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**Variability in egg production of cod
(*Gadus morhua callarias* L.)
in the Central Baltic Sea**

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1 Introduction

Stock - recruitment relationships are used in the assessment of many marine fish stocks to define biological reference points and to conduct medium to long term predictions. However, they may often not adequately forecast cohort sizes. Mathematical expressions including dome-shaped (Ricker 1954) and asymptotic (Beverton and Holt 1957) curves or more flexible functions (Shepherd 1982) were commonly assigned to describe this essential relationship. In most cases, a large residual variance within stock - recruitment relationships remained. The poor agreement was assigned to environmentally-induced variation in egg and juvenile life stage survival (e.g. Rothschild 1986), measurement errors in the dependent and independent variables (Walters and Ludwig 1981) and auto-correlation in time series (Walters 1985). Recently, awareness increased that stock indices might fail to reflect the true reproductive potential (e.g. Marshall et al. 1998, 1999) and could, thus, be responsible for a considerable amount of the unexplained variation in recruitment. In the majority of stock - recruitment relationships the spawning stock biomass (SSB) rather than the egg production was used as an index of the stock's reproductive potential assuming proportionality between both measures. However, this assumption was challenged for a number of cod stocks indicating that the SSB is not a reliable estimator of reproductive potential (Marshall et al. 1998, 1999; Marteinsdottir and Thorarinsson 1998; Köster et al. 2002). The relation of reproductive potential to the SSB may largely be influenced by the fact that SSB estimates are often derived from combined female and male maturity data or even an adult knife-edge maturity (e.g. age 3+) that do not account for temporal and sex specific variation in maturity patterns (e.g. Tomkiewicz et al. 1997). Differences in the age structure of the adult stock may add further variability, as offspring quality and quantity depends among other factors on female spawning experience (Trippel et al. 1997; Trippel 1998; Marteinsdottir and Thorarinsson 1998). Also at the individual level, variations in relative or size-

specific fecundity and viability of eggs and larvae can be substantial due to changes in female growth and nutritional condition (Kjesbu et al. 1998; Marteinsdottir and Steinarsson 1998; Kraus et al. 2000; Lambert and Dutil 2000).

The age of first maturity differs considerably between cod stocks. Baltic cod attain maturity for the first time at an age of 2 to 6 years, while for example the Northeast Arctic cod mature at an age of 7 to 13 years with the difference being probably a matter of varying temperature regimes (see review by Lambert et al. 2002). Long term historical variation in size and age at maturity of cod stocks spanning the North Atlantic were linked to increasing exploitation and related density dependent and/or genetic effects due to size selective fisheries (see review by Lambert et al. 2002). A significant temporal variation in proportion mature females and males was also shown for Eastern Baltic cod and was related to SSB (Cardinale and Modin 1999). In addition, the sex ratio of Eastern Baltic cod varies with age in a way that abundant young age classes favour higher proportions of males in the stock (Tomkiewicz et al. 1997). However, until recently only period specific combined female and male maturity ogives have been applied in the standard assessment of Eastern Baltic cod (ICES 2001a) and the application of more sensitive measures of the reproductive potential as for example egg production based on the female SSB and fecundity is far from being implemented.

Fecundity is of interest to fishery scientists as both a critical parameter of stock assessment based on egg production methods (Lasker 1985) and as a basic aspect of population dynamics (Koslow et al. 1995). In cod, annual fecundity is assumed to be determinate, i.e. the standing stock of vitellogenic oocytes prior to spawning is equivalent to the number of eggs to be spawned, and there is no evidence for de novo vitellogenesis during spawning (Kjesbu et al. 1990). Hence, fecundity can be estimated prior to spawning by counting the number of developing oocytes. Prior to ovulation mature oocytes are hydrated and cod release ten to twenty batches of buoyant eggs over a protracted spawning season.

Egg production of individual Eastern Baltic cod, for example, ranges from approximately one hundred thousand to more than ten million eggs (Kraus et al. 2000).

The individual fecundities of similar sized fish from one spawning population within a spawning season show considerable differences (e.g. Nikolskii, 1969; Osthuizen and Daan, 1974; Hislop et al., 1978) and are influenced by the availability of food (Woodhead and Woodhead, 1965; Hislop et al., 1978; Horwood et al., 1989; Kjesbu and Holm, 1994; Karlsen et al., 1995; Kjesbu et al., 1998). Indications of density dependence of fecundity were given by (i) Rijnsdorp et al. (1991) who found a negative correlation between SSB and relative fecundity for North Sea cod, (ii) Rijnsdorp (1994) who described a decrease in size-specific fecundity of North Sea plaice (*Pleuronectes platessa*) with increasing stock sizes and (iii) Bagenal (1973) who identified negative correlations between fecundity and densities in plaice from different populations. Temporal and spatial variability in individual fecundity within a spawning stock between years or between populations using different spawning grounds as described by Pinhorn (1984), Rijnsdorp et al. (1991), Kraus et al. (2000) and Kjesbu et al. (1998) might be due to one or some combined effect of these factors.

Ultimately, the amount of resources invested in reproduction depends on food supply. The interaction of food and fecundity is well studied, while atresia as a regulatory mechanism of fecundity received less attention. Descriptive literature on follicular atresia exists (see review by Tyler & Sumpter 1996) and the occurrence of atretic follicles is often discussed as part of descriptions of the seasonal changes in the ovaries of marine fish species. However, quantitative measurements of atretic egg losses are scarce (e.g. Kjesbu et al. 1991; Witthames and Greer Walker 1995; Witthames et al. 2000), though atresia is not only regarded as a fine tuning mechanism to regulate the number of eggs per batch in determinate batch spawners, but could also lead to a complete cessation of spawning activities under unfavourable conditions (e.g. Hunter and Macewicz

1985; Burton et al. 1997). For cod in the Baltic Sea, investigations of atresia as a regulatory mechanism of the individual egg production have, so far, not been conducted, though the Eastern Baltic cod stock has been studied for a long time and a considerable amount of data related to other reproductive parameters exist (reviewed in Bagge et al. 1994).

In the Baltic Sea, two distinct cod stocks exist, the western stock or “Belt Sea cod (*Gadus morhua morhua* L.)” and the eastern stock or “true” Baltic cod (*Gadus morhua callarias* L.). Meristic (Poulsen 1931; Kändler 1944) and genetic studies (Jamieson and Otterlind 1971; Schmidt 2000) as well as tagging experiments (see review by Aro 1989) indicated that the two stocks are located west and east of a borderline at 14°30' longitude near Bornholm Island with some overlap in the Arkona Sea (Figure 1). Historically, the Eastern Baltic cod stock is one of the largest in the North Atlantic region (Dickson and Brander 1993) with a long term average of SSB of 400.000 to 500.000 tonnes, whereas the stock level of Belt Sea cod was approximately one order of magnitude lower. However, due to a combination of increasing fishing pressure and low reproduction caused by unfavourable environmental conditions, SSB and recruitment of Eastern Baltic cod showed distinct time trends with the SSB declining from over 700.000t in the early 1980's to ~75.000t in 1999 (ICES 2001a).

Considerable variation in reproduction behaviour and environmental conditions on the spawning grounds exists between the two Baltic cod stocks. In the Western Baltic, cod spawning begins as early as January with a peak in March and lasts until May (see review by Bagge et al. 1994). The time of peak spawning of the eastern stock occurred from the end of April to mid June in the 1970's and 1980's gradually shifting to late July in the 1990's (Wieland et al. 2000). Key factors determining the progressive delay of spawning in this stock were found to be decreasing water temperatures during the period of gonadal maturation and the

declining stock sizes concurrent with an increase in the proportion of young individuals in the stock (Wieland et al. 2000).

