, give the impression of a constant mortality in this period.

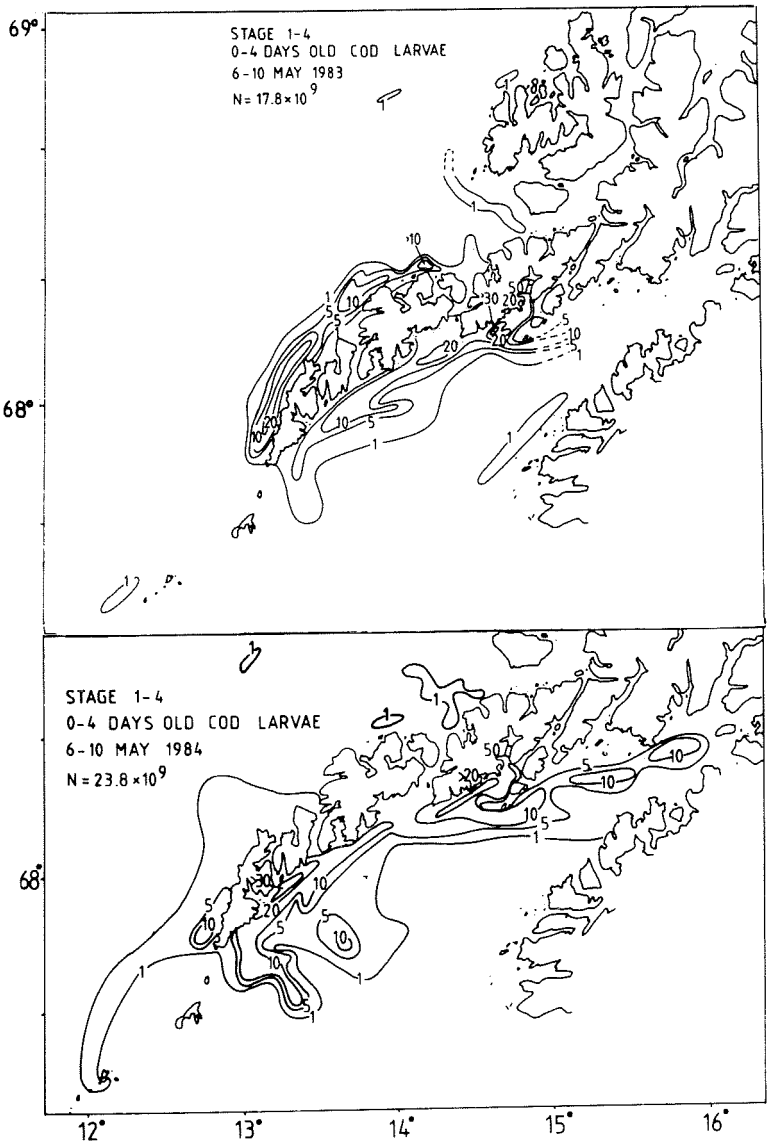


Fig. 6. The horizontal distribution of unfeeding yolk sac larvae of cod, stage 1–4.

In Fig. 11, the numbers of larvae in different age groups found in the different subareas are shown. In Fig. 12, the frequency of the different age groups on the western side of the Lofoten Islands is given. Both figures show that the only group of spawning products that to some extent was found outside the Vestfjord were the oldest larvae in 1983, while most of the other larvae were found inside the Vestfjord.

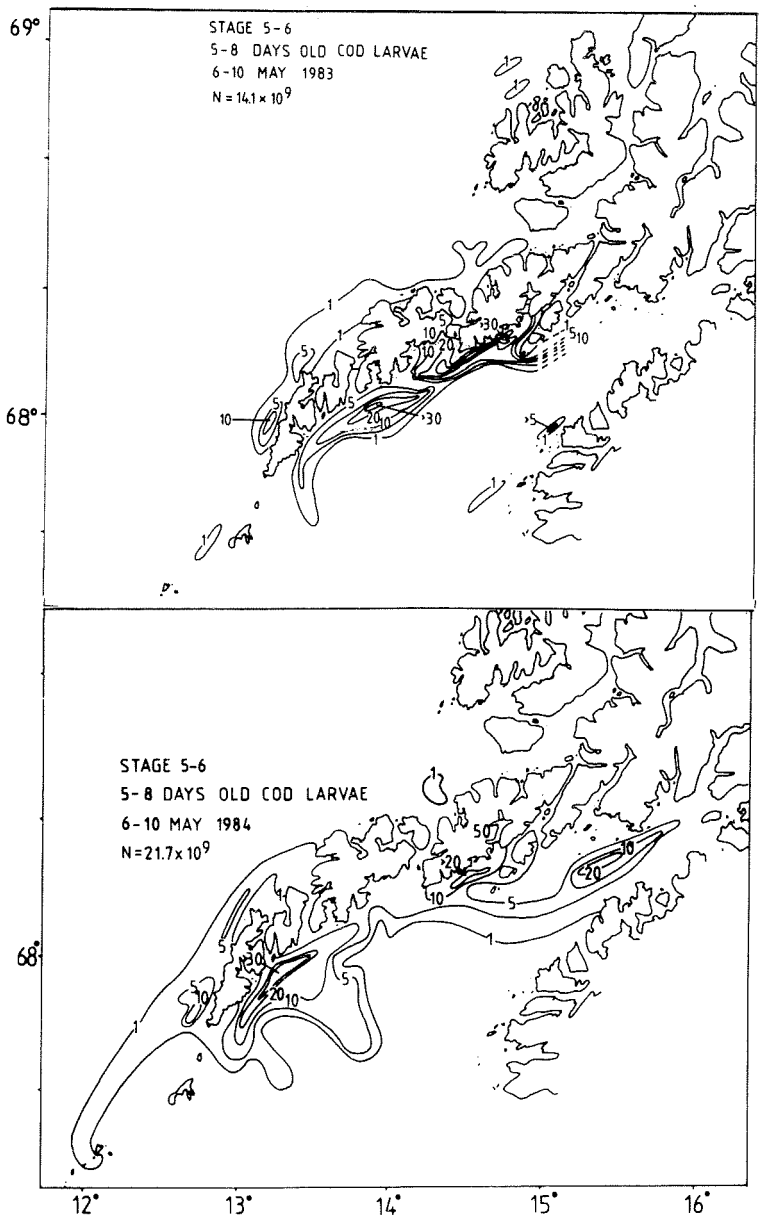


Fig. 7. The horizontal distribution of first-feeding yolk sac larvae, stage 5–6.

