Baltic **COd REcruitment** Project:
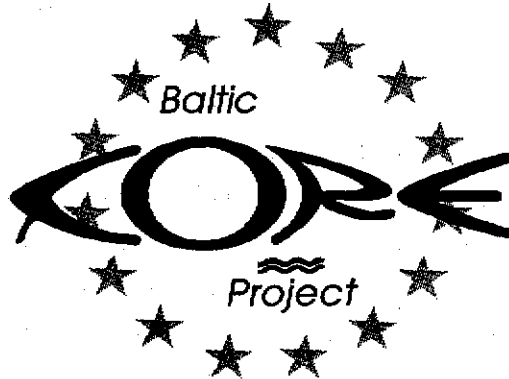
Summary of results 1994-97

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Abstract

The effects of abiotic and biotic processes on recruitment of Central Baltic cod has been studied in an EU funded interdisciplinary research project, integrating 13 institutes from 8 countries bordering the Baltic Sea. The project provides a contribution to the GLOBEC Cod and Climate Change Programme.

For statistical trend analysis, extensive time series of stock related information and environmental data have been intercalibrated and (re-)constructed. They also formed the basis for major process analysis and modelling activities.

Investigations on processes affecting the maturation, distribution and structure of the spawning stock, individual fecundity and viability of the offspring revealed a clear picture of the temporal and spatial variation in the reproductive potential of Baltic cod. Since the mid 1980s recruitment has been dependent on the reproductive success in the Bornholm Basin, while the stock component in the Gotland Basin is close to extinction.

Based on extensive field and laboratory experiments, environmental conditions and processes conducive for survival of early life stages have been described. A decrease in the water volume suitable for successful egg development and corresponding increase in egg mortalities were encountered during stagnation periods, e.g. from 1985-90. Some small and one intermediate major inflow in 1991-94 improved the hydrographic conditions, but egg survival remained still limited. Reasons are: 1) the main spawning time of cod has shifted to summer, thus most eggs released are exposed to relatively low oxygen concentrations due to fast oxygen consumption during spring/summer in bottom water layers and 2) predation by herring and especially sprat, being presently extremely abundant, affects cod egg survival substantially. Furthermore, survival of larvae requires a successful vertical migration from hatching depths to surface layers, as a

combination of low prey abundance and low light intensities does not allow successful feeding within or below the halocline.

Characteristics of the larval and juvenile populations examined (e.g. distribution of hatching dates derived from otolith analysis, drift paths obtained by 3-D hydrodynamic models) resulted in the identification of important environmental processes and biological attributes leading to increased survival success (e.g. rapid transport from spawning to suitable nursery areas). Cannibalism has been confirmed to effect the survival of juvenile cod and was estimated to be most intense in 1978-84, a period with high adult and juvenile stock size.

A series of physical/biological models have been set up to describe important processes effecting survival during successive stages of early development. On this basis, alternative stock-recruitment models have been established, incorporating environmental variability and predator/prey interaction. The models explain a considerable part of the variance encountered in cod recruitment and allowed to: 1) outline a pragmatic approach for an improvement of the stock assessment and 2) to specify a more complex approach to be utilised in medium-term stock simulation models, considering regional differences and sub-components of the cod stock in the Baltic. With regard to the fisheries management, the project results enabled a validation of some of the presently enforced management measures and resulted in recommendations for future management, including a discussion on the feasibility of an artificial stock enhancement.

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1. Organisations involved

Institute of Marine Sciences, Kiel (Coordinator)

Danish Institute for Fisheries Research, Charlottenlund & Hirtshals

Institute for Baltic Sea Research, Warnemünde

Institute for Baltic Sea Fisheries, Rostock

Institute of Marine Research, Lysekil

Finnish Game and Fisheries Research Institute, Helsinki

Finnish Institute of Marine Research, Helsinki

Sea Fisheries Institute, Gdynia

Latvian Fisheries Research Institute, Riga

Institute of Biological Sciences, University Aarhus

Dept. Systems Ecology, Stockholm University

Estonian Marine Institute, Tallinn

AtlantNIRO, Kaliningrad

2. Objectives of the programme

The cod stock in the Central Baltic is a major component of the Baltic ecosystem and has a large social and economic importance in the countries bordering the Baltic Sea. After an intermediate increase in stock size and landings in the beginning of the 1980'ies, the stock abundance was on its lowest level on record in 1992, slowly recovering afterwards. The drastic decline appears to be caused by a substantial reduction in the reproductive success coupled with high fishing mortality. As cod is the main predator in the ecosystem, the reduction in stock size influences the lower trophic levels in the food web and this has implications on the stock development of herring and sprat and their utilisation by the fishery. A comprehensive investigation on the abiotic and biotic processes influencing cod recruitment appeared to be required in order to improve the basis for assessing and managing the cod stock and also for a sufficient understanding of the role and impact of cod in the Baltic ecosystem. For this purpose a multidisciplinary research programme integrating 13 institutes from 8 countries bordering the Baltic Sea was developed. The primary goals of the project were to:

a) identify and describe the dominant biotic and abiotic processes affecting the maturation of cod and the developmental success of the early life stages of cod;

b) incorporate these key processes into recruitment models to enhance prediction of future stock fluctuations due to the state of the spawning stock, environmental perturbations, species interactions and fisheries management directives;

c) assess the biological basis and evaluate the feasibility and possible effects of cod stock enhancement programmes.

3. Summary of scientific achievements and conclusions

3.1 Trend Analysis

The Trend Analysis component of the CORE project focused on three main hypotheses related to long-term reproductive and recruitment success in this cod population:

1) reduced oxygen concentrations in the deep basins of the Baltic (caused by low intrusion rates of Kattegat water and oxygen consumption due to eutrophication) have produced conditions which are detrimental for reproductive success and recruitment;

2) physical oceanographic and food web processes occurring during the first year of life influence the abundance of prey and predators of larval and juvenile cod, thereby influencing the growth and survival of these life stages;

3) abiotic factors (e.g. temperature, salinity) directly affect the survival of cod eggs.

Analysis of these hypotheses required investigation of associations between biological variables and climate/physical oceanographic parameters, preferably using long-term data series. Many such data series existed at the start of this project so the raw material for hypothesis-testing was available and could be extended with additional observations conducted during the project period in other tasks. However, for many of the variables of interest (e.g. egg abundance, oxygen condition in spawning areas, wind speed), the individual data series were unsuitable for direct statistical analyses. Sampling and measurement techniques varied over time and/or between institutes. As a result, it was necessary to allocate a considerable effort to the preparation, intercalibration and configuration of data series for further analyses within both the Trend Analysis and Recruitment Modelling tasks. Most effort was applied to those variables and datasets which the literature suggested would have the most direct and significant influences on cod reproduction and recruitment. These variables were those relating to the production and survival of eggs and larvae and oxygen conditions at spawning sites.

A calibration of sampling methods for cod eggs and larvae showed that two long-term data series could be combined. This allowed trends in egg and larval abundances in the main spawning basins to be interpreted over several decades. During the 1970'ies, egg and larval abundances were high and relatively stable. However, abundances decreased from the early 1980'ies until the mid 1990'ies. This pattern was seen in all of the major spawning areas, the Bornholm Basin, the Gdansk Deep and the Gotland Basin. The downward trend in the Bornholm Basin stopped in 1992 and egg abundances increased in 1994 and 1995 to levels, which exceeded those, observed throughout the entire time series (1954-present). Abundances in 1996 were similar to levels observed during the entire 1970's and therefore must also be considered as high. Larval concentrations however remained low. Egg and larval concentrations in the Gdansk Deep and Gotland Basins have remained essentially zero since the late 1980'ies.

The high concentrations of eggs in the Bornholm Basin occurred during a period when cod spawning stock biomass and the abundance of a known cod egg predator (sprat) were respectively below and well above long-term averages. Improved oxygen conditions (due to saltwater inflows during the winters of 1993-94), coupled with possible changes in spatial distribution of the cod stock, increases in relative fecundity, and altered predator-prey distributions may have contributed to the high concentrations of eggs observed during the project.

The calibrated egg and larval surveys were also used to estimate the timing of peak spawning in the Bornholm Basin, and evaluate how timing varied with population age structure and water temperature. The timing of peak spawning was delayed by cold temperatures and a higher than average proportion of first-time spawners in the population. However this pattern was only evident when the spawning biomass of cod in the Bornholm Basin was low (< 40,000 t); the timing of peak spawning at higher stock levels could not be analysed, but was likely influenced by competition for food.

Environmental conditions were shown to affect cod reproduction and potentially recruitment. A new time series of water volumes having suitable oxygen, salinity and temperature conditions for cod egg development in the Bornholm Basin was constructed. A comparison of volume estimates derived from a 36-station grid in the basin and from single stations showed that one carefully chosen station can be used to estimate the entire volume of suitable water throughout the basin. This time series also showed fluctuations that were highly correlated with a similar but independent time series collected by the Latvian Fisheries Research Institute in the same area, but constructed from different hydrographic data. Latvian measurements elsewhere in the eastern Baltic also show that reproductive volumes in the Bornholm Basin have consistently been larger than those in the three other spawning areas (Gdansk Deep, southern and central Gotland Basin) since the early 1950's.

Analysis of the temporal variability in the reproductive volumes showed little evidence of an overall increase or decrease since the 1950's. However at shorter time scales, significant variation exists, and in many years (e.g. much of the 1980'ies and early 1990'ies), the Bornholm Basin was the only site which supports cod egg development. This situation changed after inflows of saline oxygenated water in January 1993, the conditions improved significantly in all basins for a short period. However, in most recent years, oxygen levels have decreased again in all areas, so that the Bornholm Basin, and to a much less extent the Gdansk Basin, are presently the only sites capable of supporting successful cod egg development.

In general in all cod spawning areas in the eastern Baltic, reproductive volumes are larger in spring (May) than in summer (August), but the seasonal decrease varies significantly between years and areas. The extent of the seasonal decline between spring and summer in the Bornholm Basin is significantly greater in years when water temperatures in the spring are warm in the surface mixing layer and the halocline. In addition, during warm years, the concentration of zooplankton throughout the central Baltic in May is significantly higher than in cold years and the seasonal decrease in reproductive volume appears to be positively correlated with the abundance of zooplankton. These associations suggest that low spring temperatures (which were found to be significantly correlated to the maximal area of ice coverage in the previous winter) affect the functioning of the pelagic food web of the Baltic, including processes (e.g. production and decomposition of organic matter) affecting cod reproductive volumes. We then considered the long-term trend in the seasonal variation itself. This analysis suggested a weak but significant increase in the seasonal decline in reproductive volume in the Bornholm Basin between spring and summer during the years 1952-1992.

Environmental conditions also have other effects on egg and larval survival. In warm years, cod larvae produced in May will experience higher food concentrations than in cold years and may be able to grow and survive at higher rates. Warmer temperatures will also directly stimulate feeding and growth rates. Wind conditions affect drift trajectories and the predominant directions of the wind that affects these trajectories varied during 1966-1996. The abundance of cod egg predators (i.e. sprat and herring) has also varied during the last 2-3 decades and one of these predators (sprat) is presently at its highest recorded level. Statistical analyses showed that sprat recruitment was not related to spawning stock biomass, but was significantly lower in years with low water temperature. The effect of temperature on sprat recruitment is possibly due to a detrimental effect of cold water on development of sprat eggs.

The overall results of the task were highly positive and all major project commitments have been met. Task activities have enabled intercalibration and (re-)construction of extensive time series of both stock-related (e.g. egg and larval abundances) and environmental information (e.g. spatially- and temporally-resolved

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hydrographic conditions at spawning sites, wind indices related to larval drift from spawning sites). These time series are matched by few (if any) other cod populations around the North Atlantic, nor by few other fish populations around the world. As a result, the time series produced in this project are of higher and more reliable quality than those previously available to the Baltic fisheries community for its various modelling (e.g. recruitment, retention/dispersion), assessment and statistical analyses. They should be an invaluable resource for the management of the cod stock and the Baltic ecosystem in the years to come, particularly if they are maintained and updated. Statistical analyses of the assembled data series have identified new mechanisms by which environmental variability can influence reproductive success, and ways that stock characteristics can interact with environmental conditions to generate variability in reproductive success. In addition new hypotheses (e.g. retention/dispersion of eggs and larvae from spawning areas, temperature effects on reproductive volumes, predators of cod eggs and larval food concentrations) have been identified that were examined in more detail in other tasks within the project.

3.2 Maturation processes, timing of spawning, spawning stock structure and distribution, egg production and quality of spawning products

The identification of the links between the adult stock component, environmental conditions, and the production of viable eggs is critical for the determination of any stock-recruitment relationship. The present section focuses on the egg production by Baltic cod in relation to the structure, abundance and distribution of the stock, size and sex specific maturation processes, timing of spawning, individual female fecundity and the viability of spawning products including contamination effects. These parameters in combination enable an estimation of the potential viable egg production by the Baltic cod. However, the age and sex composition, timing of maturation and the number of oocytes produced by individual females have been demonstrated to vary between years and areas and underlying processes needed to be investigated.

Maturity ogives and sex ratios

Extensive data on sexual and gonadal maturation of cod in different areas of the Baltic have been compiled, based partly on historical data and partly on new material from trawl surveys conducted within the project. The maturity ogives derived from the Baltic International Trawl Survey in the first quarter of the year confirmed that males in general reach sexual maturity significantly earlier than females. Differences in the timing of sexual maturation between stocks were also revealed, i.e. the cod in the eastern Baltic stock generally reach maturity at an older age than cod in the western Baltic stock. Even within stocks there is a clear trend of attaining sexual maturity at a progressively older age from the Belt Sea to the Gotland Basin. The maturity ogives were not constant over time, but showed a time trend to earlier sexual maturation at age from the 1980'ies to the 1990'ies in the Central Baltic, however, with considerable inter-annual variability.

Time series of combined as well as female and male maturity ogives have been established, taking into account the differences between Subdivisions in sex specific maturity ogives and sex ratios (see below) as well as temporal changes in the spatial distribution within the stocks. The established time series deviate substantially from the maturity ogives used in stock assessments prior to 1997, kept constant over time. As a consequence, VPA estimates of the spawning stock in numbers and biomass are reduced considerably for the 1970'ies and 1980'ies, when applying the newly established maturity ogives.

Timing of spawning activity and stock structure

The timing of gonadal maturation differed between the sexes in all areas investigated. The males reached spawning condition earlier than females and entered also the spawning areas earlier resulting in a high male abundance on the spawning grounds prior to the onset and in the beginning of the spawning period. The start and duration of the spawning period differed between areas with a progressively later female spawning period from Kiel Bight (February to June) to the Bornholm Basin (May to September). The timing of main spawning activity in the eastern Baltic did not differ substantially between areas and sexes (app. May-August), but spawning was in general of longer duration for males. The size composition of the spawning components in the various areas in the eastern Baltic changed over time and the proportion of females exceeded the proportion of males in the late spawning period. In the beginning of the spawning period an increased proportion of larger female cod was in spawning condition compared to smaller fish with a tendency to continue spawning longer as well. However, the timing of peak spawning tended to be similar for all size groups. For males, the timing of gonadal maturation and peak spawning did not differ substantially between length groups, but the duration of the spawning stage tended to be longer with increasing size.

The sex and size dependent reproductive strategies with an earlier start and a longer duration of the male spawning period compared to females suggest that the mortality of males may be higher than the female mortality rates, caused by a high fishing effort in spawning areas of the central Baltic in the second quarter of the year. The longer duration of the spawning period is also likely to increase the natural mortality of males due to a higher physiological stress level, which in combination with the earlier sexual maturation would explain the decreasing proportion of males in the stock with increasing size/age.

The compiled data on gonadal maturation and egg abundance confirmed for both stocks a clear shift of spawning activity to later months of the year within the 1980'ies and 1990'ies. Maturation data from the Gotland Basin showed no spawning of young females in March/April since 1985. A similar retardation in spawning is obvious since 1991 for intermediate sized females, whereas larger fish showed a gradual delay, but are to minor certain extend still spawning in March/April. Shifts in the spawning time have previously been related to changes in the age composition and age specific differences in the timing of gonadal maturation. The present analysis confirmed that larger females start spawning earlier than smaller ones and that the proportion of older ages has been low during the 1st half of the 1990'ies. However, an analysis of the Baltic International Trawl Survey Database (BITS) revealed a low proportion of old fish similar to the beginning of the 1990'ies already in earlier in the 1980'ies. Furthermore, the increasing proportion of older fish in 1996/97 caused by the slightly above average year-classes 1990 and 1991 did not result in earlier main spawning activity. Also in Subdivision 26, the corresponding proportion of repeat spawners was in general well above the level in Subdivision 25, especially in most recent years, while the timing of spawning is rather similar. Thus, the corresponding shift in spawning activity described for both populations can not be explained by changes in the proportion of older fish in the stock alone. This is also confirmed by the observed size-specific delay in the onset of spawning of females in the Gotland Basin. The shift in the timing of the gonadal maturation and spawning has been related to the growth rate, dependent on food supply and stock density. According to this hypothesis high clupeid and low cod stock levels should have resulted in early sexual maturation (which has in fact been shown by our analysis) as well as early gonadal maturation (which is obviously not the case).

Distribution of the stock

From the analysis of the BITS database, a general decrease in the abundance of the spawning stock is evident for all areas in the central Baltic during the 1980'ties. It is most pronounced in Subdivision 28, where in contrast to other areas, no sign of stock recovery has been observed yet. From abundance indices of juveniles it is obvious, that a substantial recruitment originated from a large spawning population in the Gotland Basin in the beginning of the 1980'ies. In the 2nd half of the decade, the abundance indices of recruits in the eastern Baltic were extremely low. This confirms the results from ichthyoplankton surveys indicating an almost complete failure of cod reproduction in the Gotland Basin in the last 10 years. The increase in the spawning stock in Subdivision 26 in recent years appears to be caused by successful reproduction in the Bornholm Basin, with the exception of 1994, when a major Baltic inflow allowed a limited reproduction in the eastern Baltic.

Related to the question whether and to which extend cod migrate from the eastern spawning areas into the Bornholm Basin to spawn, especially in times with unfavourable hydrographic conditions, a substantial increase of CPUE in the Bornholm Basin accompanied by a decrease in Gotland and Gdansk areas from March to July/August indicates that migration from the eastern areas to the Bornholm spawning area might have taken place in 1996.

Spatial distribution of cod in relation to hydrographic conditions

Hydrographic and bathymetric factors were found to influence significantly the spatial distribution of Baltic cod, thereby providing empirical evidence of strong habitat associations. The results showed that oxygen concentration and salinity were the main determinants of adult cod distribution with the habitat being defined at the upper limit by the halocline and at the lower limit by oxygen content. The effect of temperature was found not to influence the distribution pattern of neither adult nor immature cod significantly, while immature cod abundance was positively related to decreasing bottom depth within the observed range. Although the habitat preference may vary spatially and seasonally, the results emphasize that the distribution of Baltic cod is affected by hydrographic conditions as well as by bathymetry. The volume and oxygen content of the deep saline water differ substantially between areas and years, which indicates that the available preferred habitat varies both spatially and temporally and influences cod catchability and abundance estimates, as well as the stock size. The environmentally influenced distribution patterns of cod suggest that monitoring a few selected hydrographic variables during trawl surveys may improve the reliability of abundance estimates of Baltic cod.