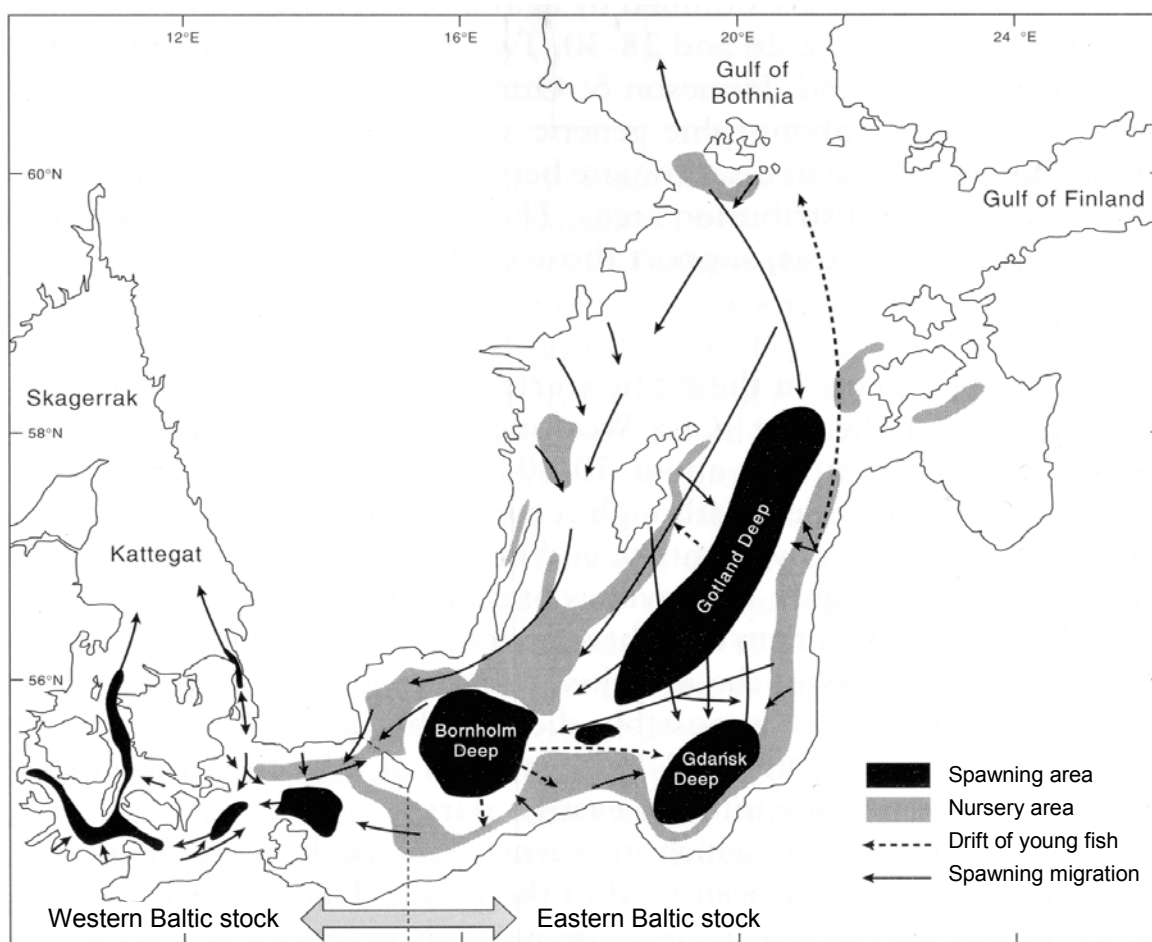


Figure 1: Distribution of spawning and nursery areas of cod in the Baltic Sea (redrawn after Bagge et al. 1994).

Environmental conditions in the Baltic Sea are characterised by a pronounced salinity gradient from west to east. The limited inflow of saline water from the North Sea in combination with a considerable fresh water inflow from river runoff in the eastern regions (e.g. Matthäus 1995) leads to permanent thermo-haline stratification and brackish water conditions.

In cod spawning areas, the ambient salinity is usually sufficient to keep cod eggs floating in the surface layers. However, salinity in the surface layers of the Central Baltic Sea is too low for cod eggs to achieve neutral buoyancy. Experimental studies revealed that the eggs of Baltic cod are neutrally buoyant at ~14 psu

(Nissling et al. 1994; Nissling and Vallin 1996). As salinities around 14 psu in the Central Baltic are restricted to deep water layers, cod eggs occur exclusively within and below the permanent halocline (e.g. Müller and Pommeranz 1984, Wieland and Jarre-Teichmann 1997) located at approximately 50 to 70 m depth (Møller and Hansen 1994). The spawning areas of Eastern Baltic cod are, thus, restricted to the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Figure 1).

Within these deep spawning layers cod eggs are exposed to variable and low oxygen concentrations depending on the frequency and intensity of intrusions of saline, oxygenated water. Oxygen content and salinity within and below the halocline were shown to be the major environmental factors influencing fertilisation rate and cod egg survival (Westin and Nissling 1991; Nissling 1994; Wieland et al. 1994). During the last decade, successful spawning was restricted to the Bornholm Basin owing to a long period with limited inflow of saline water creating anoxic conditions in the spawning layers of the Gdansk Deep and Gotland Basin (MacKenzie et al. 2000). Consequently, the stock development was heavily dependent on recruitment success in the Bornholm Basin. Based on laboratory experiments on the impact of oxygen conditions on cod egg mortality (Nissling 1994, Wieland et al. 1994) a “reproduction volume” as the water volume allowing successful cod egg development (Plikshs et al. 1993, MacKenzie et al. 2000) was defined. The reproduction volume explains a significant part of the variability in recruitment (e.g. Sparholt 1996) and has been successfully integrated into stock-recruitment relationships (see Jarre-Teichmann et al. 2000 for a review). Clupeid predation on cod eggs (Köster and Schnack 1994) and cannibalism on juvenile cod (Sparholt 1994) were shown to be further important determinants of recruitment. Still, considerable explanatory potential remains for other variables not incorporated so far. The influence of food supply for larvae and early juveniles (Hinrichsen et al. 2001), as well as temporal and spatial variation in sex ratios, female maturity ogives

(Tomkiewicz et al. 1997), fecundity (Kraus et al. 2000) and atresia on recruitment await substantiation.

In many fish stocks, time series of abiotic and biotic factors needed to study population dynamics are scarce or the data quality is poor. As a result, key factors and processes influencing reproduction and recruitment success have been difficult to identify. In the Central Baltic Sea, however, the amount of data related to cod reproduction and recruitment as well as environmental variability is comprehensive. A series of studies to examine processes influencing developmental success of subsequent life stages and their specific contribution to recruitment variability has already been conducted (MacKenzie et al. 1996; Köster et al. 2001a), but the parental influences on egg production received less attention.