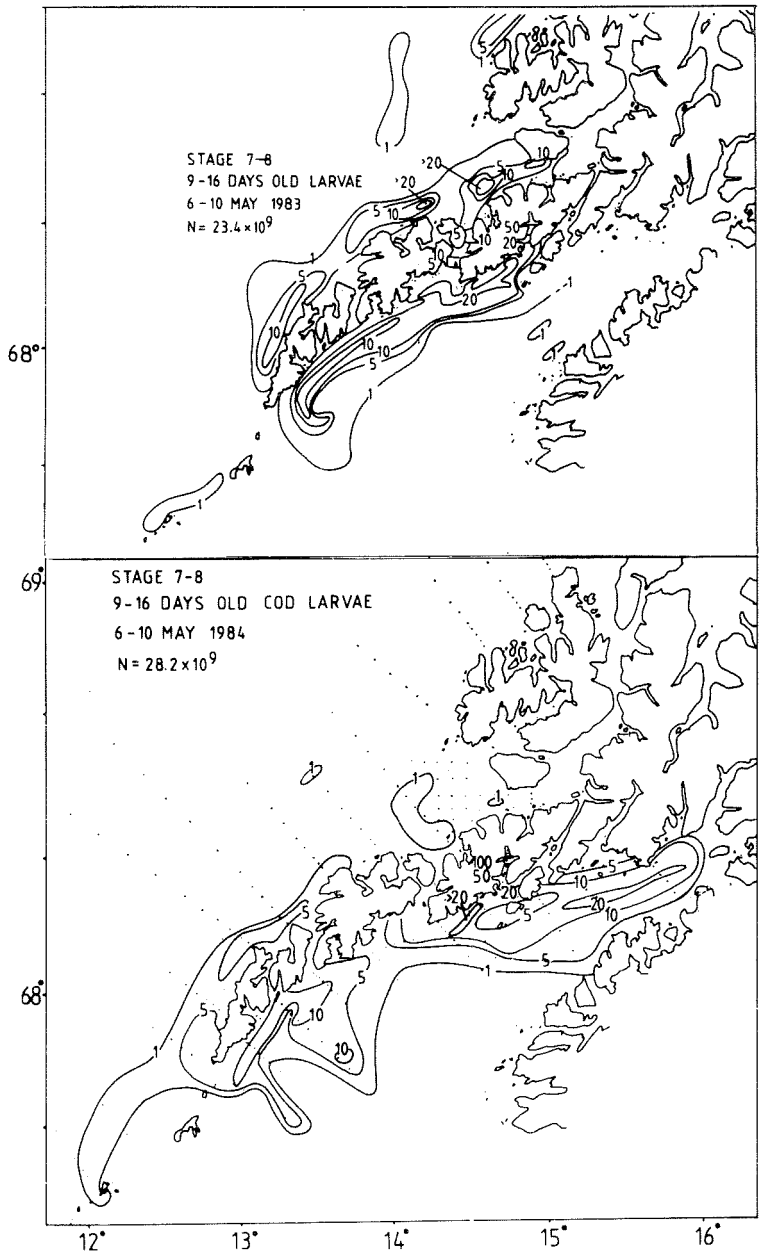


Fig. 8. The horizontal distribution of first-feeding cod larvae with resorbed yolk sac, stage 7–8.

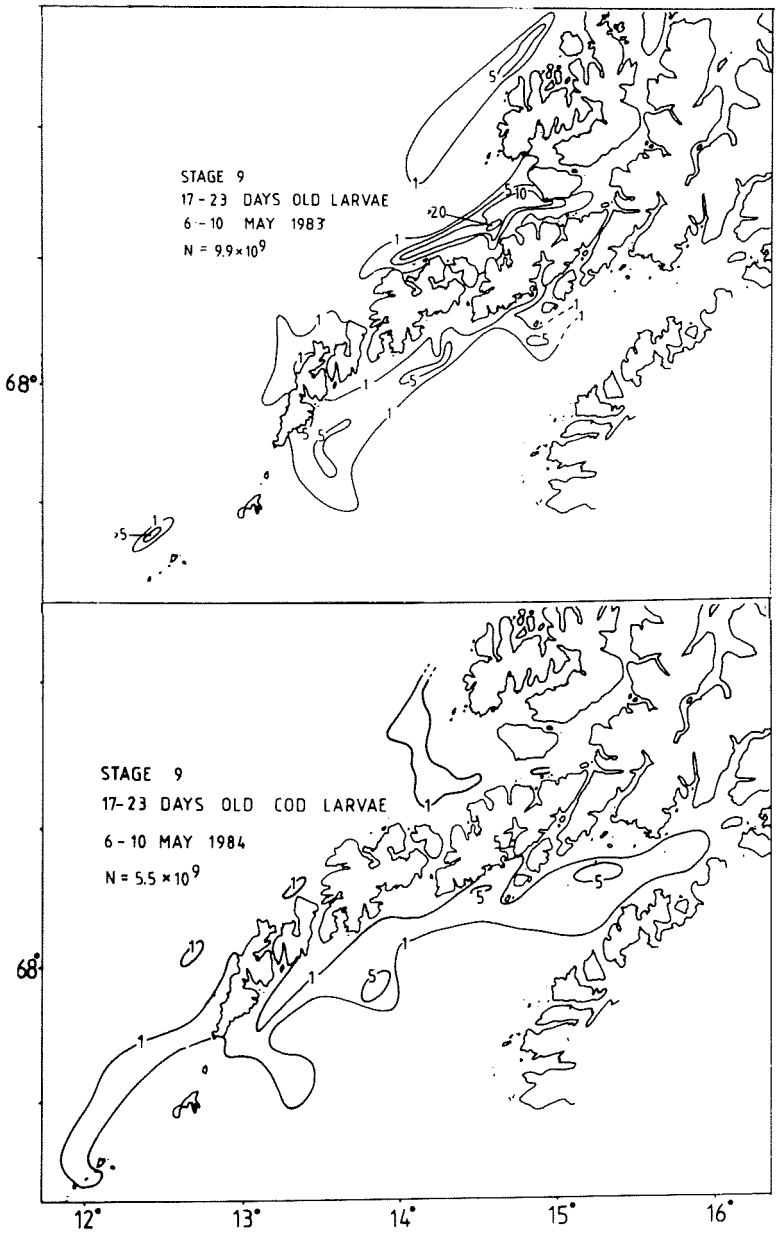


Fig. 9. The horizontal distribution of the oldest larvae, stage 9.

Table 2. The mortality from spawning to the different egg and larval stages. N = N × $10^9$, Egg = E, Larvae = L.

| Stage | Nos. of spawning product | Original number of eggs | Mortality (%) | Daily instantaneous mortality rate (Z) $N_t = N_0e^{-zt}$ |
|---|---|---|---|---|
| E4–5 (1983) | 1100 | 3235 | 66.0 | 0.09 |
| (1983) | 149 | 315 | 52.7 | 0.07 |
| (1984) | 463 | 1593 | 70.9 | 0.11 |
| E6 (1983) | 54 | 340 | 84.2 | 0.11 |
| L1–4 (1983) | 17 | 400 | 95.5 | 0.15 |
| (1984) | 23 | 403 | 94.1 | 0.13 |
| L5–6 (1983) | 14 | 620 | 97.7 | 0.18 |
| (1984) | 21 | 482 | 95.5 | 0.15 |
| L7–8 (1983) | 23 | 2600 | 99.1 | 0.15 |
| (1984) | 28 | 1524 | 98.2 | 0.13 |
| L9 (1983) | 9 | 2940 | 99.7 | 0.14 |
| (1984) | 5 | 1632 | 99.7 | 0.14 |

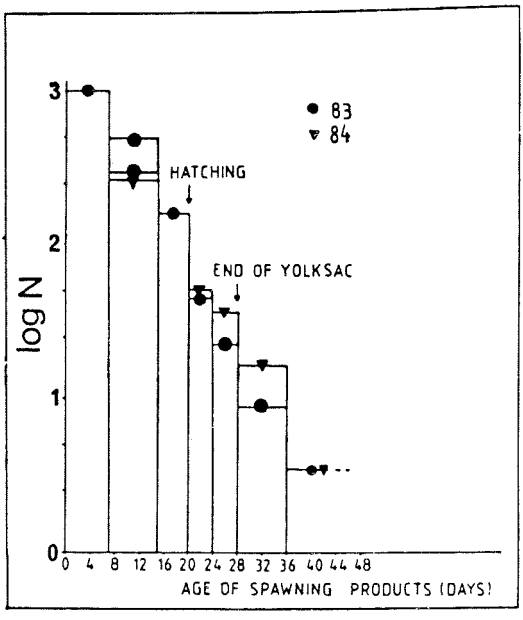


Fig. 10. The mortality of the spawning products of cod from the Vestfjord area in the period 0–50 days after spawning.