Individual female fecundity

Historic investigations on the fecundity of cod in the Baltic were rather limited in their temporal coverage and refer mainly to the western Baltic and the Gdansk Deep. Due to a relatively high variability in both absolute and relative fecundity encountered in these studies, for which the reasons were unknown, a specific analysis procedure had to be developed and the obtained results had to be investigated in order to identify significant temporal and spatial differences in individual potential egg production.

In total 1250 ovaries have been analysed originating from a 10 years period (1987-96), covering mostly Subdivision 25, but for comparative studies also other spawning areas. For each sampling date and area, relationships between individual fecundity and length as well as weight were established using different linear and non linear regression techniques. Significant differences in fecundity were determined between different years and stocks, but not between different sampling dates within one spawning period nor between different

spawning grounds. Together with fecundity data extracted from the literature, a time series of relative fecundity was established for the Central Baltic cod stock, covering the period 1976-96. Attempts to explain the obtained significant inter-annual deviations in relative fecundity (up to 33%) by hydrographic conditions (i.e. the temperature regime during the preceding winter) or the nutritional status of the females (i.e. condition factor, hepatosomatic index) were not successful. Required research actions to solve the problem were discussed and outlined, but were, due to their complexity, beyond the scope of the present project. A first approach to investigate the occurrence of atresia demonstrated that degeneration of oocytes is a frequent phenomenon in the field, however, with a relatively low intensity.

Viability of cod eggs and larvae

Differences in egg quality might be an important parameter in explaining variation in recruitment of cod. In addition to stock parameters, egg quality of cod in the Baltic might be affected by contaminants. This has been discussed since the 1980'ies when high malformation rates at early egg stages were recorded in ichthyoplankton samples.

Aiming to elucidate egg quality of Baltic cod in relation to female age/size and in comparison to other stocks, Baltic and Skagerrak cod were kept in tanks throughout the spawning season and egg and larval viability up to day 10 post hatching was assessed in subsequent batches from individual females. Incubations yielded low variability between both replicates within batches (on average 3.1±2.2% viable hatch and 7.2±5.6% larval survival) and between batches from individual females (on average 6.6±5.2 and 6.7±4.0% viable hatch and larval survival respectively) with low frequency of nonviable hatched larvae (on average 3.7±3.3%). Viable hatch for individual females ranged between 33.5 and 96% and larval survival from 68.5 to 95%.

Analysis revealed no effect of egg size on viable hatch, whereas larval size, growth, and survival during the yolk sac stage were significantly correlated to egg size (P<0.001 for all parameters). As egg size vary with female age/size and stage of spawning the results suggest that larval viability decreases with number of spawned batches during the spawning period of an individual female and increases with female age/size. Based on the relationship between egg size and larval survival, estimations of larval survival probabilities varied from 64% for a 2-year old female to 86% for a female age 6+. Comparison of viable hatch and larval survival between newly caught Baltic and Skagerrak cod revealed no significant difference between the stocks. Viable hatch averaged 85±9% for Baltic and 91±3% for Skagerrak cod and larval survival 87±5% and 87±4% for Baltic and Skagerrak cod respectively. This is consistent with reported egg survival for cod from northern Norway (80±11%). An equally high figure for egg survival of the three stocks indicates that Baltic cod is not affected by a reproductive disturbance influencing egg quality.

Incubation of eggs with malformations at early blastula stages, with normally developed eggs from the same batch as controls, revealed that viability of eggs with malformations is highly variable. The results suggest that irregular cell morphology at early blastula stages might be repaired as a number of eggs displaying malformations resulted in viable larvae, i.e. this parameter is not a consistent indicator of egg quality, as has been suggested, and should be used with caution when assessing egg viability in e.g. ichthyoplankton sampling.

The proportion of fish age 6+ in the Baltic cod stock has decreased from 8.2-11.2% in the mid 1980'ies to 1.5-2.6% in 1993/94 only slightly increasing afterwards to 3.4-4.0%. The results obtained in the present investigation suggest that the poor recruitment of Baltic cod during the 1990'ies might be caused by a low

number of repeat-spawners producing high quality eggs and consequently egg quality aspects should be incorporated in stock-recruitment relationships.

Contamination of sex products with toxic substances

Three series of successful experiments on fertilisation and egg and larval development conducted on board RV *Dana* (1995, 1996) and RV *Alkor* (1996) respectively, clearly indicated negative correlations between organochlorine contaminant concentrations of cod ovaries and reproductive success (percentages of larval hatch, survival, growth and developmental stage) of spawned eggs. The *Dana* series obtained in 1996 also revealed corresponding regional differences between the Gdansk Deep and the Bornholm Basin, i.e. significantly lower maternal condition together with lower hatching success, lower larval survival of larvae after hatch and lower developmental stage were seen in egg/larvae batches obtained from females caught in the Gdansk Deep. In contrast, comparable experiments with eggs of cod: from a) the Swedish West Coast, b) Baltic cod kept in the Lysekil for 2 years, c) newly caught Baltic cod and d) lab-raised Baltic cod did not yield similar correlations. However, the egg and larval performance showed also in general higher survival rates compared to the *Dana* and *Alkor* experimental series, which might be explained either by the fact that in Lysekil voluntarily spawned egg were used, while the field based experiments were performed with stripped eggs or that in general no high contaminant levels were detected in the Lysekil samples. The only obvious deviation between the different groups of cod in the Swedish experiments occurred in elevated DDT/DDD/DDE values in the newly caught Baltic cod eggs. The latter group was also the only one fed with Baltic sprat, whereas the other groups were fed on Skagerrak sprat, being considerably less contaminated. A first limited histological study on the occurrence and intensity of atresia in cod ovaries, of which a limited number was also analysed for organochlorines, indicated that the intensity of atresia is positively related to elevated contaminant burdens. In summary, it can be concluded that contaminant burdens occurring in Baltic cod are likely to reduce the reproduction potential to a certain extend. We do not assume that the contamination situation presently threatens the survival of the Baltic Sea cod stock as a whole, but it may still be a serious problem in certain areas.

Estimation of viable egg production

Potential annual egg production estimates of different Central Baltic cod stock components for the period 1976-96 were derived on basis of newly established female maturity ogives and sex ratios, new extensive data on individual female fecundity as well as stock size and biomass per age-group derived by area dis-aggregated MSVPA runs. Additionally, the viability of the offspring (larvae) in relation to maternal age is taken into consideration in corresponding viable egg production estimates.

To check whether the established time series are reliable, annual as well as daily egg production estimates at specific sampling dates were related to field measurements, i.e. egg- and larval abundance values obtained from ichthyoplankton surveys. Due to highly variable egg mortality rates, no significant correlations were revealed, independently whether a viability array was applied or not. However, egg production estimates of the youngest developmental stage derived from ichthyoplankton surveys were significantly correlated to the potential and the viable egg production. This indicates that the production rates determined are a reliable measure of the actual egg production by the spawning stock in the different major spawning areas of the Central Baltic.

According to the established data series, the egg production was on a rather high level in the late 1970'ies and remained on this level until 1984 (though the reproductive success had already declined). Caused by the decrease in the spawning stock the egg production declined drastically until 1991 in all major spawning areas. In contrast to the other areas, in Subdivision 25 a substantial increase in egg production was determined for most recent years, reaching nearly similar levels as in the early 1980'ies. In Subdivision 26, a moderate increase in egg production was estimated for 1995/96, reaching the intermediate levels of the mid 1970'ies. In Subdivision 28 the egg production did not show any recovery and is still on a very low level, i.e. only around 3% of the historic maximum. The relative contribution of first time and repeat spawners to the potential egg production showed considerable fluctuations in Subdivision 25, the latter being on average substantially lower than in the other spawning areas. A simple relationship between periods of high egg production by well established repeat spawners and high recruitment success could not be determined within any of the areas.

The potential egg production in 1993/94 estimated for the Western Baltic cod stock was significantly lower than in the Central Baltic, i.e. around 15% of the production. This is, due to a higher individual fecundity in the Western Baltic stock, in fact slightly higher than expected from a comparison of the corresponding spawning stock biomass values.

3.3 Physical and chemical factors acting directly on the developmental rate, mortality and small-scale distribution of eggs and larvae

For the identification and examination of hydrographic factors influencing the development and survival of Baltic cod eggs and larvae a close linkage between field, laboratory and modelling studies was established. Cod spawning areas were covered by combined ichthyoplankton/hydrographic surveys during spawning time and the impact of obtained environmental variability on developmental and survival rates was tested in controlled laboratory experiments. Subsequent numerical simulations enabled an examination which hydrographic processes acting in the Baltic have most impact on successful development of eggs and early larvae. Furthermore, the vertical distribution of larvae and their prey where investigated in relation to small-scale hydrographic processes.

Distribution and hydrographic environment conducive for survival of cod eggs and larvae

Results from 11 years of intensive field studies on the vertical distribution of Baltic cod eggs in relation to salinity, temperature, and oxygen content were summarized. The observation period 1986-96 covers a variety of common hydrographic scenarios in the Baltic: high salinity in the deep water after strong inflows (1993 and 1994), low to intermediate salinity in the deep water after weak to moderate inflows (1990, 1991 and 1992), oxygen deficiency in the bottom layer during stagnation periods (1988, 1989, 1995 and 1996) and oxygen deficiency in the bottom layer and low temperature in the intermediate layer after severe winters during stagnation periods (1986 and 1987).

It has been demonstrated that the actual salinity regime is the primary factor determining the egg distribution, whereby critical oxygen levels and temperatures have additional effects. From field observations, the tendency was identified that eggs sink towards deeper layers during development due to an increase in specific gravity. This effect has implications for the interpretation of field estimates of egg mortality.

The influence of the hydrographic parameters on the distribution patterns was analysed, and a predictive artificial neural network model for the estimation of mean ambient development temperatures encountered by

Baltic cod eggs was established, explaining 82% of the variance of predicted vs. observed relative frequencies for the full series of observations. This confirmed that salinity is the primary factor determining the vertical distribution of eggs, and that the deviations between theoretical and observed frequencies were largely due to limiting oxygen concentration and low temperature. As only slightly more than 80% of the observed variance was explained by the ANN, it is likely that additional factors also contribute to the vertical distribution of the eggs. One such factor could be the age structure of the spawning stock, which has changed considerably during the past 10 years. Small cod females produce on average smaller eggs than large females, and their eggs are less buoyant. The distribution of the eggs can therefore be expected to be shifted towards higher salinity, concurrently being subjected to unfavourable oxygen conditions limiting survival. The structure of the spawning stock and accordingly the average egg size produced by the females may therefore be a factor influencing the vertical distribution of eggs *per se*, in addition to pre-spawning adaptation of the eggs in the gonads and at fertilization in dependence of the ambient salinity. Apart from this, the ANN model can be regarded as an adequate tool to predict the vertical distribution and ambient temperature for the development of cod eggs in the Bornholm Basin.

The impact of the special hydrographic conditions on cod egg mortality was studied by comparing mortality rates estimated for time periods characterized by different environmental situations. At all sampling dates egg mortality changed considerably during development, but with pronounced differences between the different dates. Highest mortality rates occurred in the developmental period before the closure of the blastopore and just prior to hatch, in particular when critical oxygen levels in the bottom water restricted substantially the vertical range inhabited by the eggs, which corresponds well to findings from laboratory studies (see below).

Cumulative egg mortality until hatch varied from 93.6 to 98.6 % in studies based on repeated surveying of the distributional area and amounted to 99.9 % for a drift study conducted in July 1996. Thereby, the most pronounced differences between the sampling dates were found in the early egg development until the end of stage IB. Comparing the cumulative mortality until hatch of different cohorts with the reproductive volume in the Bornholm Basin a weak, but insignificant correlation is indicated for the period 1987 to 1992. Hence, either the reproductive volume alone does not adequately describe the environmental conditions during egg development or other factors than the hydrographic regime have to be considered additionally. The pronounced variation of mortality in the early egg period may indicate an impact of age structure of the spawning stock influencing the initial viability of the eggs (see below), and especially for the older egg stages predation can be an important source of mortality.

Experiments on the influence of temperature, salinity and oxygen concentration

The incubation of eggs under different oxygen levels resulted in different mortality rates, hatching success, and larval survival for eggs obtained from the same female. Combining these data with results obtained earlier in the project confirmed a significant influence of oxygen content on egg and larval survival, with minimum requirements of 2 ml/l oxygen concentration for successful hatching. The overall developmental time from fertilization to hatching was not varying significantly between the tested oxygen concentrations. These results indicate that oxygen has an important effect on mortality rates, but not on developmental time of cod eggs. Based on these laboratory results a functional relationship describing the impact of different oxygen saturation levels on the viable hatch of cod larvae was established. Temperature is an important factor controlling the rate of egg development. A direct influence of temperature on egg mortality has not

been considered in the experiments, but the results from the field studies indicate that temperature is a limiting factor only in extreme years.

The vertical migration and behaviour of young cod larvae is closely related to the developmental progress during the yolk-sac stage. Newly hatched larvae were nearly buoyant when hatching at 15 psu. They showed only limited vertical movements. With ongoing development, they lose buoyancy and became more and more active to compensate sinking. This necessity is reflected by an increase in vertical activity four days after hatching. Maximum activity was recorded between six and ten days after hatch. Progress in eye pigmentation and fin development as well as functional mouth opening takes place right in time to enable larvae to migrate and start feeding in upper water layers. Larval vertical behaviour is a combination of hop and sink. Positioning is thus mainly determined by larval activity as well as buoyancy and only to a minor extent by cruising speed. Reduction of oxygen has negative influence on survival during early larval stages and also on their activity. However older larvae were able to cope with unfavourable oxygen conditions in the experiments down to 2 ml/l oxygen concentration.

Results on the salinity requirements for fertilization success and buoyancy of eggs obtained for the western and eastern cod stock in comparison imply that the western stock could also successfully spawn in the Bornholm Basin, at least in years after an inflow, and further that both stocks can in principle spawn in the Arkona Basin. However, in stagnation periods the hydrographic conditions in the Bornholm Basin form an ecological barrier separating the Belt Sea from the central Baltic cod stock.

Measurements of egg diameter revealed no significant correlation between female condition and egg size, but between female size and egg size within the first spawned batch. Furthermore, a correlation was found between egg size and corresponding salinity required for reaching neutral buoyancy. Compiling these relationships with additional data on batch fecundity (from the literature), average specific egg buoyancy values were determined for several age groups. The results showed older females to produce more batches and eggs with a lower gravity than recruit-spawners did, i.e. these eggs will develop at shallower depths with more favourable oxygen conditions and thus have a better chance to survive. The impact of the age structure of the spawning stock will therefore be higher in years with low oxygen saturation. In the Gdansk Deep and in the Gotland Basin where salinity in the bottom layers seldom exceeds 12 psu and oxygen conditions are often unfavourable, it is likely that only well established repeat-spawners have a chance to contribute to recruitment.

Small-scale distribution of larvae and their prey in relation to small-scale hydrographic processes

During sampling with an Optical Plankton Counter and an Ichthyoplankton Video Recorder only extremely low numbers of larvae were recorded. As it was not feasible to study larval distribution and their prey in relation to small-scale hydrographic processes utilizing this material, data from sampling during 3 cruises in 1994 obtained by a multiple/opening and closing net (BIOMOC) were used to resolve the vertical distribution of larvae and their prey (resolution 5 m).

Cod larvae were found in all observed depth intervals with the highest mean abundances during daytime from 30-40 and 60-75 m, while during night peak abundances were observed between 25-30 and 70-75 m. The mean length of larvae above the halocline was significantly larger than below. Larvae < 4.5 mm length were mainly yolk-sac larvae before first-feeding and apparently concentrated below the halocline. Larvae ranging from 4.5-5.5 mm (first-feeding larvae) showed clear peaks in abundance above and below the halocline in

two occasions, while in a third they were concentrated in the upper 45 m. The 5.5-7.5 mm group (feeding larvae) aggregated in the upper 45 m during the night and spread throughout the water column during day.

No significant association during daytime between the average density of cod larvae (mean of 3 profiles) and any of the prey groups was found. Replacing the food density with food availability, which was the combined effect of illumination and food abundance, significantly improved the correlation coefficients, i.e. strong relationships were found with copepodite stages as food items.

The bimodal larval distribution observed is expected to be the result of the egg distribution and the vertical migration of larvae for optimum feeding conditions. The timing of the vertical migration of cod larvae into upper water layers coincides with the time of highest swimming activity (see above) and is undertaken long before the onset of diel migration of cod larvae.

In conclusion, this study on the vertical distribution of cod larvae in the Bornholm Basin has shown that the above/below halocline distribution in the water column is determined by larval age, as reflected in the distribution of larval sizes and stages. The upward migration of first-feeding larvae suggests that the distribution in the deep water is sub-optimal with respect to feeding. Small scale distribution (~ 5 m) of the larger feeding larvae seems to be governed by food abundance and light regime through their combined effect on food availability. The larvae aggregated on all cruises in the depth of optimum light conditions during sunrise and sunset, which are considered to be their principal feeding time. Furthermore, this aggregation was consistent in spite of large differences in temperature, thermocline depth, and subsequent water density between cruises.

Physical factors affecting the oceanographic environment

Numerical simulations required for the examination of hydrographic factors conducive for successful development and survival of Baltic cod eggs were conducted. The actual salinity regime has been clearly recognized as the primary factor determining the distribution of Baltic cod eggs and via the oxygen enrichment the survival of eggs. The modelling exercises have identified the importance of inflows of saline, oxygen enriched water masses of the Kattegat/Skagerrak region and the North Sea into the Baltic Sea on the recruitment success of Baltic cod. These inflows increase the volume of water with suitable oxygen and salinity condition for successful development and survival of cod eggs. Another candidate process to potentially increase the spawning volume is the surface wind stress resulting in enhanced mixing at and below the halocline. In contrast, the effects of winter convection on oxygen levels in the halocline seem to be limited.

3.4   Meso-scale distribution of pelagic early life stages and densities of 0- and 1-group cod

Horizontal distribution of eggs and larvae

The horizontal distribution of the youngest egg stage at main spawning time in 1986-96 was investigated for identification of areas with most intensive spawning in the Bornholm Basin. In all years, areas of high egg abundance were found mainly in the central part of the basin in water depth exceeding 75 m. The extension of the area(s) of high egg abundance increased with egg development due to dispersion, however, the older egg stages appeared to be retained within the area enclosed by the 60 m isobath due to the salinity levels they require for attaining neutral buoyancy. The horizontal distribution of cod eggs by developmental stage at main spawning time in 1995/96 differed from those observed in preceding years, and in general also from

distributions described for previous time periods when the eggs were by far most abundant in the central part of the Bornholm Basin. This, however, can be explained by two factors: 1) the inflow event in early 1993 raising the halocline and thereby influencing the vertical distribution of cod eggs allowing also the deeper distributed older egg stages to float in a wider region, 2) a shift of the spawning centre towards the basin's edges occurred.

The distribution of yolk sac larvae was closely associated with that of the oldest egg stage, whereby spatial differences in the developmental success were detected. Later larval stages are exposed to layers below the direct wind-driven surface currents, and hence their distribution patterns were strongly influenced by a return flow compensating the direct wind driven circulation. As shown for August 1991 prevailing, stronger westerly winds resulted in a rapid transport of the larvae away from the hatching sites towards shallow coastal regions in the north. Whereas in periods of low, variable wind forcing (May 1988) larvae were retained in the central part of the basin.