Several aspects of the reproductive potential including sex ratio- and maturity-at-age as well as the individual fecundity have intensively been studied. However, a synthesis of these parameters had, yet, to be conducted. For example, the fecundity of Baltic cod was investigated by Botros (1962), Strzyzewska (1962), Schopka (1970), Kosior and Strzyzewska (1979), Shapiro (1988), and Bleil and Oeberst (1996). As year specific data on the female spawning stock size and information on atresia were not available, an accurate estimation of the population egg production was hampered in these studies. Kosior and Skolski (1992) were able to show temporal variation of sex ratio- and maturity-at-age and Cardinale and Modin (1999) demonstrated pronounced time trends in the age at 50% maturity, but data on annual fecundity to calculate the population egg production were lacking in both studies. In summary, studies on reproductive potential of cod in the Central Baltic Sea covered mostly single aspects, applied methodology of different accuracy and are characterised by a lack of time series data. These shortcomings may be due to the enormous sampling effort necessary to obtain consistent data sets on stock size, structure and reproduction parameters. The results obtained within two large, international EU-funded research projects

(CORE: AIR2-CT94-1226 & STORE: FAIR-CT98-3959) enabled for the first time an accurate synthesis of important aspects of reproductive potential of Eastern Baltic cod.

In this framework, the present thesis focused on the egg production of cod in the the Central Baltic Sea. The results obtained during the work are structured into three chapters: The first section deals with the individual fecundity, its determinants and variability. In the second chapter variations in the population egg production are addressed and, finally, ovarian atresia as a regulatory mechanism of fecundity and, hence, egg production is examined.

Extensive sampling of ovaries was conducted to investigate the individual fecundity and atresia of Eastern Baltic cod. Fecundity was investigated for intra- and inter-annual variability as well as for deviations between spawning grounds within a spawning season. Information on the size and condition of individual fish as well as prey stock sizes and environmental data were used to identify possible factors determining the variability in annual fecundity. The prediction capabilities of these factors were tested to establish a fecundity model. Based on relative fecundity, which was shown to be independent of body size, the final model was used to establish a time series of predicted relative fecundities. To explore the role of atresia as regulator of the annual fecundity, the percentage of females showing atresia (prevalence) and the number of oocytes affected (intensity) were estimated. Results were checked for variability related to changes in size, maturity stage and condition to be considered when calculating the realised from the potential egg production. The total, seasonal loss of oocytes due to atresia was estimated as proportion of the potential egg production.

The potential egg production of Baltic cod at the presently only important spawning site, i.e. the Bornholm Basin, was computed for a period from 1976 – 1999. Based on stock abundance estimates from a multi-species assessment model, time series of weight at age, sex ratios and the proportion mature females (maturity ogives), the female spawning stock biomass was estimated. Multiplying the female

spawning stock biomass with the observed and modelled time series of relative fecundity yielded two data sets of potential egg production. The time series of potential egg production were complemented by independent data series of realised daily and seasonal egg production from observed egg abundance in the Bornholm Basin. These data were assumed to be representative of egg production in the field. In order to evaluate the reliability of the different time series of female spawning stock biomass and potential egg production, the stock based estimates were compared to the realised egg production. The effect of removing annual variability in sex ratios, maturity ogives and relative fecundity on the correlation between the potential and realised egg production was examined to assess their specific contribution to variation in egg production.

Finally, the difference between the most reliable estimates of the potential and realised egg production was calculated to indicate the loss of eggs due to atresia, fertilisation failure, and early egg mortality. The relative role of atresia among these processes is discussed along the exemplary estimated total atretic loss of eggs.

2 Materials and methods

2.1 Fecundity

The first part of the present study addresses the individual fecundity of Eastern Baltic cod. First, a detailed analysis of spatial, intra- and inter-annual variations in fecundity was conducted. Secondly, the power of possible predictor variables of fecundity was tested in an exploratory analysis in order to establish a fecundity model for Eastern Baltic cod.

2.1.1 Definitions

Potential fecundity is defined as the number of developing oocytes in female fish prior to spawning (Kjesbu et al. 1991). This definition considers that the realised fecundity, i.e. the total number of eggs spawned per season, can not be determined prior to spawning as a bias through subsequent atresia might occur and, furthermore, some vitellogenic eggs could remain in the ovary after spawning. **Relative fecundity** was defined as the number of developing oocytes per gram total body weight. Contrary to other investigators who used ovary free (somatic) body weight for standardisation, total weight was chosen, because weights of gonads were not available for all data sets. In the following, potential and relative potential fecundity are referred to as fecundity and relative fecundity.

2.1.2 Sampling of gonads

A total of 900 cod ovaries from fish caught in the Bornholm Basin (ICES Subdivision 25, see code of International Council for the Exploration of the Sea (ICES)) during regular German and Polish trawl surveys within the period 1987-2000 as well as 106 ovaries from the Gdansk Deep (ICES Subdivision 26) sampled in 1995 and 1996 were included in the study (Figure 2; Table 1). Two

data sets were derived from these samples by Polish and own investigations. The own data set covered the Bornholm Basin in the years 1987 – 1992, 1996 and 1998 – 2000. Polish data from the Sea Fisheries Institute in Gdynia comprised the years 1995 and 1996 in both areas, the Bornholm Basin and the Gdansk Deep. Only ovaries in the pre-spawning maturity stage 4 (Tomkiewicz et al. 2002; see Appendix Table 1) are suitable for the analysis of potential fecundity (May 1967). For this reason sampling was conducted from pre-spawning until peak spawning time. As the peak spawning of Eastern Baltic cod has shifted from end of April in the 1980's to mid June in the 1990's (Wieland et al. 2000), sampling in the 1980's mainly covered March and April, while in most recent years sampling was performed later, i.e. from April to July. Samples were randomly taken from trawl catches covering horizontally the entire spawning grounds limited by the 60m isobaths (CORE 1998).

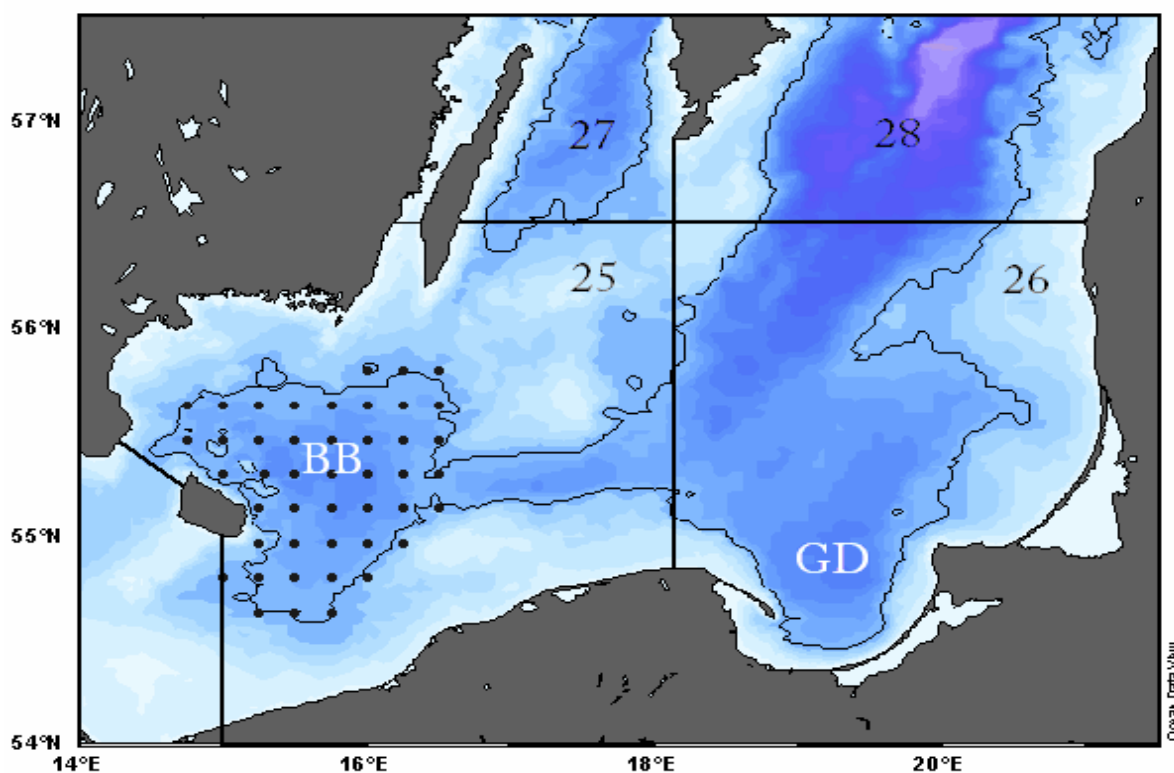


Figure 2: The Central Baltic Sea with ICES Subdivisions and ichthyoplankton sampling grid (•) in the Bornholm Basin. Cod spawning areas in the deep Basins (grey scale) of Subdivision 25 and 26, i.e., Bornholm Basin (BB) and Gdansk Deep (GD), are indicated by the 60m isobaths (solid line).