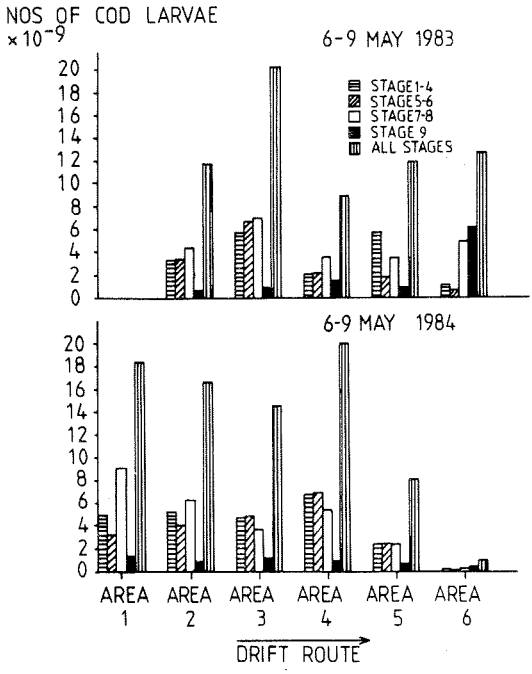


Fig. 11. The number of larvae in different age groups found in the different subareas. Area 1–Eastern Lofoten, Area 2–Austnesfj. and Hølla, Area 3–Henningsvær, Area 4–Western Lofoten, Area 5–The outer side of the Lofoten Islands and Area 6–Vesterålsfj.

## DISCUSSION

The enormous fecundity of most marine fishes is balanced by high egg and larval mortalities (Dahlberg 1979). The natural mortality in species with fast growth and short developmental time, anchovy and mackerel, is generally higher than in species which experience long incubation and larval period, e.g., cod and herring (Houde 1986). The reason for this may be that the egg and larvae of fast-growing species are less uniformly distributed than the slower-growing ones, and this makes them more vulnerable to predation (McGurk 1986).

In the present paper a large reduction in the number of the spawning products of cod was seen during the incubation and larval period. This may be due to some of the following reasons:

- The egg and larval distribution is not completely covered due to drift out of the area of investigation.
- Predation on eggs and larvae.
- Starvation.
- Physical damaging of the eggs due to wave action or stranding.
- Mortality due to genetic defects.
- Eggs or larvae infected with fungus or bacteria.

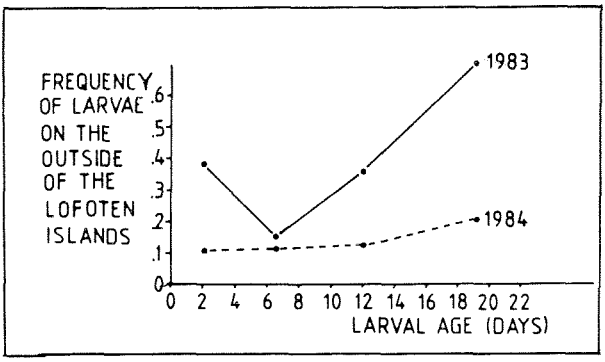


Fig. 12. The frequency of cod larvae in different age groups on the outer side of the Lofoten Islands.

The significance of mortality due to genetic defects or to fungus or bacterial attacks will not be further discussed.

The eggs are spread from the central spawning grounds due to drift and diffusion. During the first five days of the incubation period the abundance of eggs over the spawning ground decreases to 1:2.1 of the original, and the area of distribution increases 2.5 times (ELLERTSEN *et al.* in prep.). But the station grid of the coverages is laid to encompass the egg and larval distributions, and the northernly extensions were located on all coverages in both years. However, some eggs and larvae may escape out over the outer shelf area with a too-low density to be discovered by the present sampling equipment. If the mean larval abundance on the shelf area is given a value of $0.2/m^2$ surface, the total number would add up to about 1% of the estimated total number of eggs and larvae in early May (Sundby pers. commn.) (If the real density had been higher, some eggs or larvae would have been caught from time to time.) Thus very little of the observed reduction in eggs and larvae can be caused by uncontrolled diffusion and drift out of the area of investigation.

Storms and wave action may cause some mortality in cod eggs (ROLLEFSEN 1931). However, the vertical distribution of cod eggs is very sensitive to turbulent mixing of the water masses, and the cod eggs with their weak bouyancy will easily be mixed downward in the water masses due to relatively moderate energy input from wind (SOLEMDAL and SUNDBY 1981). Another reason for the relatively limited significance of wave action as an important cause of mortality in cod eggs may be that this could have put an active selective pressure on the buoyancy mechanisms in the egg.

Stranding of eggs may be a problem, especially when the Vestfjord is exposed to northerly and easterly winds which causes a near-shore distribution of the eggs (ELLERTSEN *et al.* 1981). SARS (1879) reported, "It's thrown on

shore in such enormous masses as to form, so fishermen have assured me, a layer several inches in thickness." In such cases this may have some significance to the egg mortality. Very little is reported in the literature about stranding of eggs. CLADY (1976) tells about 1% daily mortality caused by stranding of demersal yellow pike eggs in a lake. These eggs where raised up by storms and thrown on to the shore.

There is no evidence of starvation from the mortality curve in the present investigation. Heavy reductions in number during the stages totally dependent on endogenic food uptake must have other reasons. The mortality rate changes neither throughout the period of transitional feeding nor during the post-larval period. Therefore predation seems to be the most reasonable explanation of the present reduction of spawning products. The youngest stages are vulnerable to predation, but larvae will to some extent be able to avoid small predators after some time of growth and development. If, however, the larvae are starved, their ability to avoid predators will be very much reduced (NIKOLSKII 1969, WARE 1975, SHEPHERD and CUSHING 1980).

The explanation of the odd distribution of hatchable eggs which are found in the Vestfjord may be that this is a retention area (ILES and SINCLAIRE 1982). The retention time of the eggs in the Vestfjord-system is longer than can be calculated from a simple drift model, which indicates a first-feeding area in the Vesterålsfjord area. Such discrepancies between the distribution derived from a passive drift model and the real distribution found in field investigations are also reported by ILES (1986). The reason for the prolonged retention time in the Vestfjord system may be eddies or that the current system is reversed due to SW-winds. The eggs are located in the wind-mixed layer and will drift passively according to the current. The vertical distribution of the eggs is determined by turbulent mixing due to the wind. High wind impact will distribute the eggs evenly in the upper 50 meters, while during small wind velocities the eggs will concentrate near the surface (SOLEMDAL and SUNDBY 1981).