A comparison of cod egg and larval abundance in the different spawning grounds of the entire central Baltic clearly demonstrated the important role of the Bornholm Basin for recruitment of Baltic cod. It seems that the inflow event in early 1993 did not significantly change the situation in the more eastern spawning grounds. Thus, in 1993-1996 limited numbers of cod eggs were found in the southern Gotland Basin and the Gdansk Deep, with highest abundances encountered in the latter area in 1994. With one exception larvae were encountered only in the area of the Bornholm Basin, indicating a limited developmental success of eggs in the more eastern spawning areas.

Horizontal distribution and diurnal migration of 0-group cod

Distribution, density patterns and diurnal migration of metamorphosed 0- and 1-group Baltic cod were analysed in relation to environmental conditions on basis of intensive hydroacoustic, hydrographical, and trawl survey activity conducted within the project. Results contributed new knowledge on the spatial distribution, localization of nursery areas, habitat selection, and recruitment biology of pelagic and demersal stages of metamorphosed 0- and early 1-group cod.

Methodology development has included hydroacoustic measurements and integration (high frequency 120 kHz split beam echosounder) and concurrent sampling with large, fine meshed trawls. This method has been employed for the first time in the Central Baltic for detecting and localizing juvenile 0-group and early 1-group cod. In order to do so, results from supplementary experiments to measure *ex situ* Target Strengths of free swimming juvenile cod in laboratory have been made. Difficulties in applying this combined hydroacoustic and trawl sampling method have been identified, due to:

- the scattered and bottom near distribution of the juvenile cod,
- the highly stratified waters of the Baltic Sea,
- the co-occurrence of young cod with sprat and small herring (showing overlapping Target Strength values).

Hence, hydroacoustic abundance estimates of juvenile cod are more complicated to obtain compared to a situation where the juvenile cod is distributed in isolated, large patches in pelagic water layers above the pycnocline, as originally expected.

Nursery areas have been located for juvenile cod (size group 2-11 cm) in the Central Baltic, however, obtaining information on the full distribution of all potential nursery areas was not possible. The juvenile cod

occurred in all areas of the Central Baltic with varying densities, but mainly at localities with 20-80 m bottom depth, and in waters with relative high oxygen content. They seem never to aggregate in schools, which indicates different distribution pattern and behaviour of these life stages compared to the North Sea.

Stomach content analyses of juvenile cod revealed size selective feeding by identification of habitat specific pelagic or demersal prey groups, and indicated size dependent vertical distribution and migration. Trawl samples and collected hydroacoustic Target Strength data showed that pelagic juvenile are associated with the pycnocline at night or concentrate in near bottom water layers in areas with a stratified water column. In mixed water columns, i.e. in more shallow areas, juveniles were found to be more scattered in the water column.

Extended investigations on the diurnal vertical migration of 0-group cod have been performed by repeated depth stratified fisheries during night and day. For 0-group cod with a total length of 2-5 cm catch rates in the surface layer were higher than close to the bottom. At localities with intermediate water depth (from 31-60 m), catch rates of 4-9 cm long juveniles decreased in the surface layer and increased near to the bottom significantly from day to night. In shallower regions, with 21-30 m depth, such differences could not be observed in near bottom hauls. In deeper water (> 60 m) no 0-group cod was caught near to the bottom during night.

The methods used, including diet composition analyses and also checks of otolith microstructure have provided key information on processes influencing feeding and settling biology and vertical distribution (and migration) patterns of juvenile Baltic cod as well as identifying the potential for density dependent processes to limit recruitment success. The established GLM model of distribution and density of juvenile cod obtained by trawl surveys conducted within the project appears to be sensible with respect to the parameters considered and the variance structure in the data. Additionally, the results from the present study can be used in the planning process of future cod recruitment surveys in the Baltic Sea directed towards 0- and 1-group cod, as these stages now have been located and adequate gear types have been implemented. The results identified that the catchability of juvenile cod is highest during night-time indicating that estimates of juvenile abundance should be based on surveys performed at night.

Horizontal distribution of 1-group cod

The Baltic International Trawl Survey data base was updated to include 1997 survey data and corrected for errors in trawl positions and trawling time detected. Differences in fishing power of the various research vessels participating were considered in the applied GLM analyses. The obtained abundance indices of 1-group cod (numbers/ trawling hour) indicate the importance of the southern part of Subdivision 26 as a nursery area for young cod. This pattern has been observed throughout the time series, except at the beginning of the 1980's when young cod was distributed more widely. Although this analysis is a step forward to describe the distribution pattern of demersal 1-group cod throughout the available time series, there are still improvements of the analysis to be done. The data base should be revised according to new, corrected age-length keys. With respect to examine inter-annual differences in more detail, future analyses should consider spatial distribution patterns based on kriging estimation, and Latvian data from the Gotland Basin collected in 1975-95 should be included in the data base for analysis.

3.5   Predation on early life stages

During the last decade predation has been discussed as a major factor controlling recruitment of marine fish species. However, field studies that have been designed adequately for estimating predation mortalities of early life stages are scarce. Following methodological problems are suggested to be responsible for the limited success in this area:

1) identifying eggs and larvae in predator guts,
2) quantifying prey consumed by each predator,
3) determining abundances of predators
4) estimating the number of eggs and larvae available as prey.

The importance of predation on early life stages of cod in the Central Baltic has been investigated as a process potentially affecting the reproductive success of cod by covering above major work tasks by:

1) an extended literature review and re-analysis of available data bases to identify potential predators followed by an extensive field campaign to sample stomach contents,
2) performing ship board evacuation and digestion experiments,
3) estimating predator populations by trawl and hydroacoustic survey activity and age-structured models based on catch statistics,
4) determining prey abundance and production based on ichthyoplankton surveys,

Identification of potential predators

From the wide spectrum of organisms to be considered as predators of cod early life stages, a literature review and the evaluation of available databases revealed predation by the clupeids herring and sprat to be the most important process. The analysis of this process concentrated mainly on the Bornholm Basin as the presently most important cod spawning area, but was extended during the project to the more eastern spawning grounds, i.e. the Gdansk Deep and the Gotland Basin, for comparison. As other potentially important predators the scyphomedusae of *Cyanea capillata* and *Aurelia aurita* as well as sticklebacks (*Gasterosteus aculeatus*), concentrating in considerable densities in the central Baltic in summer and autumn, were identified. Cannibalism by juvenile cod on their smaller conspecifics as well as adult cod feeding on their juveniles are common processes in cod stocks and were therefore investigated during the project also. Finally garfish (*Belone belone*) were identified as potential predators on pelagic juvenile cod. However, since garfish is not caught by any standard fishing gears, a special sampling programme would be needed for a test of this hypothesis, a necessary effort beyond the scope of this project.

Predation by herring and sprat

The determined daily cod egg consumption rates by herring and sprat populations in the Bornholm Basin in comparison to corresponding egg production rates revealed a substantial predation pressure during the first month of the spawning season caused by sprat. At this time of the year spring spawning herring concentrate in their coastal spawning areas. Hence they do not significantly contribute to the predation-induced egg mortality at this time of the year. Sprat spawn in the Bornholm Basin from April to July, thus concentrating in cod spawning areas in times of high cod egg abundance. After ceased spawning activity a part of the sprat population leaves the area and remaining individuals switch from copepods and fish eggs to cladocerans as main prey organisms. With the return of the herring from the coastal areas to their feeding grounds in the

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Bornholm Basin, the predation on cod eggs by herring increases to considerable levels, especially after the peak spawning time of cod shifted to summer month.

A decline in sprat predation on cod eggs was observed in early summer during most recent years despite of relatively high cod egg abundances. Problems were encountered in explaining this trend. An investigation of a possible vertical mismatch of cod eggs and the predator due to the changed physical environment after the major inflow in 1993, resulting in a shallower distribution of the cod eggs due to increased salinity as well as a deeper distribution of the clupeids due to enhanced oxygen concentrations in the bottom layers, exhibited no final explanation. Other fish eggs occurring at times in much higher abundances than cod eggs may act as a trigger factor for fish egg consumption. Considering eggs from other fish species revealed reduced fish egg abundances for the period after the inflow, at least for early summer dates, accompanied with a change in vertical distribution of the eggs. In combination, this resulted in a substantially lower abundance of ichthyoplankton in the feeding depth of sprat, nearly explaining the observed change in feeding behaviour. Considerable changes in zooplankton abundance and biomass before and after the inflow in 1993, hypothized to lead sprat to a change their food selection, could not be confirmed.

The estimated consumption rates by both planktivorous predators are based on a new model of gastric evacuation incorporating actual ambient temperatures as well as newly compiled area dis-aggregated international catch-at-age utilized in Virtual Population Analysis (VPA) and its multispecies extension (MSVPA) to estimate predator stock sizes in specific areas of the Baltic. Downscaling from subdivision-level to single spawning grounds was obtained by historic horizontal distributions from hydroacoustic surveys conducted at different times of the year. The estimated consumption rates of cod eggs by herring and sprat populations in the Bornholm Basin exceeded corresponding egg production rates in all spring and early summer dates 1990-92, but reduced to values well below the daily production in most recent years. Also the increase in predation by herring in summer month did not compensate this lower predation pressure. Hydroacoustic surveys conducted within the project indicate a slight (herring) to moderate (sprat) overestimation of the predator stock sizes by the (MS)VPA, explaining the inconsistency between estimated consumption and production rates. However, this overestimation does not change the conclusion that predation by clupeids is a major source of cod egg mortality in the Bornholm Basin and has consequently to be considered in cod recruitment modelling approaches.

In the Gdansk Deep and the Gotland Basin, in general a low predation pressure on fish eggs through both herring and sprat populations was determined. The most likely explanation for this, is a difference in feeding depths of clupeids, which is on average considerably deeper in the Gdansk Deep and especially in the Gotland Basin compared to the Bornholm Basin. In fact, light intensities in average feeding depths in the eastern areas are on a level, where active food selection is already severely hampered, resulting probably in an none selective uptake of fish eggs. In contrast, in the Bornholm Basin especially sprat in spring and early summer actively selected fish eggs from the food supply. Significant differences in zooplankton abundance in feeding depths between the three cod spawning areas, hypothized to explain the difference in food selection, were in general not encountered. Both clupeids showed an apparent selection of older egg developmental stages, which is at least partly explainable simply by a better visibility of the older eggs due to the development of the embryo and increasing pigmentation. On the contrary, differences in egg size obviously did not affect the selection process.

In contrast to the egg stage, cod larvae appear not to be substantially affected by predation, mainly due to a limited vertical overlap between prey and predator, with the exception of early larvae hatching within and below

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the halocline. However, occasionally a significant predation on these early cod larvae by sprat occurred in the Bornholm Basin, especially when high abundances of other fish larvae were encountered in the plankton, obviously triggering sprat to switch to fish larvae as prey. Herring did not feed on these larvae at the same time, due to their small size.

Feeding on juvenile or small fish by larger herring was frequently encountered, however, on a relatively low level and mostly restricted to juvenile sprat and gobiids, independently of the investigation area. Thus, a major impact on pelagic juvenile 0-group cod is not to be expected.

Predation by scyphomedusae

The predatory impact of *Cyanea capillata* appears to be of some importance for the survival of cod eggs. However, the intensity of the predation depends on the spatial and temporal overlap between predator and prey as well as the inter-annual variation in abundance of medusae. Main factors steering the intensity of predation in the Bornholm Basin are the decrease in cod egg abundance after peak spawning season and a concurrent increase in medusa abundance as well as size. Thus, the shift in peak spawning time to summer month has increased the potential impact of predation by this scyphomedusae and for late egg cohorts also by *Aurelia aurita*. The latter scyphomedusae preys successful on cod eggs only above a size of 10 cm, which in the central Baltic is in general not reached before August. Predation by scyphomedusae on fish larvae has not been observed, however, the sampling strategy was also not directed to this process in particular.

Predation by sticklebacks

Predation on early life stages of cod by sticklebacks, occurring at certain times of the year in large quantities in the Central Baltic, has not been detected. This is due to a rather limited temporal and spatial overlap between predator and prey, i.e. the late appearance of sticklebacks in open sea areas from August onwards, after their spawning season has ceased, and their to shallow water layers restricted abundance.

Cannibalism

Predation on cod eggs and larvae by 0- and 1-group cod was rarely encountered, independent from the area of investigation and thus appear to be of no importance as a source of cod egg and larval mortality. Also cannibalism on juvenile cod by earlier cohorts of the same year-class was never observed, although the extended spawning season results in pronounced differences in sizes between early and late hatching cohorts. Both appears to be caused by a rather limited spatial overlap between potential predator and prey, as late larvae and early juveniles are normally drifted out of the spawning areas and dependent on the variable wind forcing are settling in different more shallow locations. In contrast, adult cod regularly preys upon 0- and 1-group cod, especially at high juvenile abundances (see section 3.8).

3.6 Influence of prey availability on growth, condition and survival of early life stages

Most hypotheses aiming at explaining variations in survival and recruitment of marine fish early life stages imply a direct link between feeding, nutritional condition, growth and mortality. As a consequence the effort in this section has been directed at measuring one or more of these parameters and to identify the key processes resulting in enhanced growth and condition of the early life stages of Baltic cod.

Hydrographic features resulting in enhanced feeding potential

The coupling of physical processes, primary and secondary production has been examined on the basis of cruise data obtained from 1993 to 1996, and hydrographic features which can enhance cod larval and juvenile feeding have been identified. Coastal upwelling appears to act in two modes on plankton processes. In the first case, doming influences the distribution of planktonic organisms offshore from the doming. Here, aggregation of organisms due to the interaction of circulation patterns and behaviour appears to be the mechanism as an increase in production rates is not evident for either phytoplankton or zooplankton. In this situation, the effects of nutrient injection on population size may be delayed due to; a) light limitation of the phytoplankton cells or; b) lack of chelation of metals by organics thus delaying the uptake of nutrients and increase in phytoplankton biomass. Regardless, the aggregation of planktonic organisms in these regions identifies the potential importance of this circulation pattern for creating high abundance of prey for larval and juvenile fish.

These features have also been identified to have a major effect on both phytoplankton and zooplankton production in regions where the thermocline and halocline interact with bottom topography. The high zooplankton production observed in these regions suggests an efficient coupling of primary and secondary production in the shallow waters (< 30 m around the Basin in the region between where the thermocline and halocline reach the bottom). This situation potentially creates a region of high food abundance for larval and juvenile fish in the Baltic.

The results of this study identify the need for further examination of the influence of specific oceanographic regions and intermediate scale oceanographic features in the Baltic sea on the growth, condition and survival of key fisheries stocks such as the Baltic cod. In particular these areas may become important habitats for larval and juvenile fish during periods of low food abundance in particular in early spring and late fall when food levels may be limiting to growth.

Distribution of larval and juvenile cod and their prey items

We have described the distribution of the early life stages of cod in relation to their prey items by combining information from studies on horizontal and vertical distribution of larval and 0-group cod, and microzooplankton. During the late yolk-sac and first-feeding phase most of the larvae migrate from hatching depth towards the more shallow water layers, where generally also the highest abundances of prey items (nauplii, copepodites) are observed. The abundance of larvae and prey was not found to be significantly correlated in the vertical resolved resolution, but the abundance of larvae was correlated with prey availability as defined by prey abundance and light dependent capture success.

High prey abundances during some cruises have been found associated with a characteristic doming of the pycnocline and potential upwelling of nutrients. The doming pycnocline and increased prey biomass is predominately found in the near coastal zones. Hence, larvae transported out of the Bornholm Basin may encounter higher prey abundances than larvae circulating in the deep basin, a hypothesis that could not be tested thoroughly due to the low numbers of larvae caught in contrasting areas.

The juvenile life stage of cod can be divided into a pelagic, a transition and a benthic phase with obvious changes in food environment. Juvenile cod less than 40 mm were observed to feed exclusively on pelagic prey, but at 40-50 mm the juvenile cod began to ingest benthic prey items, indicating that the settling process had begun. In the size range from 70-160 mm juvenile Baltic cod utilised exclusively benthic prey with an

increase in prey diversity observed for these larger individuals (for further information on diet composition see below).

Observation of feeding and swimming behaviour of larval and 0-group cod

Turbulence in the sea influences both the food environment for larval fishes and their ability to feed successfully. In the Baltic turbulence is generated by the wind, upwelling, and current shear and will impact feeding and growth rates of larvae or juvenile fish. In this section experimental and theoretical studies have been conducted to analyse swimming and feeding behaviour in relation to turbulence. These are the first series of experiments to report direct observations of feeding behaviour of larval and pelagic 0-group fish in turbulent water. Turbulence increases encounter rates between fish larvae and their prey. However, the results indicate that high levels of turbulence can be detrimental to the feeding success of larval cod, because turbulence can reduce the probability that larvae can successfully pursue the encountered prey. In the Baltic such episodes might occur in situations of high winds, intense upwelling, and current shear at pycnoclines. In comparison to pursuit success, attack success was very high for all levels of turbulence. This is probably because the larva approaches the prey to within a small distance, and at these scales the relative motion is negligible.

Cod larvae and 0-group diets

Diet composition of larval cod was described based on gut content analysis from larvae caught in depth stratified hauls. Diurnal and vertical feeding patterns have been identified. First-feeding was observed at a length of approximately 4.0 to 4.5 mm, but high (>80%) feeding incidence was restricted to larvae larger than 5.5 mm. The prey was dominated by copepod nauplii (88%), primarily of the species *Pseudocalanus minutus* and *Temora longicornis*. Older larvae included copepodites and adult copepods in their prey, but nauplii remained the most numerous prey in all size groups. A substantial amount of phytoplankton was only found in the diet of one larva.

The diurnal feeding patterns showed the lowest feeding incidence and numbers of prey per gut at sunrise, after which both parameters increased to maximum in the afternoon and evening. Night-time feeding was observed during a period with calm weather conditions and very high prey abundance in the surface water. The feeding patterns were determined for larvae > 4.5 mm in 4 different depth strata, corresponding to the upper mixed layer, the intermediate layer, the upper halocline and the deep water. Food intake was highest in the upper mixed layer during both day and night. During day the food intake declined slightly with increasing depth, whereas at night an abrupt drop in feeding incidence and numbers of prey per larva was observed. A pronounced increase in food intake with length of larvae was observed, therefore the decline in food intake with depth may be influenced by the fact that mean larval size decreased with depth.

The diet of 0-group juveniles was investigated with respect to the settling process and the switch from pelagic to benthic prey. Juvenile cod < 40 mm consumed exclusively pelagic prey items such as copepods and cladocerans. At a length of 40-50 mm the juvenile cod began to consume benthic prey items such as mysids and amphipods, however, copepods were still the dominant food organisms. Within 50-70 mm the dominant prey items were mysids and amphipods, with copepods comprising a minor component of the diet. In the size range from 70-160 mm juvenile Baltic cod utilised a diet composed exclusively of benthic prey. Juvenile cod were observed to utilise an increasing spectrum of prey with increasing fish size. However, prey organisms consumed by demersal juvenile Baltic cod > 90 mm were much smaller in comparison with prey sizes

reported to for other sea areas, and correspondingly prey numbers consumed were much higher. This apparent overlap in food resource utilisation among the different size groups of demersal juveniles observed in this study suggests that in areas and years with low prey abundance and high concentration of pelagic juveniles, an intra-specific competition for food resources may affect the recruitment success of Baltic cod.