Table 1: Information on the fecundity sampling campaign including sampling years and months, areas, data sources (G: own German data; P: Polish data), numbers of analysed gonads as well as length range and median length.

Year	Sampling months	Sampling area (ICES Sub-div.)	Data source	Ovaries n	Length range min/max (cm)	Median length (cm)
1987	March	25	G	64	32 / 104	56
1988	March - May	25	G	115	27 / 76	45
1989	April	25	G	65	37 / 62	48
1990	March / April	25	G	104	35 / 68	58
1991	March	25	G	77	38 / 87	51
1992	March	25	G	43	41 / 98	58
1995	April / May	25	P	114	37 / 77	50
	May	26	P	66	33 / 90	52
1996	April	25	G	37	36 / 72	55
	May	25	G	32	40 / 100	58
	July	25	G	22	37 / 82	61
1996	April	25	P	28	45 / 68	52
	April	26	P	40	42 / 75	55
1998	March / April	25	G	40	35 / 91	51
1999	April - July	25	G	65	26 / 126	48
2000	March - May	25	G	94	28 / 108	48

2.1.3 Estimation of potential fecundity

Fecundity data from the Bornholm Basin (own data set covering the years 1987-1992; 1996; 1998-2000) was obtained using a combined automatic counting and gravimetric method. On board the whole ovaries were deep frozen and kept at minus 20°C. In the laboratory samples were thawed and sub-samples of about 20g were cut out of the centre of the right ovary lap. These sub-samples were used for fecundity estimations, assuming a homogenous distribution of oocytes in the ovary (Kjesbu et al. 1996). After hardening samples in boiling water, the ovary tissue was dis-aggregated with Trypsin solution (Clem et al. 1961). Reserve oocytes (diameter < 300µm) and remaining small tissue particles were removed by pouring the samples through a 300µm mesh sized sieve.

From each ovary three sub-samples of approximately 10000 oocytes were counted with an automatic particle counter (MACRO-FLOW-PLANKTOMETER,

Hüller et al. 1991). The counted oocytes and those remaining uncounted were dried, weighted and the number of oocytes in the sample was determined separately for each sub-sample using the weight proportions. The potential fecundity was calculated by, firstly relating the dry weight of the sub-sample to its wet weight and secondly relating the wet weight of the sample and the number of oocytes in it to the wet weight of the whole ovary. The resulting three values for the potential fecundity of each individual were averaged with the mean being used as an estimate for the individual potential fecundity.

Manual counting was applied in the Polish investigations (Bornholm Basin and Gdansk Deep in 1995 and 1996). Gonads for fecundity estimations were preserved on board in Gilson's fluid. In the laboratory ovaries were dried and weighted to the nearest 0.001g. The total number of oocytes in a dried subsample, weighted to the nearest 0.0001g, was counted with a stereo microscope and the potential fecundity was estimated by a gravimetric method.

To account for potential problems caused by the different methodologies, the Polish data covering the spawning grounds in ICES Sub-divisions 25 and 26 in two years were used to analyse the spatial effect, while the temporal variability was investigated utilising the own Bornholm Basin data set.

2.1.4 Data analysis

2.1.4.1 Temporal and spatial variability in fecundity

Fecundities of different sampling years, months and areas were compared with analysis of covariance (ANCOVA). As growth in weight and length may deviate, total weight and total length were used as co-variables in separate analyses. To linearise the fecundity length relationships and to achieve normal distribution of variables and co-variables, data had to be transformed to natural logarithms. In case of significant differences, post-hoc multiple comparisons of adjusted means

(Tukey's Honest Significance Difference test (HSD) for unequal sample sizes, Spjøtvoll and Stoline 1973) were performed.

For the Bornholm Basin data set derived by own investigations an ANCOVA with weight as co-variable could not be performed as parallelism in regression lines was lacking and a different method had to be applied: If the relationships between fecundity and total body weight are linear and the intercepts equal zero, the ratio between both parameters, i.e. the relative fecundity, should be independent of body size and could be used for comparisons with one way analysis of variance (ANOVA). To test the linearity assumption, first the slopes of log – log regressions (natural logarithms) of fecundity versus total body weight were tested against one (t-tests). In a second step, the intercepts of the untransformed relationships between fecundity and body weight were tested for deviation from zero with t-tests. As an additional test to examine length effects on relative fecundity, the residuals of the fecundity – weight relationships were regressed against total fish length and the slope tested for significance. In case of significant differences in relative fecundities derived by ANOVA, a Tukey's HSD test for unequal sample sizes (Spjøtvoll and Stoline 1973) was performed again to detect between which sampling dates significant differences occurred.

2.1.4.2 Explaining variability in fecundity

The investigation of impacts of biotic and abiotic environmental factors on fecundity was based on the Bornholm Basin subset of data derived by own investigations. Two different approaches were taken: First, a multiple linear regression was performed using individual fecundities transformed to natural logarithms as dependent variable and natural logarithms of individual fish length, condition (Fulton's condition factor; $K = \text{total weight} / \text{cubic length} * 100$; Fulton 1891) and the ambient winter water temperatures (definition below) as independent variables. As growth anomaly and the prey availability (see below)

were only available on population level, condition was chosen as a variable reflecting the nutritional status of the individual fish.

The second approach was based on annual averages of relative fecundity. The following possible predictor variables were tested in order to explain variation in relative fecundity:

- **Prey availability index, P_i** , utilising the ratio of unit cod spawning stock biomass (SSB) to unit sprat (*Sprattus sprattus*; all age groups) plus herring (*Clupea harengus*; age groups 0-2) biomass in ICES Subdivision 25 in the fourth quarter preceding the spawning period (obtained from MSVPA, see below).
- **Ambient winter water temperatures** in the fourth quarter preceding the spawning period in ICES Subdivision 25. These temperatures were calculated as averages below a depth of 55 m, i.e., below the halocline, using data extracted from the ICES hydrographic database.
- **Anomaly in growth rates** of cod in ICES Sub-division 25 determined from the increase in mean weight at age between the third and the subsequent first quarter (average of age group 3, 4 and 5 weighted for their abundance, data source: ICES 1999, 2001a).

Fulton's condition factor was not included in the second analysis, as condition and relative fecundity were based on the same fish weight data biasing the relationship between both variables. In order to establish a prediction model of relative fecundity, relationships between annual average relative fecundities and the predictor variables as well as the interaction of the independent variables were determined by minimising the least squares of various uni-variate linear and non-linear regression equations. The final model was used to establish a complete time series of predicted relative fecundity (PRF) for the years from 1976 to 1999, i.e. the period covered by the multi species assessment model (MSVPA, see below).