Another explanation for the unusual distribution of eggs near to hatching may be that the egg mortality is higher on the outer side of the Lofoten archipelago than in the Vestfjord. The distribution of egg predators cannot explain this enigma, and most of the herring that feeds heavily on cod eggs is located in the Vestfjord. Other egg predators, such as Bollinopsis and medusa, are more evenly distributed, with higher densities at some distance from land in the whole area (MELLE 1985).

The reduction of spawning products throughout the period of investigation will reduce the original numbers of eggs spawned in 1983 and 1984 from $15\,000 \times 10^9$ (SUNDBY and BRATLAND 1987) to about $45 \times 10^9$ stage 9 cod larvae after 40 days. This number is about 20 times the size of a large year class as 3-year-old cod, so most of the reduction has already taken place at

this stage. In both 1983 and 1984 large year classes of cod were produced. These years followed seven bad years of recruitment. During this seven-year period very few larvae were found in the Vestfjord in early May, so it seems that the egg mortality has had som significance for the recruitment during this period. In the period 1948–1950, WIBORG (1957) found no relation between the number of larvae in Lofoten in May and the resultant year class, but recruitment is clearly a very complicated process dependent on several parameters. The relative importance of the different parameters may change with time. In one period the egg mortality may be most important, in another, the drift pattern of the costal current, and in a third, the amount of microzooplankton available for the larvae.

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# VARIATIONS IN LIVER AND BODY CONDITION DURING GONAD DEVELOPMENT OF ATLANTIC HALIBUT, *HIPPOGLOSSUS HIPPOGLOSSUS* (L.)

By

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## ABSTRACT

HAUG, T. and GULLIKSEN, B. 1988. Variations in liver and body condition during gonad development of Atlantic halibut, *Hippoglossus hippoglossus* (L.). *FiskDir. Skr. Ser. HavUnders.*, 18: 351–363.

Data were collected from Atlantic halibut *(Hippoglossus hippoglossus)* caught in gill nets and on long lines in northern Norway between September and March during the years 1981–1986. The liver is significantly depleted during the spawning season, thus indicating that it is an important energy source for the halibut in this period. The carcass seems less affected by the energy expenditures involved in the seasonal accumulation of reproductive tissues and in spawning, particulary in females where no significant sacrifice of body weight was observed.

## INTRODUCTION

In recent years there has been a growing interest in marine fish species in sea ranching and aquaculture. Owing to its high market price the Atlantic halibut has particularly received the attention of present-day aquaculturists, and rearing and farming experiments with the species are in progress at several Norwegian institutions.

The halibut is a long-lived species which is believed to spawn seasonally for a number of consequtive years (see JAKUPSSTOVU and HAUG 1988). In northern Norway the spawning of Atlantic halibut takes place at various localities within the fjords and on the edge of the coastal banks (HJORT 1905, DEVOLD 1938). Spawning, which usually takes place at depths of 300–700 m and at water temperatures of 5–7°C, lasts from December to March, with peak activity occurring between late January and early February (KJØRSVIK *et al.* 1987).

For a number of flatfish species it is known that energy reserves, which are generally deposited in liver and carcass, are considerably depleted during

the course of gonad development and spawning (LOVE 1970, DAWSON and GRIMM 1980, JOBLING 1980, ROFF 1982). Whether this is also true for the halibut is not yet known. With reference to the emerging interest in halibut aquaculture, it is obvious that this question needs to be resolved. It has relevance to the rearing of broodstocks of adult fish aimed at producing eggs and milt, and to the production of halibut food fish. This may well proceed beyond the stage of sexual maturity, since the halibut is a multi-year spawner showing rapid growth rates in body tissues even after sexual maturity (JAKUPSSTOVU and HAUG 1988).

The aim of this paper, therefore, is to study seasonal variation in the size of gonads, liver, and body tissues of wild Atlantic halibut, preparing for spawning in autumn and accomplishing the spawning in winter.

## MATERIALS AND METHODS

Halibut stocks in Norwegian waters have been quite heavily depleted in recent years (HAUG 1984, HAUG and TJEMSLAND 1986). In order to provide enough data for this study, therefore, material had to be collected over several years and from several localities. The fish were collected during 1981–1986 by gill netting and longlining at six sites in northern Norway (Fig. 1). Samples were collected from September to March from commercial catches (Vestfjord, Røstbanken, off Vesterålen), and research cruises (Andfjord, Malangen, Sørøysund). All fish were sexed, and total fish lengths (TL) were measured to the nearest centimeter. Eviscerated weights without removing head and gills (W) were recorded to the nearest 0.05 kg, while gonad weights (GW) and liver weights (LW) were recorded to the nearest 0.001 kg. All data from the different sites and years were pooled.

Gonad maturity was determined according to gross criteria using the scale given by KJØRSVIK *et al.* (1987). Thus stage 5 was maturing fish, stage 6 fish immediately before commencing of spawning, stages 7 fish with running gonads, and stage 8 fish with spent gonads. Classification of male gonads generally followed a simplified scale in that stage 5 and 6 were lumped together as "maturing fish". This was mainly due to difficulties in separating between these two stages.

In order to examine the gonad weight-to-total weight relationship, an equation of the type $GW = \alpha + \beta \cdot W$ was determined by linear regression.

The relative gonad weight, or the gonosomatic index, GI, was then examined using the ratio:

$$GI = 100 \cdot GW/W$$

The variation in GI with maturity stage and time of the year was studied by analysis of variance (ANOVA).