Analysis of otolith structure of larvae and 0-group cod

Based on laboratory experiments the accuracy of age determinations using the number of increments and comparing these to the known age was determined. The use of the otolith increment width as a measure of nutritional condition was tested in laboratory settings and related to a biochemical indicator, the RNA/DNA ratio, revealing that the biochemical and otolith reaction pattern was coupled. Measuring the level of fluctuating asymmetry (FA) in otoliths from the field caught larvae to assess larval nutritional condition coupled with RNA and DNA content analysis (see below) was performed. Fluctuating asymmetry is the random deviations from perfect bilateral symmetry, and is believed to be an indicator of developmental stability. Developmental stability can be lowered by environmental stress such as low food availability. The field caught larvae were assigned to groups in good, intermediate, and poor nutritional condition on the basis of laboratory calibration experiments. The area and the major axis length of the lapilli exhibited ideal FA. The level of FA was similar in the "intermediate" and the "good" group indicating that FA can not distinguish between well fed larvae and larvae experiencing sub-optimal feeding conditions. However, the level of FA in the "poor" group was significantly higher than in the two other groups, indicating that prolonged starvation can increase the level of FA. Hence, otolith FA is a relatively simple way to identify severely starving larvae. The effect of environmental stress factors is cumulative, and other factors may have influenced the level of FA found.

Sagittal otoliths were analysed from individual juvenile cod at different stages during transition from the pelagic to the benthic environment. High variability in otolith microstructure was evidenced among and within individuals. Newly formed secondary primordia were more abundant in non-settled pelagic individuals with variable formation (width and appearance) in settling or in newly settled demersal individuals. Otolith ring structure indicated that diel vertical migration patterns were interrupted by settling excursions suggesting that individuals explored the benthic habitat prior to settling. Large settled juveniles (>8-9 cm) had transparent zone formations deposited about one month before catch indicating transition to the demersal environment

The distribution of birth-dates of 0-group cod caught in the years 1993-96 has been determined on the basis of otolith readings. The total sequence of increments from the hatch check to the edge was only readable in 18% of the investigated otoliths, but 80% of the otoliths could be read from the accessory growth centres (AGC) to the edge. In Subdivision 24 the 0-groups could be tracked back to two spawning periods, one from the end of March to the end of May and one from July to August. The 0-group cod caught in Subdivision 25 had similar spawning periods plus an additional period from January to March. The distribution of spawning dates agree well with the observed spawning in the Kattegat, western Baltic, and Sub-decisions 24 and 25. It is suggested that the largest juveniles could originate from the southern Kattgat.

The daily growth of the 0-group cod was similar during the pelagic and benthic stage, but was retarded in the transition stage. The growth rates estimated for the period September to October correspond well with growth rates found in juveniles from Nova Scotia.

Biochemical analyses of cod larvae.

The nutritional condition and growth patterns of Baltic cod larvae are not well described considering the potential influence of the long spawning season. The quality of a prey species may influence growth and reproduction of higher tropic levels; in this case the larval cod. One important factor for this variation in quality is caused by the dietary composition of the prey. In particular, inadequate levels of the essential fatty acids (EFA) eicosapentaenoic acid (EPA; 20:5 n3) and docosahexaenoic acid (DHA; 22:6 n3) have been observed to reduce growth rates and reproductive success in marine fish species. In order to estimate variations in growth and condition of cod larvae relative to feeding regime the RNA/DNA technique was employed. RNA and DNA based indices have been calibrated through a series of laboratory rearing experiments with cod larvae. The cod larvae were starved or fed copepod nauplii reared on different algal diets with distinct essential fatty acid composition. During the laboratory experiments in Charlottenlund *Acartia* adults were fed on different algae showing variations in the essential fatty acid composition and resulting nauplii from these adults were fed to cod larvae to investigate the effect on growth and condition. In these studies the diatom *Skeletonema* had the lowest DHA/EPA ratio and the lowest amount of DHA as percentage of total lipid content of the four different algae analysed. Cod larvae fed on these nauplii showed the lowest growth rates and poorest nutritional condition compared to larvae from the other food sources. The highest larval growth rates and best nutritional condition was observed for larvae fed *Acartia* nauplii from the *Heterocapsa* based food chain which also showed the highest DHA/EPA ratio and % DHA of total lipid content. It has been shown that the growth rates of the cod larvae are correlated with the fatty acid composition of the larvae. These results clearly indicate that not only prey abundance but also prey quality influence the growth of larval cod. The results from the above experiments were then used to assess the nutritional condition and growth of field caught cod larvae with respect to vertical distribution in the Bornholm Basin. The results obtained show that the difference in growth and nutritional condition could be reflected in the indicators tested even at a very young age (~7 days). Dry weight did not increase in starving larvae and RNA content and RNA/DNA ratio decreased supporting results from other studies on cod larvae.

Estimates of growth rates and nutritional condition observed in laboratory experiment carried out in Lysekil were very low in the feeding groups indicating problems in the onset of feeding. The growth rates in the laboratory experiments conducted in Charlottenlund were comparable to previous observations based on the content of larval RNA and DNA.

The RNA/DNA-ratios of field caught larvae aged 2 to 25 days (median 10 days) ranged from 0.4 to 6.2, corresponding to levels exhibited by starving and fast growing larvae in laboratory calibration studies respectively. 70% of the field caught larvae showed RNA/DNA-ratios between the mean values found for starving and fed laboratory larvae. Larvae aged to be 8-11 days old had higher mean RNA/DNA-ratios above 45 metre than below (t-test, $p < 0.05$). The instantaneous protein growth rates were significantly higher for all larval age groups in the surface layers (t-test, $p < 0.05$). Starving larvae were found in all depths sampled (10-85 m), whereas growing larvae (positive Gpi = protein growth rate in % per day) were restricted to samples taken shallower than 45 metres. These superior growth rates above 45 metres imply that migration to the shallow water layers is a prerequisite for good nutritional condition, growth, and survival of Baltic cod larvae. The frequent occurrence of cod larvae older than 8 days in deep water in poor condition suggests that a considerable proportion of the larvae will die from starvation in the deep layers of the Baltic Sea.

3.7 Modelling cod recruitment

Incorporating stock structure, spatial distribution and female influences into estimates of annual population egg production

Annual egg production in fish populations is generally assumed to be related in a simple manner to the biomass of spawning adults. However, this assumption can sometimes be violated if population and reproductive characteristics (e.g. maturity ogives, fecundity-size relations) vary significantly over time and space. Studies conducted within the process analysis sections have shown that such variability can be significant for Baltic cod. The sensitivity of population egg production to this variability has been investigated using a simple egg production model and project-derived results based on new investigations and compilations of historical material. Egg production rates seem more sensitive to observed variations in individual fecundity (nearly 2-fold range) than to variations in either sex ratios or female maturity ogives. Estimates of spawning stock biomass may yield biased estimates of population egg production in some years. The scope for decoupling between spawning stock biomass and potential egg production is however probably underestimated by our analyses. In nature, atresia and the failure of mature fish to spawn will result in additional decoupling but the incidence of these processes is not quantified for Baltic cod and has not been included in the analyses. Moreover, our analyses assume that all females produce eggs and larvae of equal quality even though process study results demonstrate that egg and larval characteristics differ within and between females. New methodologies for accommodating correlated aspects of adult reproductive biology (e.g. relations between fecundity, maturation and growth) and within/between female effects on egg and larval characteristics could potentially be useful in improving stock-recruitment relationships. The possibility for improvement is enhanced even further when the spatial and seasonal distribution of egg production is also accommodated. This issue is particularly relevant to Baltic cod, where in the recent past, our calculations show that up to 75% of the estimated egg production occurred in areas where oxygen conditions prevented development. In general, these findings indicate that modelling efforts might benefit from using information at higher scales of resolution and dis-aggregation than those used previously.

Mortality rates of eggs and larvae caused by predators

Consumption rates of cod eggs and larvae by herring and sprat populations in the Bornholm Basin were estimated for several sampling dates within the period 1988-96 based on:

- numbers of cod eggs and larvae in individual predator stomachs and corresponding total stomach contents from sampling in the main spawning area during spawning,
- daily rations of total food as well as cod eggs and larvae by individual predators derived from performed stomach evacuation experiments and gastric evacuation modelling,
- abundance and structure of predator populations within the spawning area for each sampling date.

A comparison of daily cod egg consumption rates by the predator populations with corresponding production values obtained from ichthyoplankton surveys, enabled the determination of cod egg predation mortality rates for specific sampling dates covered (see section 3.5). Apart from this extended parametrization approach, an attempt was conducted to estimate the impact of predation by clupeids without regular extensive stomach content analysis, allowing to establish a time series (1976-96) of cod egg consumption rates. The basic problem encountered was to establish functional relationships of available food supply (the amount of cod

eggs but also other fish eggs and zooplankton) with diet composition data. This was solved by a method similar to the suitability concept used in the MSVPA, in which basically the proportion of a specific prey item to the total stomach content of a predator species is related to the standing stock of the prey available in the area. However, due to the fact, that changes in hydrographic condition effect the spatial overlap between prey and predator substantially, establishment of a relationship between suitability coefficients and the vertical overlap appeared to be necessary. The determined suitability coefficients were used to estimate consumption rates and indices of predation mortality at main spawning time on basis of actual predator and prey population sizes as well as estimated individual consumption rates. Contrary to the MSVPA approach, prey stocks are not estimated within the model, but simply observed by plankton surveys. The population size of predators were determined by conventional stock assessment models, downscaled to the spawning areas of cod by distributions obtained during hydroacoustic surveys. A further sub-model was introduced to estimate the individual food rations by predators species in dependence of actual environmental conditions, e.g. food availability. In summary, the model set-up was based on following relationships:

- the relative stomach content of fish eggs and their corresponding relative abundance in the plankton (compared to all suitable prey particles available) in dependence of the vertical overlap of predator and fish eggs as prey (see below),
- the relative abundance of cod eggs in the diet (related to the total number of fish eggs ingested) and their corresponding relative abundance in the plankton in dependence of the total abundance of fish eggs in the plankton,
- the hourly ration during the daily feeding period and the total suitable food abundance in the plankton

These relationships underlie a variety of assumptions and although most of them have been proven to be biologically reasonable and the established relationships are statistically significant, the prediction limits are in general rather wide and thus the predictive power of this procedure coupling three relationships is rather limited. Integration of identified relationships in one statistical model was impossible, as different data sets were utilized to predict different processes. Furthermore, the availability of suitable meso-zooplankton data limited the applicability of the procedure backward until 1987. Thus as an alternative, a second more simple approach was based on the assumption that:

- the ratio of cod eggs in the stomach and in the food supply (plankton) is linearly dependent on the vertical overlap of predator and cod eggs as prey.

The vertical overlap between predator and prey depends to a large extend on the ambient hydrographic conditions:

- the oxygen concentration in the bottom water limiting the depths in which herring and sprat are able to dwell during their daily feeding period, but also the depths in which egg development is possible,
- the density regime encountered, determining where cod eggs are floating in the water column, which appears to be mainly dependent on the salinity regime at which the oocyte development took place.

To establish a predator/prey overlap index for the entire time series, the average depth in which highest concentrations of cod eggs occurred and the corresponding depths in which herring and sprat during day-time concentrate had to be predicted. Based on a time series (1986-96) of vertical distributions of cod eggs in the Bornholm Basin, average levels of neutral buoyancy of the peak abundance were estimated by

calculation of corresponding weighted mean densities for stagnation and inflow periods. Both hydrographic scenarios had to be handled separately, as during stagnation, on average peak cod egg abundance was encountered at lower density levels than after inflow events. Based on information derived from conducted trawl and hydroacoustic surveys, the depths in which herring and sprat dwell during their daily feeding period, was set to the water depths at which the 2ml/l oxygen concentration was reached.

Besides the predator/prey overlap, the large fluctuations of the sprat stock in the central Baltic showing a drastic increase in the last 10 years, had a sever impact on the estimated consumption indices. A third important change within the time series was the shift in peak spawning time to summer months, incorporated into the estimation procedure of all parameters. This process resulted in a considerable predation pressure by herring on cod eggs in 1994-96, a period in which cod eggs were abundant in the plankton. On the contrary, the impact by sprat was reduced compared to preceding years.

The predation pressure for the Bornholm Basin was estimated in terms of absolute and relative indices: The first approach was based on the abundance of cod eggs as obtained by ichthyoplankton surveys and the second expresses the predation as consumption per standing stock of eggs. Despite the encountered uncertainties in the implemented procedure, especially with respect to the estimation of suitabilities, the observed changes in influential input information, i.e. inflow vs. stagnation periods, early vs. late spawning of cod, trends in sprat population size were drastic. Thus, the established time series of consumption rates are expected to capture the trends in predation pressure.

Describing feeding success of larval and 0-group cod in relation to small- and meso-scale hydrographic processes and related prey densities

Fieldwork conducted in this project revealed that growth rates of cod larvae in the Bornholm Basin were negative both in 1994 and in 1995. For example, during May-July 1994, larvae older than 11 days in the upper 45 m of the water column were losing weight at an average rate of 3.6% per day. An individual-based modelling exercise was conducted to evaluate whether these growth rates were due to insufficient food abundance. The model employs a pause-travel encounter rate sub-model developed within the project, and assumes that larvae are feeding in a calm environment. Output from this model is combined with project-derived estimates of prey concentration (see section 3.3) and capture success, and assumes that 30% of ingested matter is converted to larval body mass. Daily ingestion and growth rates of 1000 individual larvae were calculated assuming project-derived estimates of random variation in model inputs.

The model outputs showed that on average a cod larvae in the Bornholm Basin during May-July 1994 should have been able to grow at a rate of 2-3% body weight per day. This result suggests that prey concentrations were sufficient to support positive larval growth, and that the reason for the observed negative growth must be due to other factors. A geographic comparison of the food-dependence of wild larval cod growth rates revealed that growth in all other sea areas considered was positive, and that negative growth rates have only been observed in the Baltic.

Hydrodynamic modelling of retention and transport of larvae and 0-group

Combined 3-D physical oceanographic model and field sampling programmes were performed to investigate the potential drift of larval Baltic cod from the centre of spawning activity in the Bornholm Basin. The suitability of the 3-D eddy resolving baroclinic model of the Baltic for examination of the circulation and transport of larval cod has been verified by coupled field and modelling exercises during the initial components of this

programme. The implementation of a Lagrangian particle tracking technique into the model configuration allowed both projections of future distributions as well as estimates of drift trajectories thereby offering the ability to trace larvae back to their hatching sites.

The numerical simulations of larval transport were based on project developed realistic age dependent models of the vertical larval distribution. The goal of these exercises was to predict the drift trajectories of cod larvae in the Bornholm Basin, thereby aiding in the development of future sampling programmes as well as the identification of processes influencing larval retention and dispersal. Upon further refinement of the biological and physical inputs, additional model simulations have examined the variation of larval drift patterns between years of high and low recruitment success of Baltic cod. These simulations allowed an evaluation of the impact of larval drift and retention on recruitment variability and transport to areas of different benthic habitat quality. From the results of the numerical experiments it appears that variations in larval transport and hence horizontal distributions of pelagic and demersal stages of juvenile cod is caused by annual and interannual variations in meteorological forcing conditions. In years with a high number of low air pressure systems passing over the Baltic, most of the larvae initially spawned in the centre of the Bornholm Basin, are transported towards the northern coastal environment. Conversely, high air pressure over Scandinavia and the eastern Baltic Sea during the main spawning season reduces the influence of westerly wind energy, thus, early life stages of Baltic cod potentially retain within the deep water region of the Bornholm Basin. Although, rarely observed, relatively long periods of easterly winds can be identified as a prerequisite for enhanced larval transport towards the southern coastal environment. Recent research has identified the importance of transport of larvae from the spawning grounds to the shallow coastal regions for recruitment success of Baltic cod. Coastal environments identified as potential nursery areas for Baltic cod may be beneficial for larval growth and survival because they exhibit higher levels of primary and secondary production and hence food abundance than the central basin regions.

The analysis of circulation patterns in the Baltic in response to variations in physical forcing conditions has mainly focused on the identification of meteorological mechanisms influencing the retention/dispersal of cod early life stages in and around the Bornholm Basin. This spawning site being has been the most important spawning area of Baltic cod since the beginning of the pronounced stagnation period during the 1980'ies. Based on the results from numerical simulations with the Baltic Sea model and a long term wind data time series, critical levels of wind energy were derived to distinguish between years of dispersal and retention as well as to develop a transport index. This index was then utilized to identify historic variations in transport patterns for comparison with variations in cod recruitment success. Furthermore, the index was applied to identify the occurrence of within year transport regimes which when combined with information on hatch dates and growth rates of surviving 0-group cod, identify the transport regime and temporal window leading to enhanced survival success.

The physical modelling activities performed in this section supplied necessary information for establishing stock-recruitment relationship and stock assessment models being presently under development and will enhance the understanding of key processes affecting the survival success of the different early and juvenile life stages of Baltic cod.

From this component the principle physical factors identified to be influencing the recruitment of Baltic cod at present are the reproduction volume and the wind energy. It is recommended that the seasonal and inter-annual variability of physical factors are considered as substantial input parameters to improve short- and medium term recruitment predictions of the Baltic cod stock.

The hydrodynamic-ecological model FinEst

The latest version of the FinEst model was used to calculate the larval drift in the Bornholm Basin in August 1991. The larval transport studied was divided into two different parts. First, a Lagrangian approach was used, where the numbers of drifter were released in the Bornholm Basin, and their trajectories were investigated. The experiment showed the highly non-linear nature of the current system in the Baltic resulting in considerable differences in the final destinations of drifters launched within a relatively small area. On the other hand, there were pronounced differences between trajectories in the simulations, representing different initial release depths of the drifters.

The second experiment was done in an Eulerian co-ordinate system where larvae patches were released in the Bornholm Basin at different depths. Both spring bloom in April-May as well as larvae drift in July-August 1994 were simulated by the 3-D coupled hydrodynamic-ecosystem model FinEst. The main simulations were concentrated on the study of larvae drift in July-August 1994. The simulations of spring bloom gave background information and showed the model's ability to produce such features, when a size-dependent plankton food-web system and realistic loading were used. The spring bloom occurs first in the area of interest in late April and proceeds towards the northern Baltic, which is in accordance with measurements.

The larvae drift simulations were compared with the results of the Kiel model. Although, there are specific differences in the vertical model structure and in the initialization technique of both models, the present comparison of the simulated larvae fields in July 1994 revealed high correlation between the results of the different model applications. This coherence suggests that both models are suitable for future examinations of circulation patterns in the Baltic.

A conceptual model of processes acting on the early life history stages

The goal of this section is to synthesize the key results of research performed in the process analysis components of the program and, where relationships have not been established incorporate observations for other stocks in order to identify;

    a) key processes producing variable growth and survival success of young of the year Baltic cod,

    b) the attributes of individuals exhibiting enhanced survival probability.

The characteristics of survivors approach applied here has identified three processes acting to influence the survival of larval and juvenile Baltic cod. First it is indicated from the characteristics of the hatch check distributions of surviving larvae that the majority of survivors in marginal oxygen conditions are the result of the reproductive efforts of repeat spawners i.e. large females. Oxygen conditions in the deep layer act to modify the population of survivors by exerting selective pressure on both eggs and larvae.