To obtain an alternative time series of relative fecundity, a set of observed relative fecundities (ORF) was established. Individual fecundity data from the present study were supplemented by estimates of average relative fecundity of Eastern Baltic cod for 1976 - 1978 and 1983 - 1984 from Shapiro (1988) and for 1994 - 1995 from Bleil and Oeberst (1996) to prolong the ORF time series.

2.2 Population egg production

In this section, time series of **female spawning biomass (FSSB)**, **potential (PEP)** and **realised egg production** of Eastern Baltic cod in ICES Subdivision 25 were established. The reliability of the stock based egg production indices was tested by comparison with the realised egg production from ichthyoplankton surveys. The influence of removing variation in sex ratios, maturity and fecundity on egg production was assessed. The loss of oocytes from late vitellogenesis to early embryogenesis was determined by means of the difference between the most reliable data sets on potential and realised egg production. Table 2 presents an overview on the data sets used in the following analyses together with the corresponding abbreviations and included years.

Table 2: Time series on reproductive potential including fecundity, FSSB, potential and realised egg production and their abbreviations used in the analyses as well as years included in the estimation. For potential egg production five data sets were calculated using different input variables.

Time series	Abbreviation	Years included
Observed relative fecundity	ORF	1976-1978; 1983-1984; 1987-1992; 1994-1996; 1998-2000
Predicted relative fecundity	PRF	1976-2000
Female spawning stock biomass	FSSB	1976-1999
Potential egg production	PEP	
based on ORF	PEP (ORF)	1976-1978; 1983-1984; 1987-1992; 1994-1996; 1998-1999
based on PRF	PEP (PRF)	1976-1999
constant sex ratio	. / .	1976-1978; 1983-1984; 1987-1992; 1994-1996; 1998-1999
constant maturity	. / .	1976-1978; 1983-1984; 1987-1992; 1994-1996; 1998-1999
constant fecundity	. / .	1976-1999
Realised daily egg production	RDEP	1987-1988; 1991; 1993-1994; 1996; 1999
Realised seasonal egg production	RSEP	1976-1978; 1983; 1985-1996; 1998-1999

2.2.1 Stock size, sex ratio-, maturity- and weight-at-age

Population sizes of cod in the Bornholm Basin, ICES Subdivision 25, were obtained from an area-disaggregated **Multi-Species Virtual Population Analysis** (MSVPA) (Köster et al. 2001b) updated by ICES (2001b) covering the period 1976 to 1999. Abundances and biological characteristics of cod, sprat and herring, i.e. the species incorporated in the MSVPA, differ between geographical areas of the presently assessed stock units. Thus, the MSVPA runs were performed on basis of quarterly and Subdivision specific data on catch- and weight-at-age provided by ICES (1999, 2001a). Weight-at-age in the catch was assumed to be equal to

weight-at-age in the stock, exceptions being the weights for cod of age groups 0 and 1. Here, due to selectivity of commercial gear, mean values were applied for the whole period.

The tuning of the MSVPAs was performed by iteratively running Extended Survivor Analyses (Shepherd 1999) and MSVPAs exchanging updated terminal F and predation mortalities until convergence was achieved (Vinther 2001). Abundance indices utilized for tuning originated from the international bottom trawl survey directed to cod, performed annually in February/ March (Sparholt and Tomkiewicz 2000) and the international hydroacoustic survey directed to herring and sprat, conducted annually in September/ October (ICES 1998; ICES 2001a).

ICES Subdivision specific sex ratios and proportions of sexually mature females at age (maturity ogives) were applied to determine the age specific female spawning stock size. Annual sex ratios and female maturity ogives were used for the years 1988 to 1998 from the database of Tomkiewicz et al. (1997) updated by ICES (1998) containing approximately 15 000 records from national and international trawl surveys in Subdivision 25. For the period 1976-1987 five year averages extracted from the same database were used to account for less intensive sampling in those years. For 1999 the average of the years 1996-1998 was used. Sampling procedures, maturity scales and computation methods varied between the different data sets included in the database. The subset of data for ICES Subdivision 25 used in the present analysis was mainly obtained from research cruises of Danish, German and Swedish vessels. Here, a fixed number of specimens per cm length group were sampled and raised to population level by the Subdivision specific length – frequency distribution. Only data from the first quarter of the year with an adequate coverage of the total depth range were used in order to ascertain that the data reflect the pattern of sexual maturity of the total stock (Tomkiewicz et al. 1997).

2.2.2 Female spawning stock biomass and potential egg production

Stock sizes of cod were adjusted to peak spawning time defined as the middle of the second quarter within the period 1976-89 and as the start of third quarter during 1990-99 to consider the shift in spawning time (Wieland et al. 2000). These stock sizes were assumed to be representative for the entire spawning time. To calculate the adult female stock size, age specific stock abundances were multiplied with sex ratios and female maturity ogives. Weight-at-age from quarter two and three according to the above described periods were used to determine the female spawning stock biomass (FSSB):

$$FSSB = \sum_{i=1}^{i=k} N_i * S_i * M_i * W_i$$

with N_i being the abundance, S_i the sex ratio, M_i the female maturity ogive and W_i the weight at age i .

The potential egg production (PEP) was calculated by multiplying the FSSB with the year specific relative fecundity (F_{rel}):

$$PEP = FSSB * F_{rel}.$$

To obtain two alternative time series of PEP, two data sets were created with ORF and PRF as year specific relative fecundity estimates, respectively (see Table 2). To assess the separate effects of removing variability in the time series of sex ratio, maturity ogives and relative fecundity, three additional series of PEP were constructed. In these series only the ORF was chosen as fecundity estimator, but with either the sex ratio, maturity ogive or the ORF held constant (see Table 2). The constant sex ratio and maturity ogive were calculated as average per age over all years of the time series, while for constant relative fecundity the simple average of the ORF series was used.

2.2.3 Realised daily egg production

Cod eggs were sampled on combined trawl- and ichthyoplankton surveys. The ichthyoplankton gear in use was a Bongo-net (60 cm diameter) equipped with 335 and 500µm mesh sizes towed in double oblique hauls integrating the entire water column down to 2 m above the bottom (Wieland 1988). The sampling covered the entire spawning area in the Bornholm Basin of approximately 11800 km² comprising 32 to 45 stations on a 10 x 10nm grid (Figure 2; CORE 1998; STORE 2001). Station specific egg abundances per m² were averaged over all stations covered and raised to the total spawning area.

The daily egg production was calculated as the abundance of stage I eggs (Thompson and Riley 1981) divided by the stage duration estimated from stage-specific egg development-temperature relationships (Wieland 1995). Ambient water temperatures for Sub-division 25, second and third quarter, respectively, were derived from the ICES hydrographic database applying a model of the relative vertical distribution of stage IA eggs (Köster et al. 2001a). In the model, empirical vertical egg distributions of egg stage IA are related to water density profiles by fitting a parabolic function to the log relative distribution of egg stages:

$$\text{LOG}(IA_z) = a + b * \rho_z + c * \rho_z^2,$$

where ρ_z is the water density in the depth interval z . It was assumed that this distribution and, hence, the ambient temperatures would also apply to stage I eggs used in this analysis. To estimate the realised egg production rather than the viable production, dead eggs that could not be assigned to a specific stage were distributed proportionally to the relative stage-specific distribution of live eggs in the samples.