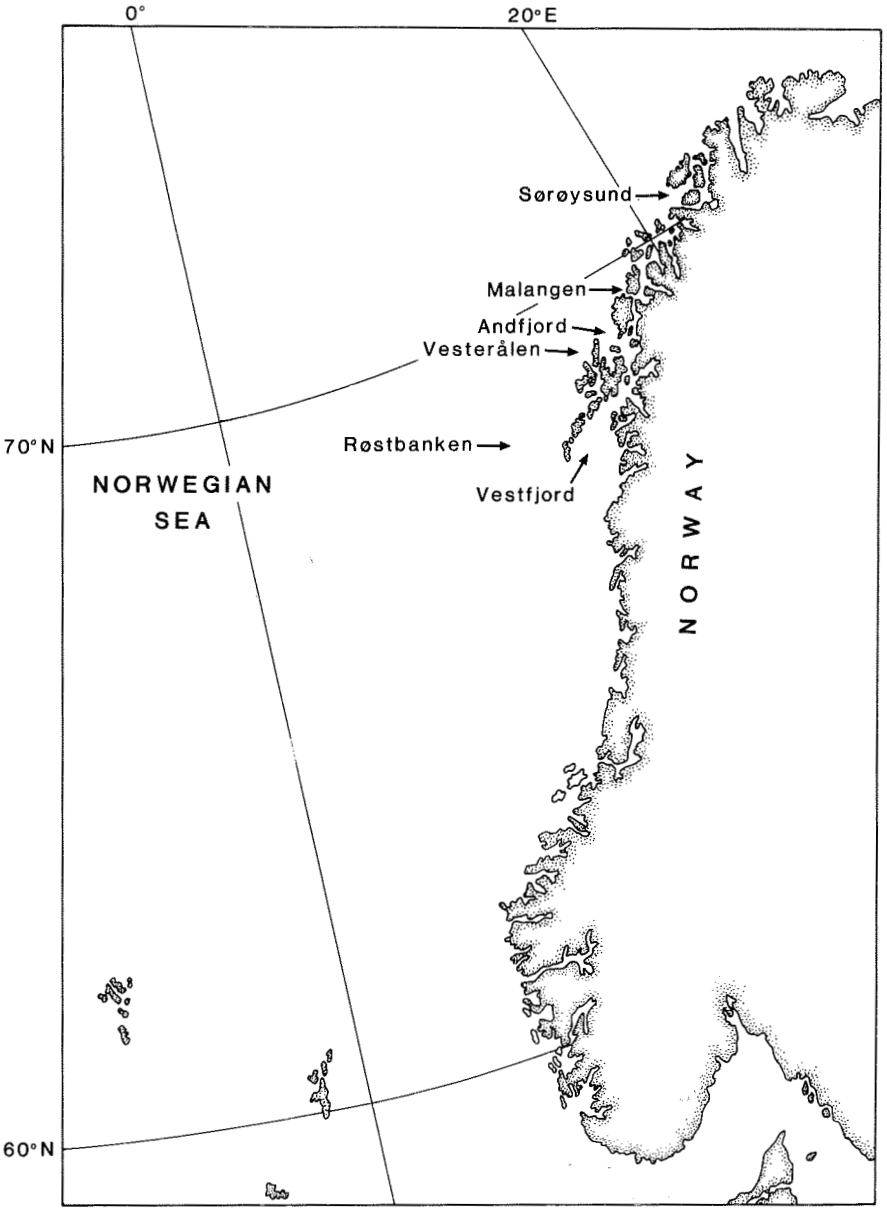


Fig. 1. The sampling sites in northern Norway.

In examining the relative liver and carcass weights, cubic growth, or isometry, of the tissues cannot be assumed *a priori*. The effect of fish lengths, which varied substantially in the present material, were, therefore, eliminated by using relative indices based on empirical length-weight relationships (Le

CREN 1951). Although several regression types can be fitted to length-weight relationships, the best fits are most often provided by a power-regression $W_t = \alpha \cdot TL^{\beta}$, which in its linearized form can be expressed as $\ln W_t = \ln\alpha + \beta \cdot \ln TL$, where $W_t$ is the weight of the tissue, and $\alpha$ and $\beta$ are the regression constant and regression coefficient, respectively (RICKER 1975).

In this paper, therefore, we chose to fit power functions to the liver weight-length and eviscerated weight-length relationships in order to estimate the precise β-values. All β-values are tested for homogeneity among fish in various maturity stages using analysis of covariance (ANCOVA). Provided homogeneity was present, pooling of the data was performed in order to calculate common β-values, irrespective of maturity stages, to be used in liver and condition indices. These indices, showing the relative sizes of liver and carcass, were defined as follows:

Liver index:

$$LI = 1000 \cdot LW/TL^{\beta}$$

Condition factor (indicating relative carcass size):

$$K = 100 \cdot W/TL^{\beta}.$$

Potential variation with maturity stage or time of the year in LI and K were analyzed by means of ANOVA.

Statistics were provided from the BMDP (DIXON 1981) programs P1R (multiple linear regression), P1V (one-way analysis of variance and covariance), and P3D (comparison of two groups with t-tests) run on a VAX computer.

## RESULTS

### *GONAD SIZE*

Regression analyses of the gonad weight-eviscerated weight relationships in males and females of various maturity stages and of the whole data set for each sex, were significant ($p<0.05$) in all cases (Table 1). ANCOVA indicated, however, that the regression coefficients (ß) of the different maturity stage groups were not homogeneous either in females ($F_{3,66} = 9.283$; $p<0.001$) or in males ($F_{2,372} = 7.899$; $p<0.001$). The highest β-values of females were recorded in fish with maturing gonads (stage 6), while in males, fish with running gonads (stage 7) had the highest β-value (Table 1). In both sexes, the lowest β-values were recorded in fish with spent gonads.

The highest mean values of the gonosomatic index, GI, were observed in females in maturity stage 6; thereafter a decrease in mean gonad index with increasing maturity stage was observed (Fig. 2). In males the highest GI-values were recorded in fish in maturity stage 5 + 6 (Fig. 2). Analyses of variance revealed significant heterogeneity among stages both in females ($F_{3,70} = 24.377$; $p<0.001$) and in males ($F_{2,375} = 39.646$; $p<0.001$).

Table 1. Relationship for fish in various maturity stages of gonad weight (GW) to eviscerated weight (W) described by linear regression equations, and of liver and carcass weights (LW and W) to total fish length (TL) described by power regression equations. N is the number of fish examined, $\alpha$ and $\ln\alpha$ are the regression constants, $\beta$ is the regression coefficient, and $r^2$ is the coefficient of correlation. In the regressions, $H_0$:B = 0; thus, rejection ($p<0.05$) means that the variation in weight can be explained by regression. * = rejection at $0.01<p<0.05$; ** = rejection at $0.001<p<0.01$; *** = rejection at $p<0.001$; ns = $H_0$ accepted (i.e. $p>0.05$).

| GONAD MATURITY | $GW = \alpha \cdot \beta \cdot W$ | | | | | $\ln LW = \ln\alpha + \beta \cdot \ln TL$ | | | | | $\ln W + \ln\alpha + \beta \cdot \ln TL$ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| STAGE | N | ß | α | $r^2$ | p | N | ß | lnα | $r^2$ | p | N | ß | lnα | $r^2$ | p |
| FEMALES | | | | | | | | | | | | | | | |
| 5 | 37 | 0.0751 | 1944.61 | 0.29 | *** | 63 | 3.2011 | –3.98 | 0.76 | *** | 39 | 3.0909 | –2.16 | 0.97 | *** |
| 6 | 12 | 0.2689 | –5079.47 | 0.89 | *** | 13 | 3.7161 | –5.31 | 0.86 | *** | 12 | 3.3013 | –2.63 | 0.97 | *** |
| 7 | 10 | 0.0635 | 2584.71 | 0.55 | * | 13 | 3.6884 | –5.33 | 0.86 | *** | 14 | 3.3926 | –2.85 | 0.98 | *** |
| 8 | 15 | 0.0217 | 215.46 | 0.37 | * | 21 | 3.7879 | –5.60 | 0.74 | *** | 20 | 3.0361 | –2.05 | 0.94 | *** |
| Combined | 74 | 0.0772 | 1228.33 | 0.28 | *** | 110 | 2.8419 | –3.30 | 0.49 | *** | 85 | 3.1293 | –2.25 | 0.97 | *** |
| MALES: | | | | | | | | | | | | | | | |
| 5+6 | 38 | 0.0580 | 148.23 | 0.15 | * | 42 | 3.6207 | –5.07 | 0.67 | *** | 38 | 3.0808 | –2.14 | 0.96 | *** |
| 7 | 304 | 0.0647 | –144.76 | 0.65 | *** | 305 | 2.9277 | –3.87 | 0.78 | *** | 308 | 3.1203 | –2.26 | 0.98 | *** |
| 8 | 36 | 0.0070 | 21.38 | 0.61 | *** | 36 | 3.2185 | –4.59 | 0.79 | *** | 36 | 3.1227 | –2.28 | 0.99 | *** |
| Combined | 378 | 0.0644 | –150.93 | 0.51 | *** | 383 | 3.2209 | –4.45 | 0.77 | *** | 382 | 3.1493 | –2.32 | 0.97 | *** |