The second process limiting survival success is the necessity for larvae to perform a vertical migration from the depth of hatching. Again, we utilized the otolith hatch check as a proxy for egg size and parental contribution. It is clear from the results presented that larvae able to successfully perform a vertical migration to the surface layer are a subset of the potential survivors and are composed of those larvae with a larger hatch check, presumably coming from females producing larger eggs with a higher energetic content.

Resolving the importance of co-occurrence of larvae and the peak abundance of their prey requires the analysis of growth characteristics of larvae and juveniles over the range of potential prey abundances available to them during the season and relation to survival success. In 1995, the majority of surviving juveniles came from the period of peak prey abundance, however, survival of this group could have been the

result of rapid transport of these larvae to the shallow coastal regions by the wind event coincident with their arrival in the surface layer. As larvae hatching after this period into the peak abundance of prey did obviously not survive, it appears that survival success in 1995 was dependent upon transport to the shallow coastal regions rather than on high abundances of prey.

Stock-recruitment relationships incorporating environmental variability

Recruitment of central/eastern Baltic cod critically depends on favourable oceanographic conditions in the deeper basins of the Baltic Sea creating a suitable habitat for the development of early life stages. The principal factors influencing the recruitment of this cod stock recognized at present are (i) the size of the reproductive volume (i.e. the volume of water with temperature, oxygen and salinity conditions which meet the minimum requirements for successful egg development), (ii) the age-structure of the spawning stock, (iii) the timing of spawning, and (iv) predation by sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) on cod eggs, as well as cod cannibalism.

In this section, recruitment at age 2 is related to parental stock size using a time series of these variables, comprising the period 1966-94. Cod spawning stock biomass and related egg production as well as sprat and herring biomass were obtained from single species (covering the period since 1970) as well as from multispecies assessment (from 1977 onwards). In addition, the influence of reproductive volume and wind energy, both adjusted for changes in the timing of spawning, as well as zooplankton abundance on cod recruitment were studied. The ACE ("Alternating Conditional Expectation") algorithm was applied in order to obtain optimal variable transformation prior to multiple regression analysis. This algorithm converges to an optimal solution. It does not produce a specific prediction equation, but rather an empirical transformation function for each of the variables. As the transformation is free of a priory assumptions on relationships between response and predictor variable, it can be used to confirm ideas on such relationships, or give new insights into these. As an alternative approach, with the potential to be used as an predictive model, a modified Ricker function was outlined explicitly accounting for environmentally-induced oscillations around multiple levels of cod stock size.

For the period 1970-94, ACE transformation revealed a slightly nonlinear relationship between recruitment per unit of total egg production as dependent variable, and total egg production and reproductive volume as independent variables, respectively. A strong nonlinear relationship was suggested for the cumulative wind energy, with a minimum at low south-westerly winds and two maxima, corresponding to strong easterly and moderate south-westerly winds. These three independent variables were highly significant ($P<0.001$) in a multiple regression model using the transformed variables, whereas sprat biomass was not. The model explained 81% of the variance encountered in cod recruitment at age 2. The amount of explained variance increased to 85% when egg production by females of age 5+ was used instead of the total egg production. Analysis of the time series 1982-94, corresponding to the lower regime of reproductive volume, showed that the same variables explained the variance in recruitment (98%), with all variables being significant at $P<0.001$ using egg production by females of age 5+. Neither zooplankton abundance nor sprat and herring biomass derived from the MSVPA, nor total clupeid biomass, were significant in the regression, and their transformations were inconclusive, depending on what other variables were used. The latter might be explained by opposite effects hidden in the data series, i.e. sprat and herring as prey for adult cod on one hand and predation by sprat and herring on cod eggs on the other, which could not be separated so far. On the contrary, the biological significance of the reproduction volume (as defining the habitat for successful

reproduction) and the wind energy (as relevant for larval transport to appropriate nursery areas) was clearly confirmed.

Stock-recruitment curves (Ricker type) were splitted into two parts, corresponding to the periods 1966-80 and 1982-94, respectively. This corresponds well to the observed shift in reproductive volume level, when in two subsequent years (1981/82) only the Bornholm Basin provided sufficient condition for successful reproduction. The smooth fit of the Ricker curves to the two regimes of high and low cod stock-recruitment, respectively, do not give any reason to reject this type of stock-recruitment relationships for central Baltic cod. A break into two regimes is made plausible by the strong change in the level of the reproductive volume after 1981, representing the carrying capacity of the environment for cod reproduction. When the environmental conditions were favourable for cod spawning, optimal recruitment was estimated at 800-900 * 10^3 t of SSB. During the past decade up to present, the reproductive volume was limited, and the Ricker curve suggests optimal recruitment at a SSB of approximately 400-550 * 10^3 t. The Ricker curves further suggest that the probability of low recruitment increases strongly at biomass levels below 250-300 * 10^3 t.

Stock-recruitment relationships in different stock components

In contrast to the preceding section, stock-recruitment relationships were constructed for different Subdivision of the central Baltic containing spawning areas with distinct hydrographic regimes, recruitment success, and stock development trends (Subdivisions 25, 26 and 28). The variability in stock-recruitment relationships established on basis of spatially dis-aggregated Multispecies Virtual Population Analysis (MSVPA, see section 3.8) and the International Bottom Trawl Survey data base (BITS, see section 3.4) were investigated with respect to the effect of environmental processes and species interactions. Based on an extensive exploratory statistical analysis, variables having significant influence on the reproductive success were incorporated into modified stock-recruitment models for single Subdivisions and utilized to establish a combined model for the entire central Baltic.

Traditional stock-recruitment relationships covering the period 1976-96 displayed significant differences in recruitment success from similar spawning stock sizes in all investigated areas in the 1970'ies when compared to the 1980'ies (see also above). The time trend in spawning population size and recruitment success appears to be rather similar in all three areas of the central Baltic until 1989. In Subdivision 25 and to a certain degree also in 26, both the spawning population and recruitment have stabilised after 1989, while the stock component in Subdivision 28 appears to be close to extinction. The major inflow event in 1993 had a positive impact on recruitment in the Bornholm Basin and Gdansk Deep, but not in the Gotland Basin, where the egg production was too low to take advantage of the highest reproductive volume within the 21 years time series occurring in 1994.

The exploratory analysis conducted on the basis of a sub-set of the time series available for Subdivision 25 (1986-96 with the most complete data set and the best area coverage by ichthyoplankton surveys, see section 3.1) revealed a significant impact of the oxygen related egg survival index as well as the predation index on the egg survival. However, the exploratory analysis was unable to explain a considerable part of the variability encountered between egg production measures and larval abundance in the same area. This indicates either an inappropriate larval sampling strategy in times of low larval abundance especially after peak spawning time shifted to summer month (i.e. a mis-match in the timing of the survey and larval abundance) or other factors than oxygen related mortality and egg predation are substantially influencing the hatching and larval survival success. In contrast, variability in larval abundance was closely related to the

hydrographic conditions in the Gdansk Deep and Gotland Basin. As environmental conditions are less favourable for successful egg survival in these areas compared to the Bornholm Basin, other processes are obviously of minor importance for hatching and larval development success.

The viability array applied for the egg production by the spawning stock in Subdivision 25, accounting for differences in larval viability due to egg size (see section 3.2) did not explain significant changes in the abundance of larvae nor deviations in survival rates, i.e. changes in the stock structure are not affecting the viability of the larval production in a statistically significant way. However, as the buoyancy of eggs is related to egg size, it is nevertheless expected that changes in the stock structure have a significant impact on survival rates of the egg production. In section 3.3, a first attempt has been conducted to couple the age structure in the spawning stock and egg buoyancy via female age/egg size and egg size/egg buoyancy relationships obtained from laboratory experiments. Due to a present lack of knowledge on the relationships between egg size and female attributes such as size, condition and batch number, the inclusion of this approach into stock recruitment models appears to be premature.

A multiple regression of recruitment at age 0 on larval abundance, including the sum of oxygen in the reproductive volume and the larval transport index obtained from drift modelling revealed a highly significant fit explaining 70% of the variance in recruitment. However, larval abundance explained 65% of the variance alone leading to the utilization of the simple linear model as a first approach for predicting recruitment success. In Subdivision 26 a similar relationship was obtained, however, the fit of the model was not satisfactory and for Subdivision 28 no significant relationship could be established at all. This can be explained by the fact, that recruitment success occurred despite the lack of larvae in the ichthyoplankton surveys. This indicates either a problem in sampling efficiency of the gear in use at low larval abundance (noticed already above), or a transport of pelagic 0-group into the eastern basins. The latter process is confirmed by the comparison of trawl survey results and MSVPA output and is also indicated by the fact that the larval transport index is negatively related to recruitment in Subdivision 25 (see below). This limits a possible utilization of a larval abundance index (corrected for drift out of the survey area and correctly timed) for prediction of recruitment to Subdivision 25.

For estimation of cannibalism rates of 0-group cod, significant linear regressions of predation mortalities obtained by MSVPA on spawning stock biomass were established.

The final statistical model for prediction of recruitment at age 0 based on the potential egg production by the spawning stock in Subdivision 25 explained 74% of the variance. Besides the egg production (corrected for egg predation by clupeids), the sum of oxygen in the reproductive volume was introduced as a significant variable, and the larval transport index as a variable being nearly significant. The regression coefficient of the latter variable was negative, i.e. recruitment success appears to be negatively related to high wind stress, suggesting that retention in the basin and low turbulent mixing leads to increased recruitment success. The wind energy index is also a measure of the percentage of larvae drifted from the spawning to the nursery areas. Thus, this result is biologically sensible, when interpreting it as a transport into neighbouring Subdivisions, for which evidence exists (see section 3.8).

The statistical models established for the eastern spawning areas were simpler than the one obtained for the Bornholm Basin. However, as only in the latter area permanently a certain water volume suitable for cod egg reproduction was available (of course in varying quantities), other factors like egg predation and larval drift have a regular and also more pronounced influence on the reproductive success of cod. On the contrary, in the Gdansk Deep and especially the Gotland Basin the hydrographic regime did (in general) not allow

successful egg development in the period 1981-92. Thus, only relatively simple models were required for these areas to achieve a reasonable explanation of recruitment variability (60-70% explained variance).

Although recruitment was log-normal rather than normally distributed and multiplicative instead of additive processes may be more appropriate to describe some of the acting processes, the log-transformed models did not predict recruitment better, but consistently underestimated high recruitment in the beginning of the time series. Additionally 1st order autocorrelations of recruitment were encountered regularly in all log-transformed models, whereas it was not in the un-transformed models.

To obtain an indication about the sensitivity of the parameter estimates and the predictive power of the established statistical models, re-fitting of the models over different shorter time periods utilizing a sub-set of the data series was conducted. The exercise clearly demonstrated that the models derived for the different Subdivisions are able to capture the trend of decreasing recruitment success during the 1980'ies and an increase in the early 1990'ies, though they overestimated recruitment in the most recent years and regularly underestimated recruitment in early years of the time period to a certain extent. However, if a subset of the years with maximum observed recruitment were included in the model fitting, the deviations between observed and predicted recruitment were found to be acceptable. In particular exclusion of the recruitment estimate for 1979 increased the model performance. This was not interpreted as a mis-specification of the model, as the observed recruitment in 1979 appeared to be overestimated by the MSVPA. Given the relatively low sensitivity in the parameter estimation and a reasonable predictive power, the statistical models developed in this section will:

a) enhance presently used short-term stock predictions, by estimating recruitment at age 2 two years in advance. These estimates are based on the most recent spawning stock size and structure (in particular its egg production), hydrographic conditions and predator abundances. Validation of egg production can be performed from egg survey results and utilized for validation of the spawning stock size, with larval survey results as an independent data source for predicting recruitment success,

b) improve medium-term projections (ICES 1997a/Assess:12) to predict cod recruitment at any given age for simulation of various fishing activities and fisheries management strategies in different Subdivisions under assumed environmental scenarios, i.e. oxygen concentration in and extension of the reproductive volume, wind forcing regulating larval and pelagic 0-group retention and transport but also causing inflow events (this interdependence is not incorporated so far), considering also predator/prey interactions affecting egg and juvenile mortality rates,

c) allow the determination of robust biological reference points (ICES 1998/J:1) considering their sensitivity to environmental perturbations and species interactions taking into account area specific trends in stock and recruitment development as well as basin specific environmental regimes, predator/prey interactions and fishing activities.

3.8 Improvement of multispecies stock assessment models

The Multispecies Virtual Population Analysis (MSVPA) is presently the most important tool to determine the abundance of 0- and 1-group cod in the central Baltic, i.e. to quantify the amount of survivors and thus determine the reproductive success of cod. Furthermore, cannibalism has recently been discovered as a rather strong self-regulatory mechanism of the Baltic cod stock and is consequently of major importance for any predictive model of cod stock development. Following tasks were covered during the present project:

1) Assess the reliability of predation mortalities of 0- and 1-group cod estimated by the MSVPA, which includes:

   a) an evaluation of the stomach content analysis and data compilation procedure,

   b) considering intra-cohort cannibalism, trawl feeding and feeding on discards as possible processes introducing bias,

   a) assess the time and area effect of sampling on the diet composition,

   b) check MSVPA output by independent data, especially in view of a possible prey switching due to changes in predator/prey overlap and density dependent processes.

2) Updating relevant input databases :

   a) stomach content database up-date to cover underrepresented areas, years and quarters,

   b) include cod cannibalism in the western Baltic MSVPA,

   c) complete revision of the quarterly catch and weight at age per Subdivision,

   d) revise consumption rates based on up-dated stomach content database, new gastric evacuation models considering ambient temperature in relation to yearly distribution patterns of predators.

3) Conducting MSVPA runs incorporating results obtained above and improving the methodology with respect to:

   a) an implementation of a reliable and practicable tuning procedure,

   b) an exploration of the effects of different alternative suitability sub-models on predation mortalities and subsequent recruitment estimates,

   c) conducting spatially dis-aggregated MSVPAs to determine recruitment and spawning stock sizes in different areas of the central Baltic characterized by specific spawning habitats and nursery areas, including a validation of spatially dis-aggregated MSVPA results.

As progress in the above activities appeared to be essential for some of the research tasks covered in the present project, but the available resources did not allow to allocate adequate research effort in all areas mentioned above, a project within the EU 4th framework TMR programme "Spatial structures in multi-species fisheries models for the Baltic Sea" was set up (FAIR GT 95 5933) and an ICES Study Group: "Multispecies Model Implementation in the Baltic" was established, serving as the platform for coordination of effort outside the project (ICES 1997/J:2).

Reliability of predation mortalities of 0- and 1-group cod estimated by the MSVPA

Based on a recompilation of cod stomach content data considerable cannibalism rates of juvenile cod in the Central Baltic were computed by the Working Group on Multispecies Assessment of Baltic Fish during its meeting in 1993 (ICES 1994/Assess:1). Before, cannibalism was regarded to be of minor importance, as cod as prey was detected rather seldom in the diets. Due to this judgement, the analysis and reporting procedure on cod as prey was not standardized to the same extent as for herring and sprat, especially before guidelines were set-up by the Study Group on Cod Stomach Data for the Baltic (ICES 1989/J:2).

A critical point in the conducted stomach sampling scheme identified is, that in some areas most or a considerable part of the stomachs have been collected on trawl surveys directed to the estimation of cod year-class strength, thus mainly covering areas were juvenile cod are expected to be more abundant. From comparisons of stomach content data obtained in different areas of the Western Baltic, a time and area effect on the amount of cod found in cod stomachs is indicated. For the Central Baltic a comprehensive analysis of

juvenile cod distributions in relation to the area and depths dependence of the diet composition has been conducted (see below).

The stomach content analysis procedure established by the various laboratories for the two different multispecies assessment areas was rather consistent, but differed slightly between the areas, due to a difference in prey composition. Thus an introduction of a major bias by different methodology applied in different laboratories can be excluded.

The stomach content compilation procedure for cod as prey has been reviewed, while compiling corresponding data for the Western Baltic. No major problems were encountered. The Latvian data on cod as prey are available on a more detailed level and should be integrated into the database, avoiding assumptions made in the compilation of missing information. It would be preferable if the Polish data could be submitted in the same way.

Trawl feeding is a problem that will bias the predation mortalities considerably when not handled appropriately while sampling and analysing stomach contents. However, the impact on cod as prey is probably not higher than for other prey species and thus according to Swedish data collected in 1992-94 well below 10% with respect to the stomach content in weight.

A rather limited overlap of size frequencies of consumed and discarded cod has been demonstrated for the Western Baltic, an area where considerable portions of the catches are discarded in some years. As the length frequency of cod eaten by cod in the Central Baltic is rather similar to the Western Baltic, it can be concluded, that preying on discards may occur, but has definitely no major influence on the estimated predation mortalities of cod.

In conclusion, it appears to be likely that the amount of cod found in cod stomachs is to a certain degree biased, however, the order of magnitude is not expected to result in a substantial overestimation of the predation mortalities determined for the Central Baltic. Independent of the basic stomach content data, problems in estimating predation mortalities were encountered with respect to the suitability sub-model implemented in the MSVPA (see below).

Database updating

The revision of the basic input data for both assessment areas included:

- update and correction of the quarterly catch at age and weight at age for stock units used so far,
- complete revision of the quarterly catch at age and weight at age data per Subdivision (25-32) for the period 1977-96 ,
- update of stomach content data in both multispecies areas until 1994,
- inclusion of cod as prey in the Western Baltic.

The complete revision of the quarterly catch at age and weight at age according to Subdivisions enabled changes in stock units as appropriate, e.g. applying the same as in the singlespecies assessment, but also separate runs for different Subdivisions (see below). The revision was based on national reports submitted to the Assessment Working Groups. Gaps in the data were identified and a detailed substitution scheme was developed, discussed within the Baltic Fisheries Assessment Working Group (ICES 1997/Assess:12) and distributed for comments to the various national laboratories. Based on received feed back, errors in the data base were eliminated. These data are expected to form the basis of multi- as well as singlespecies assessments in the future.

A considerable amount of new data has been integrated into the cod stomach content database, which now includes data up to 1994. Additionally cod as prey has been included into the Western Baltic database. In connection to the database updating, the procedure of compiling stomach contents was modified as follows:

- introduction of a weighting procedure for averaging over Subdivisions, which accounts for yearly variability in the distribution of the predator,
- inclusion of intra-cohort cannibalism of cod age-group 1+ by shifting prey ages one year back (so far cases in which cod ingested cod of a similar age had to be excluded from the MSVPA).

Consumption rates

After updating the stomach content database by including new data and revising the weighting procedure for the calculation of relative diet compositions and total stomach contents, the individual quarterly consumption rates had to be re-calculated accordingly. Several improvements of the food consumption estimation procedure were possible:

- application of new evacuation models (developed within the EU-project FAIR 95 604; CORMA), considering the environmental temperature and the predator weight as variables using different fish species as prey,
- inclusion of inter- and intra-annual variability in the consumption by incorporation of yearly and not only quarterly variable stomach contents, corresponding ambient temperatures considering also shifts in the distribution of cod, and predator weight at age reflecting changes in growth rates over time in the evacuation model.

The improved consumption rates are on average higher than the old estimates, which corresponds to results obtained when updating consumption rates of North Sea cod utilizing a similar model.