To obtain yearly values of the **realised daily egg production (RDEP)**, survey specific estimates were averaged over a three-month period encompassing the main spawning period, i.e., April-June up to 1989, May-July from 1990-1992 and

June-August from 1993-1999 corresponding to the shift in spawning time. The RDEP was calculated for years with a minimum coverage of three surveys including 1976-1978, 1983, 1985-1996 and 1998-1999.

2.2.4 Realised seasonal egg production

The calculation of the **realised seasonal egg production (RSEP)** based on the youngest egg stage (IA) required an extensive coverage of the spawning period with ichthyoplankton surveys. Only years with at least six egg surveys, i.e., 1987-1988, 1991, 1993-1994, 1996 and 1999, were considered. The survey specific daily egg production was calculated as above but using egg stage IA. According to Daan (1981), daily cod egg production of the youngest egg stage is normally distributed over time. A transformation to natural logarithms converts these normal distribution curves into parabolas. Based on these assumptions, second order polynomials were fitted to the transformed survey specific daily egg production for each year by applying the least-squares method. The area beneath the fitted curves was estimated by numerical integration of re-transformed data to obtain the RSEP.

2.2.5 The influence of sex ratio, maturity and fecundity on relationships between potential and realised egg production

The agreement between FSSB as well as PEP based on ORF and PRF and estimates of the realised egg production (RDEP and RSEP) was examined in a regression analysis. To investigate the effects of removing variability in sex ratios, maturity ogives and fecundity from PEP, the three manipulated PEP time series and PEP based on ORF were regressed against RDEP and RSEP. The differences in explained variances between the relationships applying manipulated PEP's and the original PEP based on ORF were determined to assess the separate influence of each constant variable. Assuming that the RSEP and PEP

based on ORF are reliable estimates of the annual potential and realised egg production, their difference was calculated as an indicator for the loss of eggs due to atresia, fertilisation failure and early egg mortality. The difference was estimated as average ratio as well as from the linear relationship between RSEP and the PEP.

2.3 Atresia

The analysis conducted to study atresia was based on intensive gonad sampling in 2000 covering the period from pre-spawning time until spawning had ceased. Histological sections of these ovaries were used in stereological analyses (to estimate volume quantities from a two-dimensional plane) to quantify the total number of atretic eggs in the ovary. Differences in the proportion of females showing atresia and the intensity of atresia in these females were studied with respect to size, maturity and condition leading to an estimate of the total, seasonal atretic loss of oocytes in the stock.

2.3.1 Sampling of gonads and histological methods

Atresia of cod from the Bornholm basin (ICES Subdivision 25) was investigated in the 2000 spawning season covering the pre-spawning and spawning time from April to August with four trawl surveys. On each survey 12 to 15 trawl sets on a 10 by 10 nm grid were conducted over a period of max. 6 days covering the different areas of the spawning ground limited by the 60m isobath. Assuming a quasi synoptic sampling and an even distribution of cod over the spawning ground, material from each cruise was treated as a homogenous sample. In total 311 ovaries of different maturity stages were sampled for histological analysis (Table 3).

Table 3: Sampling dates, sample sizes as well as length range and median length of females sampled in ICES Sub-division 25 in 2000 for investigations of atresia.

Sampling dates	Ovaries n	Length range min/max (cm)	Median length (cm)
April, 21 st – 26 th	75	21 / 73	43
May, 25 th – 28 th	74	26 / 77	46
July, 06 th – 09 th	104	31 / 59	45
August, 03 rd - 05 th	58	37 / 104	45

Fish were dissected directly on board and total length was measured to the nearest cm. For each specimen total and gutted body weight, as well as liver and gonad weight were recorded to the nearest gram. In addition, the displacement volume of ovaries was determined to convert weights to volume for the stereological analysis. The maturity stage of each fish was determined applying the 10 stage macroscopical scale of Tomkiewicz et al. (2002) (see Appendix Table 1). From each ovary a cross section of tissue of approximately 1cm thickness was dissected from the centre of the right ovary lap and preserved in Bouin's solution (1 part acetic acid (glacial), 5 parts sodium phosphate buffered Formalin (36%), and 15 parts saturated Picric acid solution); the remaining tissue from ovaries in maturity stage four was deep frozen for analysis of potential fecundity as described above. After fixation, the histological samples were dehydrated in increasing concentrations of ethyl alcohol (70 - 96%) and embedded in paraplast historesin. Sections were cut at ~3 μ m using a non-motorized rotary microtome. After washing in ethyl alcohol and xylol, sections were stained with h matoxilin and eosin counterstaining (H & E) enabling the identification of atretic oocytes and the judgement of developmental stages.

2.3.2 Stereological analysis

All sections were microscopically screened to validate the macroscopic maturity stage according to the criteria described in Tomkiewicz et al. (2002) and for the

presence of atretic oocytes. The nomenclature and characteristics used to identify and describe atretic stages followed those of Bretschneider and Duyvene de Wit (1947) and Lambert (1970). The detailed stereological analysis to estimate the number of atretic oocytes was based on the first part of the alpha stage including only oocytes that still retain some of the characteristics of cortical alveoli, vitellogenic or final maturation/hydration oocytes (Witthames and Greer Walker 1995). In contrast to Hunter and Macewicz (1985), who defined the end of the alpha stage as total resorption of the oocyte, the end of the truncated alpha stage is characterised by complete resorption of the yolk, but remnants of the zona pellucida are still present. This truncated alpha stage is better suited for the stereological analysis, because atretic oocytes could be easily distinguished from normally developing oocytes and at the end of the original alpha stage the structure's boundaries become irregular and the distinction from empty follicles becomes difficult.

To quantify the total number of alpha atretic follicles per ovary, the theorem of DeHoff and Rhines (1961) was applied, which is based on the assumption that a section samples a volume equal to the diameter of the oocytes. First, the number and diameter of alpha atretic oocytes in the entire histological section or a sub-area as well as the size of the area were determined from light microscope images taken with a digital camera (NIKON COOLPIX 995). Measurements were performed using the freeware image analysis program NIH-Image (available at <http://rsb.info.nih.gov/nih-image/>). In any section larger particles are more likely to be represented than smaller ones and are correspondingly overestimated in area counts. Hence, the numbers of atretic oocytes were determined separately for three size classes according to their developmental stage, i.e., pre-vitellogenic to early vitellogenic (average diameter 0.05mm), vitellogenic (average diameter 0.15mm) and final maturation plus hydration (average diameter 0.17mm). Final maturation and hydration were grouped, because with breakdown of the chorion hydrated eggs lose the hydrolysed yolk and do not retain their original size. In a

second step, the sampled volume for each size class of atretic oocytes was calculated by multiplying the sampled area with the corresponding average oocyte diameter (theorem of DeHoff and Rhines 1961). The number of atretic oocytes of each size category in the corresponding volume was then raised to the ovary volume. Finally, the total number of alpha atretic oocytes of all size categories in the ovary was obtained by summing up the numbers per oocyte size classes:

$$N_o = \sum_{i=1}^{i=3} V_o * N_{iA} / A * d_i,$$

where N_o is the total number of atretic oocytes in the ovary, V_o the volume of the ovary, N_{iA} the number of atretic oocytes of size category i in the section area A , A the section area, and d_i the average diameter of oocytes of category i .

The proportion of females containing ovaries with alpha atretic oocytes in relation to individuals without atresia was designated as **the prevalence of atresia (P_a)**, the total number of alpha atretic oocytes per ovary as the **intensity of atresia (I_a)**. The intensity divided by the corresponding potential fecundity predicted from the year specific fecundity – length relationship (see results, Table 3) was defined as **relative intensity of atresia (RI_a)**.