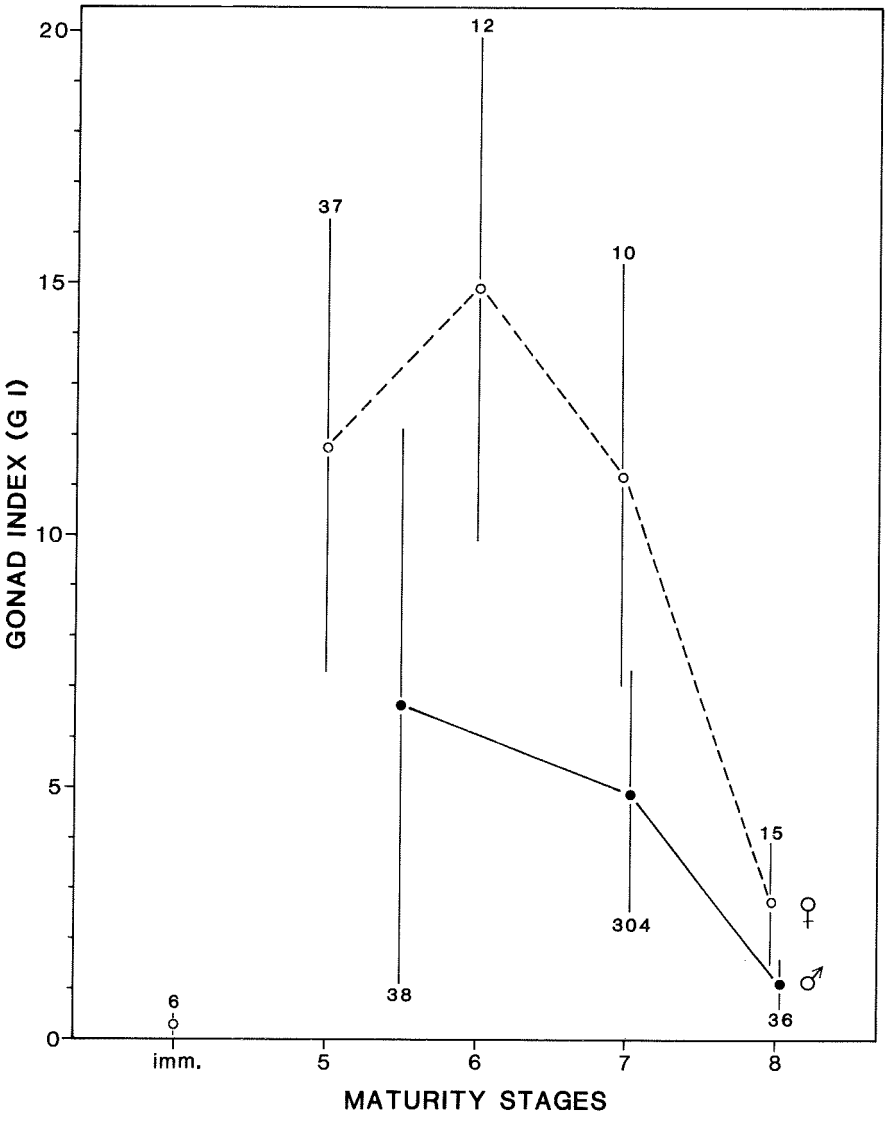


Fig. 2. Mean gonad indices (GI) per maturity stage of halibut females (stipled line). The mean values of males are also given (solid lines). Standard deviations are indicated by the bars and the numbers of examined fish are given.

In both sexes the mean GI values increased during autumn, reaching the highest values in November (males) and December (females). Thereafter, the average gonad sizes decreased (Fig. 3). ANOVA revealed that the observed variation in the monthly means of GI was significant both in males ($F_{6,371}$ = 40.919, $p<0.001$) and in females ($F_{6,67}$ = 2.317, $p = 0.043$).

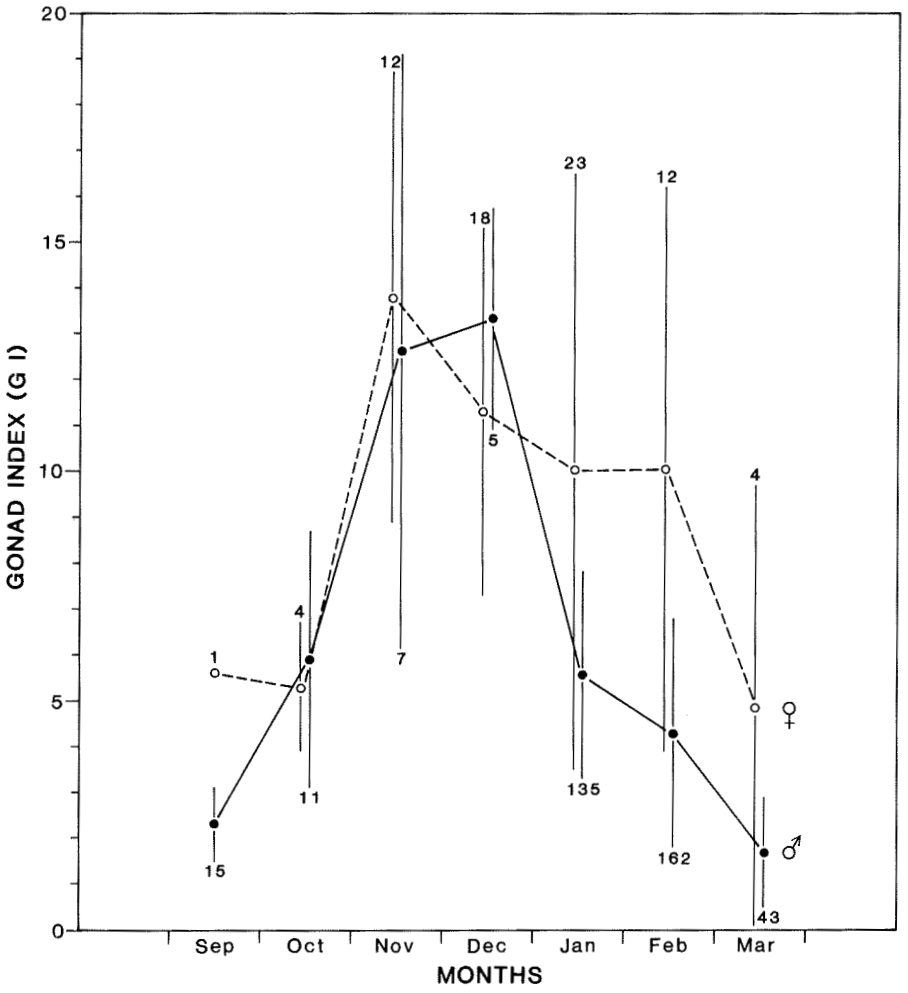


Fig. 3. Mean monthly gonad indices (GI) for halibut males (solid line) and females (stipled line). Standard deviations are indicated by the bars and the numbers of examined fish are given.