Tuning of MSVPA

Adequate tuning of a MSVPA is a prerequisite for a reliable output of the analysis. Up to now, the tuning procedure conducted by the ICES Multispecies Working Groups was in general rather rough. The singlespecies terminal-F values were applied after splitting them into quarterly values based on quarterly distribution of the catches and estimated population sizes in the beginning of the years, according to ICES 1996/Assess:2. To assess the impact of the choice of terminal F values on the estimated stock sizes of predator and prey a sensitivity analysis was performed, which resulted in the following conclusion:

- the MSVPA estimates of herring and sprat abundance are rather robust towards errors in the estimation of the cod terminal F in the final year,
- the MSVPA appears to be considerably more stable than singlespecies VPAs for prey species suffering from high predation mortalities, e.g. sprat,
- nevertheless, the impact of erroneous terminal-F values is considered to be a major problem requiring an adequate tuning of the MSVPA.

The Multispecies Working Group (ICES 1992/Assess:16) suggested to couple the XSA with the MSVPA, which appears to be a constructive idea. It was, however, expected to be rather impracticable to re-run tuning programmes and MSVPAs several times while inspecting output statistics (ICES 1997/J:2). To check the practicability, test runs were performed to investigate the convergence behaviour of successive XSA and

MSVPAs runs for the different stocks included in the Central Baltic. In general, the iterative running of XSAs and MSVPAs was rather unproblematic, as changes in predation mortalities had only limited impact on the determination of terminal-F sets, even for age-groups regularly preyed upon by cod. Sprat with lower numbers of age-groups in the calculation and higher predation mortalities in oldest age-groups showed the highest sensitivity and cod the lowest. Especially the latter fact is stabilizing the MSVPA as changes in terminal-F values for cod have an impact on the predation mortality of the prey species.

As a conclusion from this section, it appears that the implemented procedure of iterative singlespecies tuning and running of MSVPAs is a suitable procedure to improve the reliability of the MSVPA output. In this context, it has to be considered that excluding not fully recruited age-groups from the tuning changes the tuning output even when keeping all input data constant.

Cannibalism rates derived from MSVPA runs with alternative and without suitability sub-models

MSVPA runs conducted with cod as prey have changed the perception of cannibalism to that of a strong self-regulatory mechanism in the Central Baltic cod stock, which lead to the suggestion to utilize MSVPA instead of VPA estimates for establishing stock recruitment relationships. However, are the high cannibalism rates estimated for 0- and 1-group cod an artefact introduced by the suitability sub-model in use ? This question has been addressed in the present section, which mainly consists of two components:

a) a summary of cannibalism-related output derived from revised MSVPA runs for the Central and Western Baltic assessment areas,

b) attempts to estimate cannibalism rates for the Central Baltic cod with an alternative and without any suitability sub-model implemented in the MSVPA as well as utilizing independent estimates of predator stock sizes.

The results obtained, were compared with respect to time trends in the occurrence and intensity of cannibalism, giving an indication about the reliability of the predation mortalities estimated for Baltic cod by the MSVPA.

For both stocks a pronounced cannibalism on 0-group and to a lesser extent on 1-group cod has been estimated by the standard MSVPA. On average 37% and 17% of these age-groups are removed by predation from the Central Baltic stock. Thus, a year-class looses on average 47% of its individuals from age 0 to 2 due to cannibalism. The predation mortality of cod is lower in the Western Baltic. On average 19% of the 0-group and 9% of the 1-group are consumed per year. Predation was estimated to be most intense in 1978-84, a period with high adult and juvenile cod stock sizes in both areas, followed by a steady decline in stock, recruitment and cannibalism until the early 1990'ies and an inverse trend afterwards.

The original suitability sub-model of the MSVPA was created for the application in the North Sea model, because only stomach content data for 1981/82 were available. Based on a high amount of stomachs sampled in a short period of time quarterly suitability coefficients were determined and applied as constants to other years. This suitability sub-model has also been used in the Baltic MSVPA up to 1992, when a modification was introduced. The limitations and advantages of both models have been intensively discussed (ICES 1994/Assess:1), but no consensus about the method to be preferred was reached. In contrast to the North Sea, the database on cod stomach contents for the Baltic Sea contains stomach data for nearly all years, quarters, and Subdivisions inhabited by cod. This allowed a check of the performance of both suitability sub-models by comparing simulated and observed relative contents of cod in cod stomachs. Alternative approaches circumventing any suitability sub-model by using only available stomach content data

coupled to either predator stock sizes obtained by the MSVPA or abundance indices from trawl surveys were additionally computed, as:

a) it appears to be inconsistent that weight at age varies between years, and even worse shows a time trend and suitability coefficients remain constant, although weight at age are used to determine them,

b) considerable changes in the relative distribution of adult cod and their potential prey, juvenile cod, occurred in relation to the decline of the Central Baltic stock, which may violate the assumption that an average suitability coefficient calculated for the entire period reflects the mean relative spatial distribution of predator and prey as well as the probability that the predator will catch the prey once encountered.

Using the original stomach data together with MSVPA generated predator stock sizes revealed a peak in cannibalism on age-group 1 in 1977/78. This is a direct consequence of the stomach data showing highest relative contributions of cod in the diet in these years and relatively high predator abundance. In contrast, the application of the suitability sub-model in the presently used standard MSVPA set-up resulted in highest cannibalism rates in 1980/81. This maximum in cannibalism is driven by a high abundance of 4-5 year old cod (year-classes 1976/77), for which age-group 1 as prey has a high suitability coefficient. The same trend in predator stock size and structure is, of course, also valid for the calculation without suitabilities, but here the predator stock driven increase in predation is overwritten by the impact of the original stomach contents.

In summary, the application of a suitability sub-model (refers to both models) instead of using the original stomach data, creates a temporal dynamic of cannibalism mostly dependent on the predator abundance and the age structure. By averaging the suitability coefficients, extreme values in the observed stomach contents are homogeneously distributed over the whole time series, leading to a generally higher level of cannibalism in most years, but omitting the maxima in 1977/78. The tendency of the suitability sub-model to smooth outstanding stomach content data and to distribute them over the whole time series leads to a better correlation with the survey derived index of the predation mortality than using the stomach data directly. The comparison of determined M2 indices with estimated M2 values generated by the standard MSVPA is though no test on the reliability of the magnitude of predation mortalities, because the used survey data are no absolute abundance estimates. Nevertheless, the better correlation of the MSVPA with the survey based estimates may indicate that application of a suitability sub-model is the preferable procedure, rather than omitting it, even in the case when stomach sampling coverage is rather good. Based on the better fit of predicted vs. observed fractions of cod in cod stomachs, it appears that the new suitability sub-model presently chosen for the standard set-up of the MSVPA in the Baltic performs better than the original version still implemented in the North Sea MSVPA.

Independently whether cannibalism and recruitment is estimated via a normal MSVPA or on basis of original stomach content data using predator stock sizes obtained by MSVPA, the stock recruitment relationships showed two different levels in recruitment, i.e. a phase of high recruitment from 1977-80 and of relatively low recruitment after 1982. The fact that on the lower tray low recruitment occurred at same SSB levels as high recruitment in the beginning of the time series, indicates substantial environmental influence on recruitment. However, if the environmental conditions are suitable for reproduction, cannibalism driven by the size and structure of the predator stock, the spatial overlap between predator and prey and probably also the availability of other suitable prey has a considerable impact on the survival of juvenile cod. The singlespecies set-up showed the same discrepancy between the periods favourable and unfavourable for recruitment, but it underestimated the difference between high and low recruitment levels. This is due to the fact, that

cannibalism especially at high juvenile cod (prey) and adult cod (predator) stock sizes accounts for a considerable part of the mortality of juveniles before reaching age 2 (the recruiting age in singlespecies assessment).

Inter-annual variability of cannibalism and impact of prey abundance and distribution as obtained from MSVPA independent information

The inter-annual variability of cannibalism as well as density and distribution dependent effects on cannibalism were investigated utilizing information obtained during trawl surveys conducted in the eastern Central Baltic. During the period 1963-90 cod contributed on average 2.8% (weight) and 1.1% (occurrence) of the total stomach content of cod. Cannibalism was mainly recorded for cod > 35cm. The size of consumed cod was in general between 5-15 cm. Cannibalism occurred in restricted areas and exhibited strong inter-annual variability, with a significantly different intensity between the periods 1969-75, 1976-79 and 1980-90. Until 1980 the cod population in the Central Baltic inhabited mainly near bottom layers of the central basins. A high abundance of recruits was encountered in 1976-79. During the 1980's, stagnation resulted in the reduction of recruitment and the adult cod population changed its distribution from demersal to pelagic mode of life during the first half of the year. Thus, low abundance of young cod and the changed distribution of older fish resulted in low cannibalism rates during 1980-90, a feature which the present MSVPA is not able to model, due to the implemented suitability sub-model assuming constant suitabilities the covered time period.

MSVPA runs for different areas of the Central Baltic

As the abundance and biological characteristics of the three species incorporated into the MSVPA for the Central Baltic are rather different between geographical areas within the presently assessed stock units and are also rather variable in time, spatially dis-aggregated MSVPA runs have been performed. This allowed to establish actual spawning population sizes and structures contributing to recruitment of cod in the different spawning regions characterized by distinct hydrographic conditions, thus defining regional or basin specific population recruitment. After the revision of the catch and weight at age data according to quarter and Subdivision, a suite of independent MSVPA runs was conducted for Subdivisions 25, 26 and 28, i.e. areas in which major cod spawning areas are located: the Bornholm, Gdansk and Gotland Basin. This procedure does, however, not include migration, being accounted for by fluctuations in the catch at age data only.

A rather synchronized development of cod recruitment and population sizes was revealed for Subdivision 25 and 26, with also the absolute estimates being rather similar. Highest recruitment was computed for the period 1976-80, with a steady decline until the beginning of the 1990's and a moderate increase in most recent years. The spawning stock biomass reached highest values of 140000-180000 t in each area in 1979-83, with a time lag of two years in the increase in Subdivision 25. Lowest levels of spawning stock components were reached in 1991/92 with a subsequent increase to a level corresponding to the beginning of the time series (120000 t in each area). The differences between both areas, i.e. a more pronounced decrease and a time lag in the subsequent increase of SSB in Subdivision 26, can be explained by a more limited recruitment success in the Gdansk Deep due to the in general unfavourable hydrographic conditions. Recruitment and spawning population size in Subdivision 28 showed a similar trend within the first half of the period covered. However, maximum values of recruitment and SSB were only about 50% of those encountered in the other areas and the decline continued nearly to extinction of the stock component, showing also no reverse trend after the 1993 inflow.

Substantial difference in the cannibalism level between the different areas was computed, with lowest predation mortalities in Subdivision 25 from 1978-85. In later years the values were rather similar in Subdivision 25 and 26, with a tendency of higher predation pressure in the eastern area in most recent years. This deviation in predation mortality is coupled to a considerably lower suitability of juvenile cod as prey of adult cod in Subdivision 25. In Subdivision 28, the predation mortality declined from high levels in 1983 to virtually being absence in 1990.

The determined F at age for cod did not indicate any substantial problems induced by migration between Subdivisions, however, as corresponding signals are rather indirect, this is no validation of MSVPA results. Also a gradual shift of the cod population out of areas with unfavourable conditions into the Bornholm Basin might have happened not detected by the VPA procedure. However, the synchronized development of cod recruitment and population sizes in Subdivision 25 and 26, based on completely independent information, indicate that the obtained trends are reliable. Independent of remaining uncertainties (see below), the output of the spatially dis-aggregated MSVPA runs have been utilized in the establishment of area specific stock recruitment relationships.

A special validation of the spatially dis-aggregated MSVPA results was performed utilizing independent information on abundance and biomass obtained from survey activity within the project as well as compilation of available historical data. In connection to the validation attempt, it is discussed whether abundance indices from trawl, hydroacoustic and ichthyoplankton surveys can be used for tuning VPA´s, as the utilization of more than one reliable abundance index (the international bottom trawl survey) would improve the tuning output and thus, the accuracy of most recent stock size estimations to be utilized in short-term projections.

The comparison of various cod stock biomass and abundance indices obtained by hydroacoustic and trawl surveys indicate a declining trend of the stock component in Subdivision 25 in most recent years, which is not obvious from the MSVPA. Comparing egg production values estimated via MSVPA based female spawning population size with corresponding production rates from ichthyoplankton surveys showed a quite reasonable fit for the period since 1986, but confirmed an overestimation by the MSVPA in 1996, probably caused by tuning problems. Latvian trawl survey data directed to the spawning population in the Gotland Basin confirmed the trend derived by the MSVPA for Subdivision 28 and indicated further for most recent years, that the population size determined for Subdivision 26 by the MSVPA is restricted more or less entirely to the Gdansk Deep and not the southern part of the Gotland Basin.

The distribution of the cod stock among the Subdivisions of the Central Baltic as obtained from the MSVPA shows substantial deviations from the relative distribution pattern derived from the international trawl survey, utilized for tuning the MSVPA. In the trawl survey the distribution is changing with age, especially in the juvenile stage, which might have three reasons:

1) area specific mortality rates: varying cannibalism rates were determined by the MSVPA for the different areas, however, as they were incorporated into the stock estimation, they do not explain the differences encountered, neither do the fishing mortalities, as they are probably negligible for age-group 1,

2) a shift in distribution, especially within the 2nd year of live, either by passive drift or by active migration of larger juveniles,

3) area specific differences in catchability of the bottom trawls in use.

In principal neither of the processes will distort the MSVPA results substantially, as long as neither the relative loss nor gain of juveniles to and from another area nor the unaccounted natural mortalities are changing over

time. Processes acting constantly will influence the absolute production of juveniles per adult, but should not change the recruitment pattern. However, not only the distribution of the juveniles changes, adult cod are known to undertake spawning migrations, especially from northern and eastern areas into the Gdansk Deep and the Bornholm Basin. The intensity and extension of this migration depends probably on the hydrographic conditions, with a shift to more southern and western spawning areas, when environmental conditions are unfavourable in the Gotland Basin. Relative CPUE-values obtained from conducted trawl surveys in the Bornholm Basin and the Gdansk Deep within the spawning season 1996 in fact indicate a spawning migration of cod from Subdivision 26 into 25. In relation to time trends of increasing proportions of the stock component concentrating in Subdivision 25, it should be pointed out, that there was nearly no deviation between the trawl survey and MSVPA proportions in 1992-94, but again afterwards, which may be related to a tuning problem, rather than migration.

Incorporation of predation on early life stages of cod in multispecies assessment tools

The performed literature review, the evaluation of available stomach content databases and the subsequent sampling of diet compositions of potential predators on early and juvenile life stages of cod in the Baltic identified predation on cod eggs by herring and sprat as well as to a lesser extend by scyphomedusae as the only relevant predation processes effecting the reproductive success (apart from cannibalism on juveniles already integrated into the MSVPA). Modelling cod egg predation by clupeids within the present MSVPA and MSFORE models is in principal possible, but would require to incorporate consumption and suitability sub-models on number and developmental stage (instead of biomass units and age) and to introduce an appropriate smaller time scale (reduce the time intervals from quarters to months).

Reformulation of the MSVPA algorithms to calculate predation mortalities based on prey numbers, is in principal possible. To adjust the MSVPA algorithm to prey stages instead of age-groups also appears to be possible without major difficulties. Major difficulties, however, are expected to arise from the necessity to introduce smaller time scales for which basic input data (e.g. catch at age and weight at age) are not available and are hardly possible to obtain. All together the necessary changes in the algorithms, the programme structure and the data handling are expected to be a major task, beyond the scope of this project. Thus, modelling predation on cod eggs right from the beginning independently from the MSVPA, but using MSVPA output as input (e.g. predator stock sizes) appeared to be more feasible. An attempt to model cod egg predation by clupeids accordingly has been conducted and the results were incorporated in the established area specific stock-recruitment relationships.

3.9   Evaluation of stock enhancement programmes

Stock enhancement through release of cultured juveniles is a common practice in freshwater systems. It has also been shown to be an effective method in ranching of anadromous fish species (e.g. salmonids). In coastal and marine systems, stock enhancement has received increasing attention world-wide. The most advanced experience has been reported from Japan where early trials with kuruma prawns and red sea bream have - over the years - yielded promising results, mainly to enhance local fisheries. The pertinent literature on ranching and enhancement of local cod stocks has been reviewed. Major efforts were made in Norway and some Baltic States to test the feasibility of juvenile production in various systems while also testing growth, migration, and recapture rate of released fish. The results of historic and recent trials are summarized. Particular attention was paid to the evaluation of various tagging methods (e.g. external tags,

internal tags, chemical tags, implanted electronic ships). Comparative studies on the possible interactions between wild and cultured released juvenile cod were also reported, placing major emphasis on possible genetic interactions between wild and cultured stocks, growth differences, and specific differences in feeding habits and migrational behaviour. Finally the issue on density dependent mortality is discussed in relation to the scale of release necessary to achieve a measurable impact. A comparative evaluation was conducted of the profitability of Japanese and European approaches to marine fish larviculture production for sea ranching programmes.

From this study it is concluded that the potential effect of stocking on enhancement success requires criteria that determine the optimum choice from a palette of operational scenarios suitable for the given area (e.g. geographical area of release, target species, choice of habitat characteristics for release, choice of conditioning method to improve fitness for survival, rearing techniques close to natural conditions to prevent early domestication effects, choice of stocking level and duration of the programme (matching with predicted natural recruitment), and finally choice of ownership and management units including harvesting practices).

The performed review identified several positive aspects with regard to the development of cod ranching programmes:

- reared juvenile cod show a high growth rate, a good condition factor, and favourable liver indices. On release they are often notably larger than their wild counterparts. In some cases the 0-group may be nearly as big as the wild 1-group fish. Good condition factors allow them to withstand a period of poor feeding after release, but this effect is uncertain and only verified in studies with Norwegian coastal cod,

- after release, the reared cod revert towards the wild fish habits in terms of diet, feeding efficiency and anti-predator behaviour, and this is achieved in just a few weeks, thus indicating the option for effective short-term adaptation,

- reared and wild cod have similar growth rates in the sea and tend to remain in the same area, although some cod release studies show (Danish Limfjord) that fish moved considerable distances. Norwegian cod from local stocks released near the open coast also tended in some areas to move greater distances laterally.

Some critical conclusions must also be drawn from the literature review:

- despite good growth and adaptation to habitat, released cod may not be as fit for survival as wild ones. Netting may initially easily capture them and they also may not be as fast in response to escape from predators as wild conspecifics. Japanese studies with red sea bream (*Pagrus major*) indicate that early conditioning and step by step adaptation from close confinement to semi-enclosed and open water areas may greatly help to mitigate these effects,

- there is so far no evidence that released cod have enhanced the local (Norwegian) stocks at stages when they were supposed to recruit to fishery, despite the fact that they have augmented the local stocks during the first few months after release. This indicates that under specific circumstances, year class strength may remain unstable even after the 0-group phase, particularly in coastal fjord cod populations,

- there exists some evidence of density-dependence and low pre-recruit survival when the abundance of 0-group cod is high and this may be counter productive to stocking.

The lack of suitable tagging and monitoring techniques for released fish and the lack of quantitative methods to follow released stocks in sufficient numbers so that stocking effects on conventional fishery yield can be reliably judged is still a bottleneck. The possibility of tagging the released fish with genetic markers may be a promising method that can provide the data required. The presently developing modern internal tags that record the movement of fish in relation to environmental cues (temperature, light, pressure) are certainly promising to gain more insight in what triggers outmigration of on-growing fish.