2.3.3 Statistical analysis

Five 10cm length categories from ≤ 30 cm to >60 cm were established. Differences in P_a between length classes and maturity stages were compared with Chi – squared tests for comparison of multiple samples. Condition (Fulton's condition factor; $K = (\text{total weight} - \text{gonad weight}) / \text{cubic length} * 100$; Fulton, 1891) and liver index ($HSI = \text{liver weight} / (\text{body weight} - \text{gonad weight}) * 100$) were investigated for differences between specimens with or without atresia applying t-tests.

Intensities (I_a) and relative intensities of atresia (RI_a) were investigated for influences of maturity stage, fish size and condition measured as Fulton's K and HSI. The analysis was carried out in two steps. As the assumptions for parametric tests were not met, first, the effects of maturity stage were tested with non parametric Kruskal Wallis tests. In the second step, an exploratory analysis was conducted to detect correlations between I_a , RI_a and fish length, weight and both measures of condition.

In addition to atresia, the potential fecundity of females in maturity stage four was determined according to the methods described in section 2.1.3. To investigate similarities or dissimilarities of patterns in individual fecundity and atresia, relationships between the residuals of the fecundity - length and weight relationships were related to the RI_a .

3 Results

3.1 Fecundity

3.1.1 Fecundity and fish size

Best fits for relationships of potential fecundity and total fish length were given by power equations with exponents close to three ($r^2 = 0.46$ in 1995 to $r^2 = 0.98$ in 1999; Table 4). Although the best fits for the relationships between total body weight and potential fecundity were also given by low order polynomial or power equations, they were considered to be linear within the Bornholm Basin data set, because the exponents were close to one. Tests of linearity for these relationships revealed for eight out of ten years no significant deviation of the slopes of log – log regressions from one when 95% confidence limits were applied. For 1989 a minor deviation was detected with a probability value of $p > 0.04$, while for 1991 a major deviation from linearity was found (Table 4). Untransformed linear relationships between fecundity and weight were highly significant for all years ($r^2 = 0.72$ in 1988 to $r^2 = 0.98$ in 1999; Table 4). A significant intercept of these relationships was detected in 1989 (Table 4), but isometry was only slightly violated ($p = 0.02$). For none of the years length dependence of relative fecundity was detected ($p > 0.05$; Table 4). Within this data set relative fecundity was, thus, considered to be independent of body size and used for the analysis of inter-annual variability in fecundity. Contrary, the log – log analysis of the 1995 and 1996 data from Polish fecundity investigations revealed a deviation from linearity for one out of four samples (1995, Bornholm Basin). Additionally, the intercepts of linear relationships between fecundity and weight differed significantly from zero for the Gdansk Deep in 1995 and 1996 as well as for the Bornholm Basin in 1995 (Table 4). Hence, data from the Polish investigations were not included in the temporal comparisons

of relative fecundity, but used in a separate analysis to investigate spatial variation between spawning grounds.

Table 4: Fecundity relationships, significance levels and results for the tests of assumptions of relative fecundity. Each data set includes information about sampling time, area and source, fecundity - length and weight - relationships. For linear regression equations of fecundity versus body weight, the corresponding explained variance (r^2), the intercept (y_0) and the p-value (p_y) for the intercept to differ from zero is given. In addition, regression statistics for the residuals versus fish length, as well as for the log transformed fecundity - weight relationships are presented.

Year	Sampling months	Sampling area (ICES Sub-div.)	Data source	Fecundity - total		Intercepts			Slope residuals versus length		Slope log _{fecundity} versus log _{weight}		
				length relationships	weight relationships	r^2	r^2	y_0	p_y	β_e	p_e	β_w	p_w
1987	March	25	G	$F=49,76*L^2,51$	0,76	$F=584,6*W+105944$	0,76	105943	> 0.3	0.09	> 0.4	1.06	> 0.05
1988	March - May	25	G	$F=9,33*L^2,92$	0,68	$F=617,6*W-14111$	0,72	- 14110	> 0.7	- 0.03	> 0.7	0.97	> 0.05
1989	April	25	G	$F=0,54*L^3,66$	0,76	$F=799,5*W-206819$	0,75	- 206819	> 0.02	0.11	> 0.3	1.19	> 0.04
1990	March / April	25	G	$F=23,47*L^2,76$	0,74	$F=754,8*W-11815$	0,85	- 11815	> 0.9	0.02	> 0.8	1.04	> 0.05
1991	March	25	G	$F=18,05*L^2,77$	0,77	$F=630,4*W-56807$	0,74	- 56807	> 0.5	0.12	> 0.2	1.24	> 0.001
1992	March	25	G	$F=2,61*L^3,26$	0,93	$F=697,9*W-75182$	0,96	- 75182	> 0.4	- 0.04	> 0.8	1.04	> 0.05
1995	April / May	25	P	$F=150,33*L^2,23$	0,46	$F=430,5*W+293344$	0,44	293344	< 0.01	0.03	> 0.7	0.70	< 0.01
	May	26	P	$F=98,48*L^2,32$	0,80	$F=442,3*W+157691$	0,82	157691	< 0.01	- 0.02	> 0.8	0.90	> 0.05
1996	April	25	G	$F=12,12*L^2,94$	0,75	$F=788,9*W+151499$	0,77	151498	> 0.3	0.05	> 0.7	0.90	> 0.05
	May	25	G	$F=185,56*L^2,28$	0,79	$F=734,6*W+256725$	0,84	297999	> 0.08	0.08	> 0.6	1.05	> 0.05
	July	25	G	$F=0,44*L^3,75$	0,84	$F=998,2*W-375983$	0,8	-375983	> 0.3	0.02	> 0.9	1.16	> 0.05
Sum 1996	April / May / July	25	G	$F=13,53*L^2,92$	0,77	$F=846,3*W+3515$	0,8	35135	> 0.8	0.02	> 0.8	1.02	> 0.05
1996	April	25	P	$F=25,06*L^2,73$	0,67	$F=731,1*W+93200$	0,73	93199	> 0.6	- 0.07	> 0.7	0.78	> 0.05
	April	26	P	$F=393,74*L^2,04$	0,67	$F=491,1*W+507333$	0,65	507333	< 0.001	0.06	> 0.07	0.95	> 0.05
1998	March / April	25	G	$F=116,65*L^2,35$	0,71	$F=616,5*W+171600$	0,73	171641	> 0.3	0.02	> 0.5	1.04	> 0.05
1999	April - July	25	G	$F=27,63*L^2,71$	0,98	$F=775,1*W+42761$	0,98	42761	> 0.25	0.10	> 0.4	1.05	> 0.05
2000	March - May	25	G	$F=55,67*L^2,55$	0,77	$F=739,3*W+90356$	0,84	90356	> 0.3	- 0.01	> 0.8	0.98	> 0.05

Note: β_e and p_e : Slope and respective significance level of the slope; β_w and p_w : Slope and probability level for the slope to differ from one. G: German data set, P: Polish data set.

3.1.2 Seasonal variability in fecundity

A comparison of sampling months within one season was conducted for 1996, i.e. the only year in which sampling covered a large range of the pre-spawning and spawning season with sufficient sample sizes for each date. Relative fecundity values determined in three sampling months (April, May, July) in the Bornholm Basin did not show significant differences ($n = 91$; ANOVA $p > 0.58$). Seasonal variations in body condition (Fulton's K) did not confound this result, as relative fecundity showed a minor decrease from April to July concurrent with a minor increase in the condition factor (Figure 3). A post hoc multiple comparison of means revealed that differences in condition between April and July were significant at the 95% confidence level.