*LIVER CONDITION*

Power curve regressions fitted to the liver weight-total length data were highly significant ($p<0.001$) in both males and females in all maturity stages (Table 1). ANCOVA showed that the regression slopes ($\beta$) from the different gonadal maturity stages were homogeneous in females ($F_{3,102} = 0.678$; $p = 0.568$) as well as in males ($F_{2,377} = 1.867$: $p = 0.156$), thus permitting the use of combined $\beta$-values (2.8419 and 3.2209 for females and males, respectively, Table 1) when calculating the liver index in each of the sexes. Both the combined regressions were highly significant ($p<0.001$). The liver indices thus became:

Females:

$$LI = 1000 \cdot LW/TL^{2.8419}$$

Males:

$$LI = 1000 \cdot LW/TL^{3.2209}$$

A general decrease in mean LI was observed with increasing maturity stage in adult fish of both sexes (Fig. 4). ANOVA revealed that the observed intermaturity stage heterogeneity of LI was highly significant both in males ($F_{2,380} = 24.057$, $p<0.001$) and in females ($F_{3,106} = 33.719$, $p<0.001$). In immature females the mean LI was similar to those observed in maturity stage 6–8 females, but significantly lower ($p<0.001$) than those observed in stage 5 females.

ANOVA shows that the monthly mean values of liver indices (Fig. 5) vary significantly during the period of investigation in both males ($F_{6,376} = 9.684$, $p<0.001$) and females ($F_{6,103} = 12.585$, $p<0.001$). In the males, the mean LI decreased clearly during the whole period from September to March inclusive. In females, relative liver weight did not start to decrease until December. After January, a slight increase in the mean LI of females again occurred.

*BODY CONDITION*

Power curve regressions fitted to the eviscerated weight-total fish length data of females and males in various stages of gonadal maturity were highly significant ($p<0.001$) in all cases (Table 1). ANCOVA indicated that the regression coefficients of the different maturity stages were homogeneous in females ($F_{3,77} = 1.382$; $p = 0.255$) as well as in males ($F_{2,376} = 0.067$; $p = 0.935$). This permitted the use of combined β-values (3.1293 for females, 3.1493 for males, Table 1) when calculating the condition factor in each of the sexes. The condition factors (K) thus became:

Females:

$$K = 100 \cdot W/TL^{3.1293}$$

Males:

$$K = 100 \cdot W/TL^{3.1493}$$

As revealed by ANOVA, mean values of the condition factor calculated for sexually mature fish in various maturity stages (Fig. 4) vary significantly in males ($F_{2,379} = 14.391$, $p<0.001$), but not in females ($F_{3,81} = 1.965$, $p = 0.126$). In males, a general decrease in mean K with increasing maturity stage was observed. No significant differences ($p<0.05$) were observed between the mean K-value for immature females and those observed in mature females.

In males, the mean monthly K-values were quite stable in autumn (September–November), followed by a decrease to a lower level maintained from

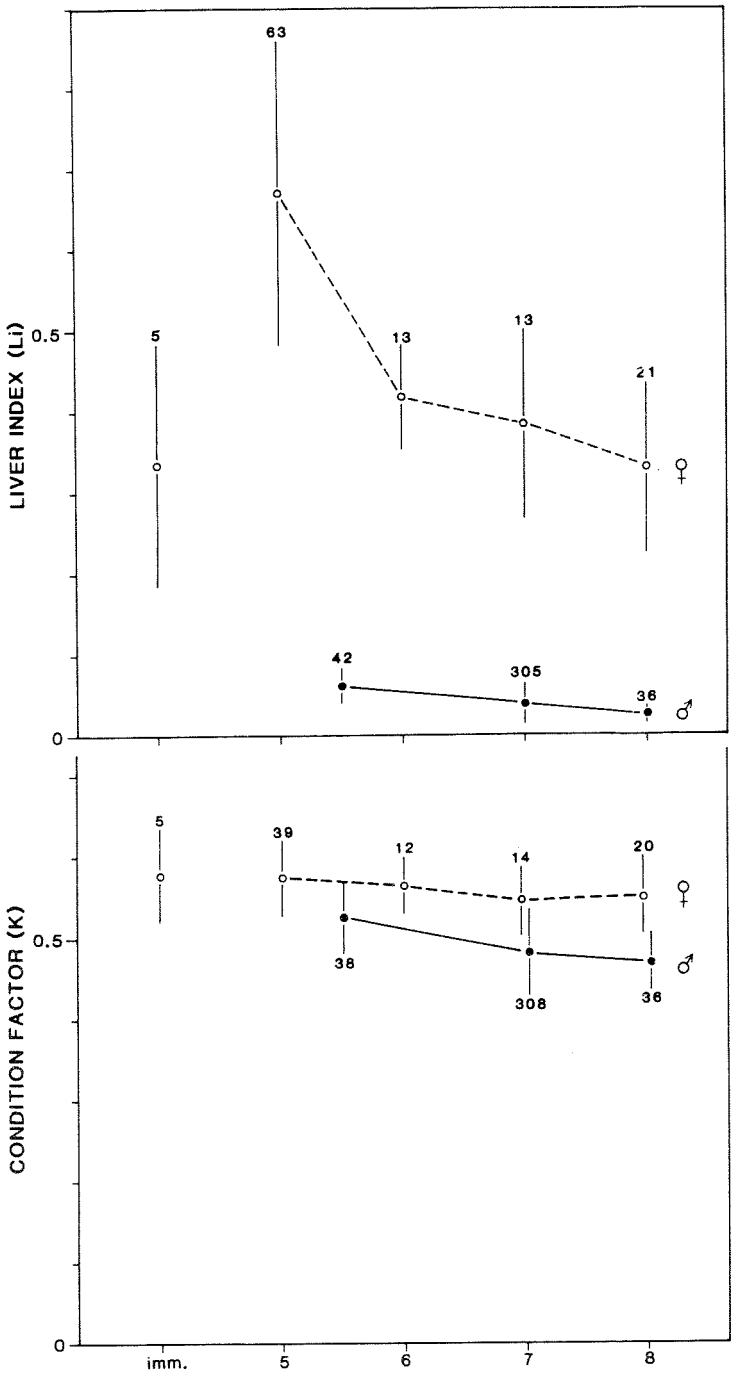


Fig. 4. Mean liver indices (LI, above) and condition factor (K, below) per maturity stage of halibut males (solid lines) and females (stipled lines). Standard deviations (bars) and numbers of examined fish are given.

December through March (Fig. 5). ANOVA revealed that this observed heterogeneity among monthly mean values of the condition factor in males was highly significant ($F_{6,375} = 5.795$, $p<0.001$). The female monthly mean values of K appeared to vary in the same manner as for the males (Fig. 5), but an analysis of variance revealed no significant variation between months in the females ($F_{6,78} = 1.749$, $p = 0.121$).