The first step of the Japanese sea ranching programmes focused on basic research for mass production of fingerlings. One can certainly learn from the experience gained there. Relevant publications and research work, especially on Baltic cod, is slowly becoming available. Judging from the Japanese experience, a 10 years lead time will be necessary to work out a certain technology for a reasonable and cost-effective mass incubation and rearing technique. Similar scenarios and large-scale logistical approaches will have still to be worked out for cod in the Baltic Sea where specific hydrographic and ecological conditions occur which differ greatly from other areas. Presently, the results of the mass-incubation and rearing trials with Baltic cod are still not satisfactory. The quality of the spawning stock and the resulting egg quality may partly affect survival potential. It needs further to be emphasized that little is known about O-Group behaviour and performance in Baltic coastal waters while nothing is known about the optimal strategy for points and frequency of release. It is recommended that tagging studies are undertaken to provide some insight on the subsequent influence of growth, mortality and out-migration of 0-group cod before any large-scale release tests for cultured specimens are undertaken.

4.   Description of potential practical applications

4.1   Application of project results in stock assessment

The present project has identified key processes affecting the egg production by the spawning stock, the viability of the offspring and the subsequent developmental success and survival of early and juvenile cod life stages, described their variability in space and time, compiled related long-term data series, implemented a series of coupled biological/physical sub-models and established statistical models relating recruitment success and environmental as well as predator/prey interaction processes. In terms of the potential utility of the achievements in stock assessment, the results can be grouped into two broad categories on the basis of the length of time before they could be expected to be implemented in stock assessments.

The first group of results includes those, which have direct impact on some of the key inputs to stock assessment models or their modification, and which have been documented to be statistically significant over several years of study. This group of results could potentially be incorporated in the near future (1-4 years) into existing stock assessment procedures with relatively little, minor changes in methodology.

The second group includes those which either have improved our understanding of processes affecting the interactions between stock structure, recruitment and the environment, or which require further documentation of effects to ensure robustness of the observed relationships (e.g. over longer time periods, in contrasting environmental situations). The impact of these results on inputs to current stock assessment models is therefore less direct, because they have addressed scientific issues, which lie outside the scope of traditional stock assessment procedures. If these findings should be used, these procedures will have to undergo modest to major changes. Since such developments require time and dedicated effort, this group of results may need a longer period (e.g. 5-10 years) before being used quantitatively in stock assessments.

However they have a more immediate impact on the nature and direction of research that could be followed in the future (e.g. fully document observed relations that are based on limited temporal/spatial coverage, develop the modifications to existing stock assessment procedures to include new types of scientific information).

Identified processes with the potential to be considered in future stock assessment of Baltic cod:

a) Maturity ogives and sex ratios showed inter-annual variability and a general trend of increasing proportions of females with age. In addition there was a significant trend to later maturity from west to east in the Baltic.

b) Relative fecundity varied significantly between years (up to 33% deviation), but not with female size or age, within a spawning season, or between spawning areas within a given year.

c) Spatially dis-aggregated egg production estimates based on research vessel survey indices of adult distributions or output of area dis-aggregated MSVPA models show large spatial variability between years, which can lead to high levels of production of eggs in areas which cannot support egg development.

d) Larger females generally produce larger and more buoyant eggs. These eggs also produce larvae, which have a higher survival probability after hatch than larvae, which hatch from smaller eggs. However, between-batch and between-female differences in egg size make generalizations difficult.

e) Significant differences in contamination level were found between Subdivision 25 and 26, with the latter showing higher contamination, lower hatching success and lower survival after hatch. Furthermore, significant relationships exist between maternal age and most investigated xenobiotics; however hatching success or survival after hatch was only related in some cases significantly to body burdens of specific individual xenobiotics.

f) Estimates of daily egg production derived via determined SSB values are on average 2.3 times higher than the corresponding production of the youngest egg stage IA obtained by ichthyoplankton surveys. The difference is probably due to atresia and limited fertilization success.

g) The timing of spawning has varied substantially over the last 2 decades, related to both, stock characteristics (e.g. age structure and abundance) and to water temperature. The present main spawning period is June to August and as a consequence the egg production is exposed to relatively low oxygen concentration even after inflow situations due to oxygen consumption in the bottom water.

h) Production of egg development stage III as estimated from ichthyoplankton surveys per unit of potential egg production by SSB (and alternatively also egg production of stage IA from ichthyoplankton surveys) is significantly related:

   – positively to oxygen content in the reproductive volume at peak spawning time and a corresponding oxygen related survival index (Subdivision 25) or the reproductive volume adjusted to peak spawning time (Subdivision 26 and 28),

   – negatively to predation by clupeids; the impact of predation was considered only in Subdivision 25 as in other areas consumption rates were of minor importance.

i) Larval abundance is positively correlated with egg production by SSB, and larval abundance per unit of egg production by SSB is positively correlated to the sum of oxygen in the reproductive volume (Subdivision 25) and the reproductive volume (Subdivision 26 and 28).

j) Recruitment at age 0 (as obtained from area dis-aggregated MSVPA runs) is positively correlated with:

   – the egg production by SSB corrected for predation (correction only in Subdivision 25),

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- the sum of oxygen in the reproductive volume (Subdivision 25) or the reproductive volume (Subdivision 26 and 28),

- negatively correlated with a cumulative wind energy index, expressing wind stress and direction as a measure of transport to nursery areas or retention on spawning grounds (applied in Subdivision 25 only). A possible explanation may be a transport of larval and pelagic juvenile out of Subdivision 25 at strong westerly winds, which is confirmed by the distribution of age-group 1 cod derived from trawl surveys showing high abundance of recruits in the southern part of Subdivision 26, also in years with rather unfavourable hydrographic conditions in the Gdansk Deep. However, a positive signal of a high transport index resulting in enhanced recruitment is also here not obvious, which is not un-expected as the transport index covers temporally only the larval phase. Apart from this, correlation analyses for the entire Central Baltic conducted have clearly demonstrated that recruitment at age 2 is positively correlated with strong south-westerly and easterly winds,

- not correlated with changes in viability of the larval production as estimated from interrelations between spawning stock age/size structure, egg size and larval survival relationships.

k) Recruitment at age 0 is positively correlated to larval abundance in Subdivision 25 and 26. In Subdivision 28, recruits (age 0) were expected from the model runs and also observed as age-group 1 in trawl surveys, but were in a number of years not found in larval surveys. This indicates either problems with the catchability of the ichthyoplankton gear at very low larval abundance or drift/migration of juveniles into the area.

l) Recruitment at age 1 and 2 is affected by cannibalism through adult cod (mean annual removal: 5-43% at age 0 and 30-47% at age 1). Considerable variability in cannibalism (smoothed out by MSVPA) appears to be related to prey densities and spatial prey/predator overlap.

m) The present situation of the cod stock in the Central Baltic can briefly be summarized as follows (based on the area disaggregated MSVPA runs):

- The stock component in Subdivision 28 is close to extinction, with a presently very low egg production by the spawning stock, i.e. not able to take advantage of the 1993 major Baltic inflow resulting in 1994 in the highest reproductive volume in the Gotland Basin since 1977. However, the inflow replaced especially deeper parts of the bottom water, resulting in an intermediate layer with very low oxygen concentration but having densities sufficient to keep at least a part of the cod eggs floating and thus not sustaining their development. Thus, even at a higher egg production it is quite uncertain, whether the single major inflow event would have enabled a substantial reproductive success.

- The component in Subdivision 25 dominated the stock in the late 1980s and early 1990s with the lowest level on record in 1992 and an increase afterwards. Although the hydrographic conditions were unfavourable for successful egg development in the Gdansk Deep up to 1993, an increase in this stock component is obvious since 1991, indicating recruitment originating from the Bornholm Basin. In the most recent assessment year, the spawning stock biomass was estimated to be approximately 120000 t in each area, which is in the order of the 1976/77 levels and the highest on record since 1984.

- The stock trend obtained by the singlespecies assessment (ICES 1997/Assess:12) and also by the MSVPA showed a relatively stable stock in most recent years. This result is contradicted by decreases in stock estimates from hydroacoustic surveys, CPUE from trawl surveys directed to the spawning stock and ichthyoplankton-based egg production estimates. The overestimation of the stock in most recent assessments might be due to time trends in the catchability in the trawl survey data used for

tuning, caused by changed hydrographic conditions. This hypothesis remains to be investigated and was beyond the scope of this project.

From the above summarized information on processes influencing the reproductive success and recruitment of cod as well considering the present stock situation, the following modifications of current assessment procedures and methodologies can be recommended:

ref. a)

The significant variations in adult reproductive biology (e.g. between years and areas) need to be considered when estimating the reproductive potential of the stock. Sensitivity analyses of egg production estimates show that failure to do so, can lead to considerable over- or underestimates of the true egg production depending on the direction of the variability relative to the average value. Time series of project-derived maturity ogives have already been implemented in last year's cod stock assessment (ICES 1997/Assess:12). However, instead of using the entire spawning stock estimate it is recommended to utilize only the female spawning stock biomass (as a measure of egg production, preferably at spawning time, e.g. 1. July), because the sex ratios heavily depend on age (increasing female proportions with age). The data base for implementation of this result (i.e. age-specific sex ratios and female maturity ogives) has been set up within the programme. In addition, comparison of estimated potential egg production by the spawning stock with egg production rates derived by ichthyoplankton surveys shows that utilization of annual maturity ogives is preferable to 5-year averages (given a sufficient data quality).

ref. b)

Relative fecundity varied significantly between years but not in dependence of body size/age and of seasonal effects. Factors determining the relative fecundity (not yet known) appear to influence the entire stock rather than a sub-component. These findings allow monitoring of fecundity with relatively restricted effort. Relative fecundity data should be combined with age/size structure and maturity/sex ratio information to produce annual estimates of population egg production. However, if reliable fecundity data are not available, the female spawning stock biomass is a useful alternative measure of egg production. Investigations on the determining factors causing changes in the sexual maturation (probably coupled to growth) as well as in the individual fecundity should be encouraged, to enable prediction of changes caused by environmental perturbations and variability in the food supply.

ref. c)

Present assessment practice (e.g. ICES 1997/Assess:12) assumes no spatial or seasonal variability in either egg production or environmental conditions that favour survival of early life stages. Methods for producing dis-aggregated data series and models that incorporate information at these dis-aggregated scales need to be developed, and comparative analyses using aggregated and dis-aggregated data sets and models need to be conducted (see j and m).

ref. d)

Established relationships between female size and age vs. average size of produced eggs and egg size vs. larval survival after hatch, coupled to annual stock structure data revealed a rather limited variability in the viable egg production. However, the differences in buoyancy related to the egg size appear to be more important as a feature steering the survival success of the egg production, especially at unfavourable oxygen conditions. At present this impact of the stock structure on the vertical egg distribution is ignored in the

modelling approaches conducted in the programme as it should await results from still ongoing research activities, outlined in the corresponding process analysis section.

ref. e)

Contamination levels in adult females and sex products differed between the Bornholm Basin and the Gdansk Deep. The latter area showed higher contamination levels of ovaries, lower hatching success, and lower survival after hatch. A lower recruitment originating from a similar egg production, however, is not obvious from the conducted analysis, but the process may be masked by an introduction of pelagic juvenile stages by the current system. Due to the complexity of the problem and different interpretation possibilities the outlined findings are to date hardly applicable in present stock assessment procedures.

ref. f)

The significant relationship obtained between potential egg production estimated via the population size of spawning females in combination with relative fecundities and the actual egg production from ichthyoplankton surveys demonstrates the potential to use ichthyoplankton surveys to derive (MS)VPA-independent estimates of population sizes. A prerequisite for application of this method is sufficient knowledge about the timing of the spawning activity as well as stock structure and fecundity information, which have been made available for a time series in the present project, but also have to be monitored in future.

ref. g)

Due to eutrophication, oxygen introduced by an inflow event is consumed faster today than in former decades, with a corresponding increase in egg mortality rates. This does not affect short-term recruitment predictions, as the most recent hydrographic measurements can be utilized when making these predictions, but medium- to long-term simulations should take this process into account when assuming environmental scenarios.

ref. h)

The significant positive relationships between the production of eggs in advanced developmental stage per unit of total egg production and the sum of oxygen in the reproductive volume or the reproductive volume itself and the negative relationship to predation by clupeids (at least in the Bornholm Basin) established during the programme are a prerequisite for an inclusion of these factors into stock-recruitment relationships.

ref. i)

The correlations between larval abundance and egg production (from SSB) as well as larval abundance per unit of egg production and reproductive volume showed a relatively high amount of unexplained variance. The high scatter encountered in the relationships may indicate that larval survival is related to other factors not considered in the analysis. A potential candidate process in this respect is the ability to utilize available food resources, as indicated by in general very low growth rates of larvae encountered in the field. Thus, a considerable part of the unexplained variance experienced in the established stock recruitment relationships could be introduced at this stage, a fact which should be considered when planning future recruitment related research initiatives.

ref. j)

Established stock recruitment models incorporating egg production from SSB (corrected for predation: Subdivision 25), the sum of oxygen in the reproductive volume (Subdivision 25) or the reproductive volume (Subdivision 26 and 28), the larval transport index (Subdivision 25) and cannibalism rates can be used in stock assessment in a number of ways.

- Short-term stock and catch projections to predict the recruitment at age 2 two years ahead, instead of simply assuming an average recruitment observed over a certain time period (e.g. ICES 1997/Assess:12). The prediction should be based on following observations obtained by regular monitoring as well as model output:
  - the most recent female spawning stock biomass,
  - last and present years hydographic conditions in different spawning areas,
  - egg predation pressure by clupeids,
  - the cumulative wind energy index as a measure of transport of larvae and pelagic O-group to suitable nursery areas or retention on spawning grounds,
  - cannibalism on juveniles.
- In medium-term projections (ICES 1997/Assess:12) to predict cod recruitment at any given age for simulation of various fishing activities and fisheries management strategies in different Subdivisions considering predator/prey interaction and environmental scenarios including above mentioned variables.
- In the determination of biological reference points, and considering their sensitivity to environmental perturbations and species interactions.

ref. k)

The significant positive correlation between recruitment and larval abundance demonstrates the potential to use larval surveys to derive a (MS)VPA-independent recruitment estimate that could be used in short-term predictions at least for Subdivision 25. However, a prerequisite for the application of this method is knowledge about the timing of spawning (see also g). A difficulty in the implementation might be to identify the relatively narrow time window of high larval abundance in the spawning area when spawning times are shifting.

Resolution of the horizontal and vertical distribution of young of the year pelagic and demersal juveniles accomplished during this programme enables in principal the development of 0-group surveys to obtain recruitment estimates. This, however, needs further methodological improvements for a regular application in stock assessment.

ref. l)

Besides testing of the MSVPA modelling approach with respect to the reliability of the estimated cannibalism rates, a series of methodological improvements related to the present multispecies assessment was accomplished:

- complete revision of quarterly catch and weight at age data with Subdivision as smallest area unit allowing separate or combined assessments of different area combinations as required,
- updated stomach content database and enhanced area weighting procedures when averaging stomach contents over different areas,
- improved consumption rate estimates,
- implementation of a practicable tuning approach.

With respect to the latter achievement, data from surveys conducted within the project, e.g. CPUE from trawl surveys covering the spawning stocks as well as ichthyoplankton surveys (see f) could be used as alternative data-sets in tuning procedures.

Apart from these improvements, we have identified two problems in the present multispecies assessment, which we were not able to solve completely within the present project period:

- The suitability sub-model in use is unable to predict the seldom events of high cannibalism and instead distributes the predation mortality, mainly in dependence of predator stock sizes and structures, more or less evenly over the entire time series, thus overestimating regularly cannibalism rates compared to independently computed predation rates. Based on a test of the performance of different suitability sub-models as well as computation of predation rates without suitability sub-model, the best behaving alternative was selected. Within the frame of the still ongoing EU TMR grant (FAIR GT 95 5933), this subject will be more closely investigated in future.

- Recruitment at age 0 is estimated in the MSVPA via the predation mortality caused by the adult stock in the same year (i.e. basically the spawning stock). Consequently the estimated recruitment is to a certain degree dependent on the spawning stock biomass either entering directly or indirectly (via the egg production by SSB) in the stock-recruitment models. Of course also other factors (e.g. the catch history of the cohort, residual mortalities and predation mortalities at higher age-groups) influence the recruitment estimate. At high cannibalism rates, however, the impact may be considerable and may artificially create a linear relationship between recruitment at age 0 and the SSB. Utilizing recruitment at age 1 in stock-recruitment relationships may circumvent this problem and test trials indicated a limited impact of the described interdependency in the case of Baltic cod only. However, corresponding sensitivity analyses are strongly recommended.

ref. m)

Substantial improvements of the MSVPA and their input data bases achieved within the project have already (ICES 1997/Assess:12) and will also in future enhance the fish stock assessment in the Baltic, e.g. in the following ways:

- The newly compiled and completely revised catch and weight at age data base is expected to form the common basis of stock assessment for Baltic cod, herring and sprat in the years to come.
- The incorporation of cod cannibalism in the western Baltic MSVPA allowed for the first time the introduction of predation mortalities in last years assessment for the Western Baltic stock.
- The estimation of predation mortalities of herring and sprat, referring for the first time to standardized management units, enabled the utilization of updated predation mortalities in the assessment of both clupeid stocks.

Apart from this, running a suite of independent MSVPAs for different Subdivisions and the area dis-aggregated analyses of the BITS data base have changed our perception of the reproductive potential of the central Baltic cod substantially. For example, a high reproductive volume in the Gotland Basin will have no beneficial effect on the cod stock recruitment at present and in future, unless a successful re-colonisation of the area by a sufficient spawning population occurs. Of course, migration will have an impact on the precision of the stock estimates obtained by the MSVPA in different areas; however, the validation performed did not indicate a major impact on the spawning stock estimates. Also problems related to the age determination of cod (e.g. ICES 1997/J:1), mis-reporting of catches and discarding (ICES 1997/Assess:12) effect the reliability of the assessment of the stocks. Apart from these uncertainties, the importance of the spawning population in the Bornholm Basin for successful reproduction is evident from the presented results and should consequently be considered in the stock assessment as well as in the management of the cod stock.

4.2   Implication of project results for fisheries management

Prior to the onset of the present programme, recruitment success of the Central Baltic cod was related mainly to the degree of oxygen depletion in the near bottom water layers of the spawning areas, affecting the developmental success of the eggs floating in this depth. Renewal of oxygen supply is mainly depending on the inflow of high saline water from the North Sea through the Skagerrak/Kattegat and the Western into the Central Baltic. Salinity has been realized as a further limiting environmental factor, influencing the fertilization success, and also temperature was described to have a certain impact on egg survival. Besides hydrographic conditions, two biological processes were demonstrated to have an impact on cod recruitment: the egg production, measured in general as the spawning stock biomass and the cannibalism on juvenile cod.