## DISCUSSION

The observed significant heterogeneity among slopes (β-values) of regressions of gonad weights against eviscerated weights indicates that this relationship varies with the stage of maturity both in female and male halibut, i.e., fish have gonads of different relative weight proportions depending on their state of maturity. In the females, fish in maturity stage 6, namely the last phase of vitellogenesis before the oocytes start to absorb fluid and are released from the ovary follicles, had the steepest slope (Table 1). This indicates that the larger females in this stage generate larger ovaries in proportion to eviscerated body size than do the smaller females, as compared with other maturity stages. According to DE VLAMING *et al.* (1982), who critically reviewed the use of the gonosomatic index in studies of breeding in fishes, such heterogeneity among females in different maturity stages is commonly observed also in other fish species. These authors discussed the biological significance of such size-related heterogeneity, and especially pointed out that body size might have a greater impact on relative ovary weight when females had "ripe" ovaries than when ovaries were inactive. This is highly consistent with our present observations. There seems to be less variation of β-values with maturity stage in males than in females, although the pooling of stages 5 and 6 in the males complicates more precise intersexual comparison.

At the individual level, the mean GI's reached their highest values in fish in maturity stage 6 (females) or 5 + 6 (males) (Fig. 2), which is quite natural since this is the latest stage of gonad maturity before the spawning starts and drains the gonads of gametes and weight. At the population level, the continuous decreases in mean GI from November–December to March (Fig. 3) is consistent with the conclusion of KJØRSVIK *et al.* (1987) that this is the spawning season of the species. The increase in mean GI values from September to November–December emphasizes that this is a period of intense accumulation of reproductive tissues by the species. The observed heterogeneities of regression slopes mean that dividing gonad weight by eviscerated weight may have a different result depending on the phase of the gonad cycle. Thus, the GI may provide a misleading indication of gonadal activity, and the validity of comparing mean values among maturity stages and months is, therefore, debatable.

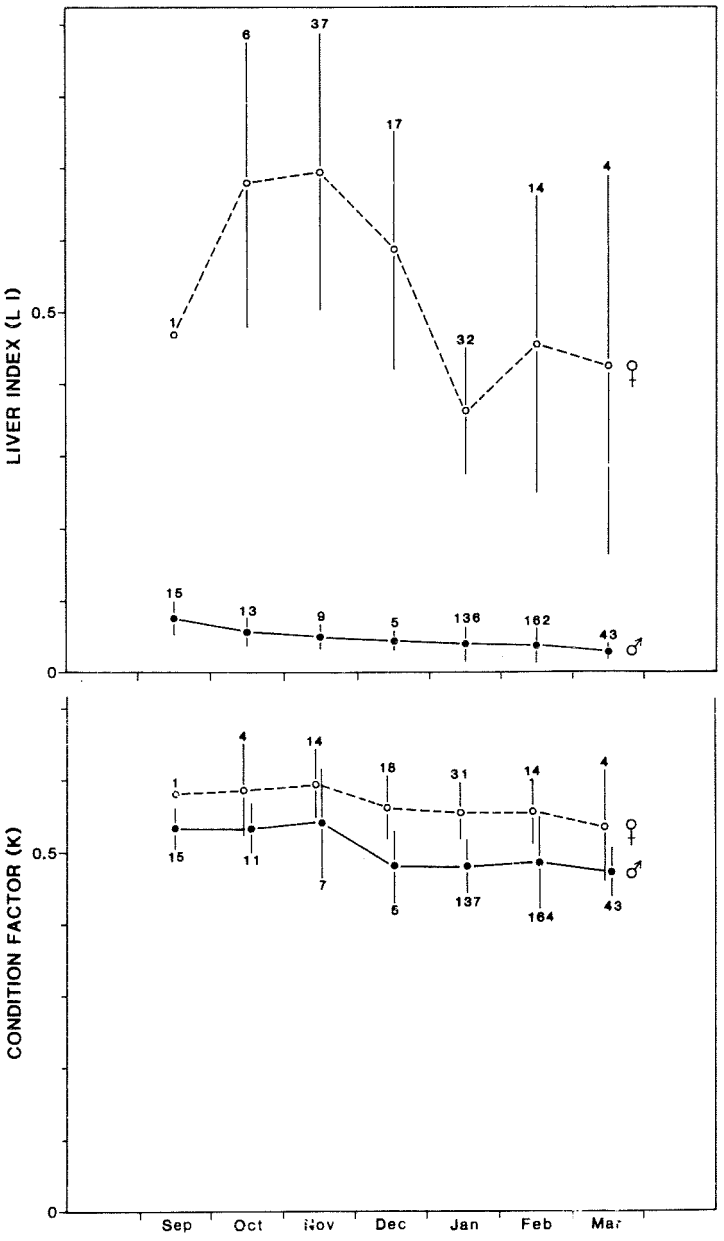


Fig. 5. Mean monthly liver indices (LI, above) and condition factor (K, below) for halibut males (solid lines) and females (stipled lines). Standard deviations (bars) and numbers of examined fish are given.

No significant variation with stage of maturity was observed in the β-values either in the regression of liver weight on total length or in the regression of eviscerated weight on total length. This applied to both sexes, and indicates that single regressions, based on pooled material irrespective of maturity stage, can be expected to adequately describe both the above-mentioned relationships for female as well as male halibut.

It is generally accepted that in flatfish, the main energy reserves are usually deposited in the liver and muscle tissues (Love 1970). Our results suggest, however, that in halibut these two different tissue types are differently affected by the costs of spawning. Obviously, the liver is significantly reduced as the maturation process proceeds (Fig. 4), leading to a significant decrease in mean relative liver weight (LI) throughout the spawning season (Fig. 5). Thus, it seems reasonable to conclude that the liver is an important energy source for female and male halibut during preparation for spawning. This is supported by studies of the lipids and fatty acid profiles of the species (Haug *et al.* 1988). The carcass seems, however, much less affected by the energy expenditures involved in the seasonal accumulation of the reproductive tissues. Certainly, the males show a little, but still significant, decrease in relative body weight during gonad maturation (Fig. 4) and during the first part of the spawning season (Fig. 5). This was, however, not the case in females whose sacrifice of general body weight in order to build up ovaries seems minimal. The observed difference between females and males in mobilizing muscle tissue into reproductive tissue seems to support previous suggestions of sexual differences in physiology and growth/energy strategies of male and female halibut. These differences are also manifested in the female growth rate being far in excess of the males after the attainment of sexual maturity (Mathisen and Olsen 1968, Jakupsstovu and Haug 1988), and in the generally higher lipid levels in several tissues of females as compared with males during spawning (Haug *et al.* 1988).

In general, the energy reserves of flatfish are considerably depleted during the course of gonad development or starvation which usually accompanies overwintering and spawning (Dawson and Grimm 1980, Jobling 1980, Roff 1982). With its low level of general body weight sacrifice during spawning, the Atlantic halibut follows this trend only in part. No doubt the food intake of the species is reduced during spawning (Devold 1938, McIntyre 1953). We suggest, however, that feeding most probably does not cease completely, and that the general physical activity, particularly in females, is reduced to such an extent that a minimal loss of energy is ensured during spawning.

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