The present programme has in principal confirmed the dependence of egg survival on the hydrographic conditions within and below the halocline. The 'reproductive volume' in which egg development may be successful has been defined by threshold levels in salinity (> 11 psu), oxygen concentration (> 2 ml/l) and temperature (> 1.5°C). However, it has also been demonstrated that this reproductive volume is neither simply proportional to egg survival, nor to subsequent recruitment success. The non linearity in the relationship is caused by intra- and inter-annual variability in egg buoyancy, resulting in variable portions of the eggs floating inside the reproductive volume. Even in years with a large 'reproductive volume' there may exist extended water layers outside this volume, in which eggs are floating according to their buoyancy but will not survive due to low oxygen or temperature levels. The vertical distribution of cod eggs is depending on:

- the salinity conditions during the oocyte ripening process and to a lesser extend during fertilization, i.e. in years subsequent to a major Baltic inflow event, the cod eggs will on average have higher specific gravity and will thus float at higher salinities, violating the upper boundary of 11 psu,
- the spawning stock structure, as larger females produce on average larger eggs with a higher buoyancy,
- the developmental stage of the egg, as older eggs have a tendency to increase their specific gravity, i.e. have neutral buoyancy at higher salinities.

The hydrographic conditions relevant for the egg development are depending on the specific regional and temporal distribution of the spawning effort:

- large reproductive volumes in areas of rather low egg production (e.g. the Gotland Basin in 1994) or small reproductive volumes in areas of relatively high egg production (e.g. the Bornholm Basin in 1990) will result in unexpected low or high values for total egg survival respectively, if these regional differences are not considered,
- the shift in main spawning time to summer months, as observed since the beginning of the 1990'ies, results in an exposure of the eggs to declining oxygen concentrations even after winter inflow events, as oxygen consumption rates are high in the bottom water layers of the Central Baltic deep basins,
- egg survival rates are related to the oxygen conditions also above the developmental threshold of 2 ml/l, i.e. a large water body with 3 ml/l oxygen concentration will not necessarily result in a higher egg survival than a smaller water volume with higher oxygen concentration.

Based on these results, the following processes were described and subsequently modelled within the programme:

a) the vertical distribution of cod eggs in relation to the hydrography,

b) the regional and temporal distribution of the egg production,

c) the buoyancy in relation to the age/size structure of the spawning stock,

d) the egg mortality rates in relation to oxygen concentrations above the developmental threshold level.

The models obtained from the available data base are in some cases still rather restricted in their predictive power and will require some further investigations for instance in topic c). Nevertheless, some clear implications for the fisheries management in the Baltic are obvious already at this stage. These are shortly summarized below:

1) The Bornholm Basin is the only spawning area in the Central Baltic where cod is regularly reproducing; spawning effort in the Gdansk Deep is to a large extent unsuccessful under normal stagnation conditions, and also inflow events do not guarantee high egg survival in this area, if suitable water masses are not introduced at a certain right time into the Gdansk Deep. In the Gotland Basin the situation is worse, as the stock component is close to extinction since the end of the 1980's, and it appears very doubtful that the egg production is still sufficient to utilize even favourable environmental conditions.

Implication 1): Great care should be taken to preserve the Bornholm spawning component of the central Baltic cod stock, as this component presently sustains the stock. The fish migrate between areas, so a complete preservation will not be possible. However, it appears to be unlikely that cod encountered in pre-spawning concentrations in the Bornholm Basin will migrate to the Gdansk Deep and Gotland Basin to spawn, especially as long as the hydrographic conditions are more unfavourable in the latter areas.

2) Hydrodynamic modelling exercises have confirmed the importance of inflows of saline, oxygen enriched water masses from the North Sea into the Baltic as the main process increasing the volume of water suitable for successful egg development. Another candidate process to increase the reproductive volume is the surface wind stress resulting in enhanced mixing at and below the halocline, however, with considerably less impact. Also the effect of winter convection on oxygen levels in the halocline appears to be rather limited. Hydrographic situations in the Central Baltic are not predictable with sufficient precision 1 or 2 years ahead, however, monitoring in winter (February/March, utilizing the existing monitoring system) allows predictions about the hydrographic conditions during the subsequent spawning time (May to August).

Implication 2): Maximum egg production has to be ensured in an area of suitable reproductive conditions. As a standard option during stagnation conditions this would be the Bornholm Basin. In case of inflow events, the most suitable area will depend on the magnitude of the inflow, the wind forcing and the salinity of the inflowing water in relation to the bottom water in the Bornholm Basin. It is possible to predict whether an inflow will reach eastern spawning areas, however, prediction whether the inflowing water masses will turn south into the Gdansk Deep or north into the Gotland Basin is difficult.

3) Timing of spawning is important, as it will affect the potential of the stock to utilize the environmental conditions conducive for egg survival. The shift in spawning time is related to variation in ambient temperature conditions as well as changes in stock density and stock structure. However, predictions on the basis of measurable variables are presently not possible and can be derived from trend (autoregressive models) only.

Implication 3): High recruitment success (as occurred in the 2nd half of the 1970'ies and early 1980'ies) is not to be expected as long as the main spawning time remains in summer months and following from 1) no rebuilding of the spawning component in the Gotland Basin has happened; the latter depends on recruitment from other areas.

4) The viability of offspring from large females is higher than that from small females and first time spawners. Larger fish produce on average larger eggs being more buoyant and thus, having a higher survival probability and additionally resulting in larger more viable larvae being probably the ones successfully completing the vertical migration into upper water layers. However, egg size is varying significantly also among batches from one female, being intermediate in the beginning of the season, largest during an early intermediate period, and smallest from late batches.

Implication 4): Care should be taken to maintain a sufficient number of well established repeat spawners in the stock and to ensure maximum egg production in early and intermediate periods of the spawning seasons (large females start spawning also earlier and hydrographic conditions are normally better).

Apart from the direct impact of hydrographic conditions on the fertilization success and survival of cod eggs, a series of other abiotic and biotic processes were identified to effect the Baltic cod recruitment success:

5) The relative potential egg production by individual female cod varies significantly between years, for which the reasons are largely unknown. The sex ratio in the stock changes significantly with age, i.e. a spawning stock consisting of a large number of young individuals will produce substantially less eggs than the same biomass consisting of old fish (a fact which has been realized before). Consequently the egg production determined by ichthyoplankton surveys is significantly better correlated to the female spawning stock biomass than to the entire spawning stock. This correlation can be improved, if the inter-annual variations in the maturity ogives and sex ratios are considered, based on yearly monitored data.

Implication 5): The spawning stock biomass is an uncertain measure of egg production, especially if maturity ogives are not monitored regularly. Spawning stock biomass related reference points refer to and should in principal be based on the potential egg production of the stock. This cannot be predicted yet with sufficient precision, but using the female spawning stock biomass would provide already a better measure than the total adult stock biomass. This does, however, not mean that the size of the male spawning stock is irrelevant for the reproductive success, especially if size associated mating occurs in cod.

6) Due to the low exchange rates of the deep water masses, highly persistent toxic substances accumulate in the Baltic deep basins. The project results indicate a link between contamination burden

(organochlorine pesticides and polychlorinated biphenyls) of cod ovaries and reproductive success of the offspring. As contamination is related to age/size of the fish, its negative effect may counterbalance to some extend the advantage of the higher buoyancy and general viability of offspring produced by large females. However, differences in the contamination load were found to be more pronounced between different areas of the Central Baltic than between different age/size-groups from the same area. Ovaries from the Gdansk Deep had significantly higher pollutant burdens, and the performance of the eggs and larvae from that area were correspondingly significantly worse, than from the Bornholm Basin. This indicates that pollution is rather an area related problem than threatening the survival of the Baltic cod stock as a whole.

Implication 6): None related to fisheries management at present. The area specific differences in contamination and subsequent impact on the viability of the spawning products have to be ascertained. However, it is difficult to establish significant relationships as a complete analysis of the occurrence of xenobiotics is extremely resource demanding and interactions between different contaminants difficult to describe. Thus, enzymatic tests indicating the presence of xenobiotics should be implemented in future studies.

7) Clupeids, especially sprat are the preferred prey of cod, but they are also important predators on cod eggs in the Bornholm Basin, utilizing the same spawning area and having largely overlapping spawning times. Oxygen conditions conducive for cod egg survival result in a limited vertical predator prey overlap, i.e. ensuring high egg survival. In unfavourable environmental situations, predation increases and by this limits egg survival even more, especially as clupeids are apparently selecting older egg stages, i.e. those surviving. Due to the shift in cod spawning time to summer months, predation intensity by sprat has decreased, but is partly compensated by herring returning in early summer from their coastal spawning areas.

Implication 7): As the Bornholm Basin is the most important spawning area for sustaining the cod stock, egg predation by clupeids is a fact to be taken into account in the management. A fishery on sprat in the Bornholm area should preferably concentrate on pre-spawning seasons to avoid heavy by-catches of spawning cod, staying in the water column above the deep layers of low oxygen concentration while spawning. On the other hand, cod depends on sprat as a food resource; thus, a proper management of the sprat stock is required, leading to multispecies management (see below).

8) High and variable mortality rates are not only effective during egg development. Survival of larvae, in this area, requires especially a successful completion of vertical migration from hatching depths to surface layers. Within and below the halocline, prey abundance and light intensities are both combined not sufficient for a successful start of external food intake. Through the examination of characteristics of the larval and juvenile population, such as the otolith derived hatch dates and application of 3-D hydrodynamic modelling approaches, environmental processes and biological attributes have been identified, which lead to increased survival success during this phase of development. Sequential sampling of the population has demonstrated that the highly viable offspring from large females, which are in addition transported rapidly to nursery areas, have the highest potential to survive. From the 3-D hydrodynamic modelling, typical meteorological situations have been identified and related to year

class strength, which either force the transport of pelagic life stages into suitable nursery areas or keep them on the spawning sites.

Implication 8): The tools now available can be used to a) identify important nursery areas in a given year, allowing in principal to ensure their conservation (e.g. reduce by-catch of pelagic juveniles in pelagic fishery on sprat and herring) and to b) contribute to short-term recruitment predictions.

9) Cannibalism effects the survival of 0- and 1-group cod substantially in specific years/periods. Highest predation mortality rates were encountered in the late 1970´ies and early 1980´ies with significantly higher cannibalism and suitability coefficients in the eastern spawning areas compared to the Bornholm Basin. These regional differences were caused by high abundances of demersal juvenile cod in certain areas (e.g. southern Subdivision 26) overlapping with the adult stock especially at specific hydrographic situations.

Implication 9): As cannibalism in the Baltic is enforced by the parental stock, it has to be considered in the management of the stocks as a potential self regulatory mechanism. The direct effects on biological reference points, and on responses of populations to strategies for stock rebuilding in relation to environmental factors still have to be assessed quantitatively. Cannibalism levels were low during the last 10 years, especially as a relatively high proportions of the adult stock concentrated in Subdivision 25, while juveniles were growing up to a considerable extent in Subdivision 26 and 28.

10) From the review of past and present research programmes on stock enhancement of cod and other species it is concluded, that enhancement success will depend on the optimum choices of operational scenarios, which are particularly suitable for certain areas in the Baltic. Most of the essential criteria from other areas are not fully applicable and site specific ones are not yet sufficiently studied.

Implication 10): Stock enhancement is presently not to be considered as a suitable management option to sustain the Baltic cod stocks or successfully enhance their stock development with economically acceptable effort. It is recommended to conduct specific tagging studies on the time-size-release window and simultaneously study possibilities to improve the cost-effectiveness of fry production.

Management measures enforced in 1998

The Baltic cod is managed by the International Baltic Sea Fisheries Commission (IBSFC) as one unit covering all Subdivisions 22-32. However, ICES considers the stocks in two units (Subdivisions 22-24 and Subdivisions 25-32) and advice is provided separately on them. The main tools of cod stock management has been Total Allowable Catch (TAC) and also technical measures, i.e. fishing rules. The fishery in 1998 is regulated by following rules:

a) A TAC of 145 000 tonnes for 1998, of which 140 000 tonnes is allocated with effect from 1. January 1998. The remaining 5 000 tonnes will be considered at the next session of the IBSFC in September 1998 in the light of available scientific information and advice, no fishery on cod for industrial purposes,

b) a minimum landing size 35 cm south of latitude 59°30' N,

c) the weight of undersized cod may amount to 5% of the weight of the total catch of cod, the by-catch of cod in the herring and sprat fishery shall not exceed 10% by weight and no more than 5% of this cod by-catch shall be undersized,

d) it is prohibited to use trawls, Danish seines or gillnets having a mesh opening (measured when wet) smaller than that specified for fisheries listed below:

gillnet: 105 mm,

trawls and Danish seines with special selectivity devices such as exit windows or any other design with at least a selectivity at a level of 50% retention length of 38 cm (Danish and Swedish exit windows): 105 mm normal trawl and Danish seines: 120 mm,

e) fishing ban in 1998 from 10. June to 20. August (both days included),

f) fishing ban in the Bornholm Deep from 15. May to 31. August (both days included, in the maritime area defined by the lines connecting the coordinates: 55°30'N and 15°30'E; 55°30'N and 16°10'E; 55°15'N and 16°10'E; 55°15'N and 15°30'E).

Evaluation of presently enforced management measures

Total Allowable Catches (TAC)

According to project results, the TAC for 1998 of 145 000 tonnes is most probably too high to sustain the cod stocks above the MBAL level (at least in the Central Baltic), especially when taking into account the indicated overestimation by the last assessment conducted by the Baltic Fisheries Assessment WG (ICES 1997/Assess:12) and accepted by the Advisory Committee on Fisheries Management.

Minimum landing size

The present minimum landing size of 35 cm will allow participation of the majority of males at least once in their lifetime in the spawning activity, if not caught just prior to their first spawning period. However, most of the females in the Central Baltic are not sexually mature at this size, independent of the inter-annual variability, long term trends, and area differences detected. Keeping in mind implication 4), a minor change in minimum landing size is not expected to increase the viable egg production substantially, implying that either a substantial increase in minimum landing size and corresponding mesh-size regulations or a substantial reduction of the female mortality would be required to improve the viable egg production notably.

Fishing ban in 1998 from 10. June to 20. August

The fishing ban will cover probably most of the spawning season in the Central Baltic, however considering implication 3) and 4), it starts too late to ensure a high egg production originating from large, early spawning females and early to intermediate batches. A significant improvement with respect to the reproductive success of cod would be a start of the ban in mid May, considering especially the Bornholm Basin (see below). Given the present hydrographic situation, implications 1) and 2) would indicate that the fishing ban in eastern areas of the Central Baltic has only limited impact on the recruitment success, as the environmental conditions are expected to be unfavourable for egg survival in the Gdansk Deep and Gotland Basin. However, opening the fishery in these areas, while closing it in Subdivision 25 would probably result in a

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heavy reduction of the remaining stock in these areas, with the component in the Gotland Basin being already close to extinction.

Fishing ban in an area of the Bornholm Deep from 15. May to 31. August

According to project results for the years 1986-96, high egg abundances were found mainly in the central part of the Bornholm Basin in which the water depth exceeds 75 m. In the years 1990-1996, the egg production in the closed area as observed from ichthyoplankton surveys in July (the peak spawning time since 1993) varied between 3% and 32% of the total egg production in the Bornholm Basin. For the years 1994-1996 the proportion was lower (3-14%) than for the former time period (17-32%), due to a change in regional distribution patterns caused by the major Baltic inflow in 1993. A more effective measure to ensure undisturbed spawning would be a closure of the whole central Bornholm Basin from 15. May to the 20. August.

General fisheries management considerations

Changes in hydrographical conditions affecting the reproductive success of cod are irregular or semiregular events, which are very hard to predict and beyond of fisheries management control. However, a proper combination of closed areas and closed seasons may give some possibilities to allow undisturbed spawning in the main spawning grounds having favourable environmental conditions for egg survival. From implications 1) to 3) it is evident, that the spawning area to be protected is first of all the Bornholm Basin, basically sustaining the Central Baltic stock. Depending on the hydrographic conditions in the preceding winter, other spawning areas may be closed for the fishery before the onset of spawning activity to use favourable environmental conditions. This adaptive strategy would of course require a flexible enforcement of fisheries management regulations, but would probably secure highest possible benefit from the reproductive effort of the stock.

One of the main targets of cod management in the Baltic has been to safeguard spawning stock biomass above MBAL levels (240 000 tonnes for the Central Baltic stock) to reduce the risk and probability of low year-class sizes. Following implications 1), 2), 4), 5) and potentially 6), the cod management should aim to sustain a certain MBAL for the Bornholm Basin, preferably consisting of a high proportion of well established female repeat spawners. To increase the amount of older females eventually needs a change in minimum landing size and corresponding mesh-size regulations, and thus the overall exploitation pattern of cod. However, this change just postpones peak mortality about 0.5-1.0 year depending on the new minimum landing size and mesh-size. In fact to ensure a higher share of older females in the spawning stock addresses a constant fishing mortality or a total effort management strategy reducing mortality rates.

From implication 3), a strict conservation of remaining cod in Subdivision 28 and the northern part of Subdivision 26 may be indicated to rebuild a certain spawning stock component being able to use potentially favourable environmental conditions in the Gotland Basin. However, the interrelationships between this basin and the bordering areas are at present poorly understood. Recruitment in the Gotland Basin is most probably originated in the Bornholm Basin and to a lesser extent in the Gdansk Deep. Reaching sexual maturity, the fish will probably either migrate back into the areas of their origin or stay in the Gotland Basin, if suitable environmental conditions are encountered. An unconditional stay in the area by a majority of the population appears to be unlikely. This indicates that a proper management of the stock component as a separate identity is hardly possible.

From implication 7) and 9) it is evident, that recruitment of cod not only depends on the amount as well as temporal and spatial distribution of the viable egg production in relation to environmental conditions, but also on predator/prey interactions. Cannibalism, at present, appears to occur on a comparably low level in the Central Baltic, due to limited spatial overlap and low abundance of prey and predator. In general, the spatial and temporal overlap of predator and prey is forced by a set of abiotic and biotic processes and the interactions are additionally influenced by the occurrence and abundance of alternative prey species. This and the feed back mechanisms between cod and sprat (as major prey of cod and predator of cod eggs at the same time) make medium- to long-term predictions of cod and also sprat stock development extremely difficult. Although it has been demonstrated that multispecies interactions have direct effects on biological reference points (e.g. ICES 1998/J:1), at present there are no firm recommendations how multispecies aspects should be taken into account when setting biological reference points for specific stock complexes such as cod, herring and sprat in the Baltic.

Apart from the demonstrated biological interactions, the existence of technical interactions and technical regulatory measures imply the need to define biological reference points in an ecosystem or at least a multispecies context. In fact, ideally, control rules should be multidimensional. Estimates of F_{pa}, B_{pa}, F_{lim} and B_{lim} for each stock of concern should be conditional on the status of the other stocks in the assemblage.

If a recovery plan needs to be developed, then in order to ensure recovery of the stock of concern, that plan should incorporate actions for all other (relevant) species in the assemblage. Another important factor of relevance to mixed fisheries is the need to take into account the ability of fleets to switch between stocks and the possibility that latent capacities may be mobilized in response to fisheries regulations and/or markets. Reductions in quotas for one species (cod) may result in increases in fishing pressure on other species (e.g. herring and sprat as well as flounder in the Baltic at the present). Quota reductions in combination with technical interactions may also result in increased discarding and increased cryptic mortality, both of which may be difficult to measure and incorporate into stock assessments.

Multispecies considerations and technical interactions as well as the pronounced impact of environmental variability on the reproductive success of cod are the reasons why it may not be feasible or practical to construct generic harvesting control rules. Adaptive annual case-by-case decisions based on careful stock and environmental monitoring appears to be the only feasible approach for a successful management of Baltic cod at the present level of fishing capacity. Economically more reasonable could be the approach to substantially reduce the fishing capacity in general, adapting it to an average productivity of the system.

5. Acknowledgement

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