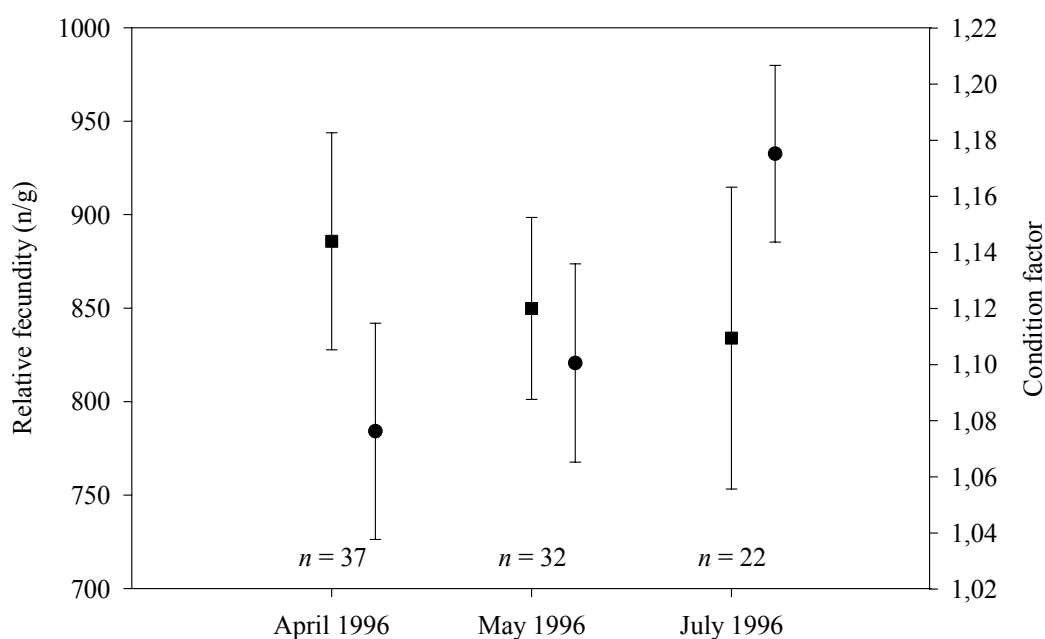


Figure 3: Average relative fecundity (■) and condition factor (●) for three sampling dates in 1996. Relative fecundity refers to total body weight, condition is calculated as Fulton's condition factor referring to total body weight and total length. The vertical lines give approximation for the 95% confidence limits of Tukey's HSD-test for unequal sample sizes.

The ANCOVA of log transformed potential fecundity and log total length as co-variable further corroborated this result ($n = 91$; ANCOVA $p > 0.90$). Consequently, varying sampling dates within one year were neglected in the following analyses of variations in fecundity between years and spawning sites (see sections 3.1.3 and 3.1.4).

3.1.3 Annual variability in fecundity

Relative fecundity varied significantly between years in the Bornholm Basin ($n = 758$; ANOVA $p < 0.001$). Homoscedasticity, a prerequisite for performing analyses of variance, was slightly deteriorated (Hartley's F-max test: $p < 0.05$; Levenne test: $p > 0.05$) caused by a low variance of individual relative fecundities in 1992. As analysis of variance is quite robust against departures from homogeneity of variance this was neglected in the interpretation of the results. Relative fecundity values of each sampling year were normally distributed.

Three homogenous groups of means (no significant differences) were identified by Tukey's HSD test. These are displayed in Figure 4 as annual averages of relative fecundity together with the approximation of the 95% confidence limits for the test. The years 1987 - 1989 and 1991 belonged to one group displaying the lowest relative fecundities. Though 1992 and 1998 were not significantly different from the first group, they formed together with 1990 a group of intermediate values, whereas 1996, 1999 and 2000 formed a group of the highest relative fecundity values significantly different from the first group. 1996 differed significantly from the low and intermediate group, while 1999 / 2000 differed only from the lowest group. The maximum observed difference in relative fecundity between 1991 and 1996 was 33% (setting maximum to 100%).

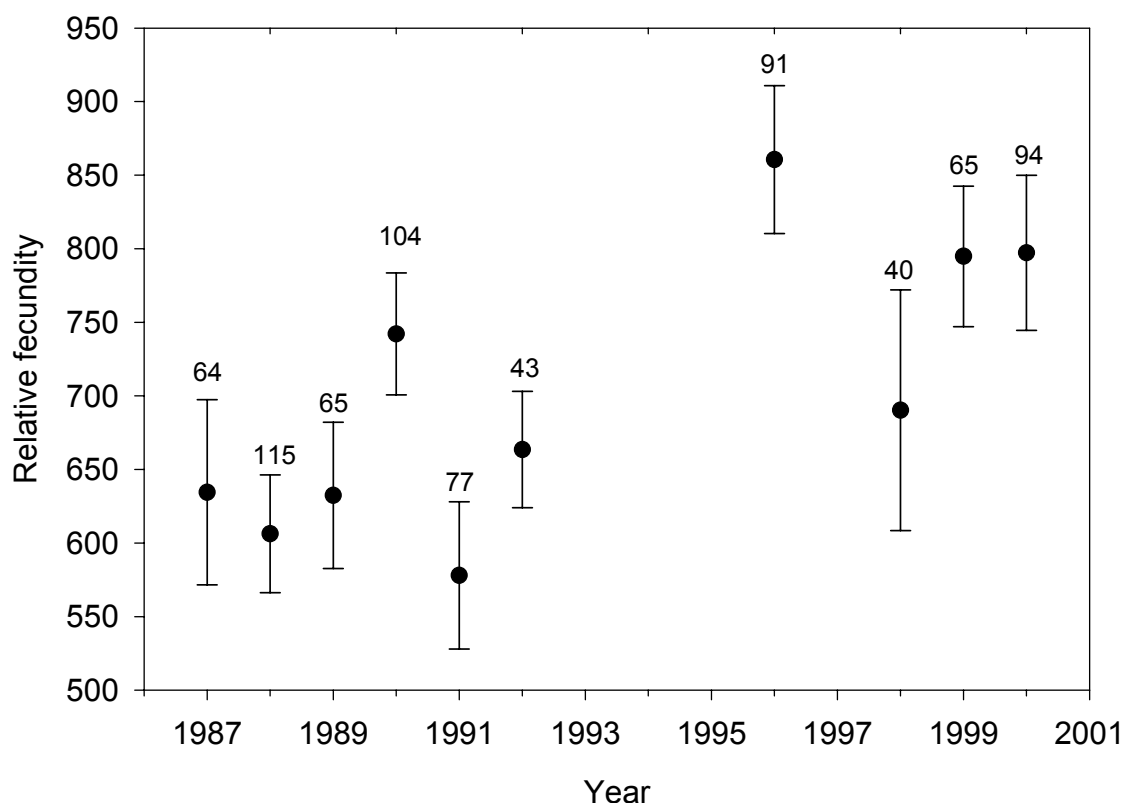


Figure 4: Annual averages of relative fecundity (based on total body weight) in ICES Subdivision 25. The vertical lines give an approximation of the 95% confidence limits of Tukey's HSD-test for unequal sample sizes, numbers represent sample sizes.

The ANCOVA for the log length adjusted log potential fecundities showed also highly significant differences between years ($n = 758$; ANCOVA $p > 0.001$). Thereby, the ANCOVA assumption of homogenous variances of variable and co-variable was severely violated (Hartley's F-max test: $p < 0.05$; Levenne test: $p < 0.05$). As severe misinterpretation of the results would mainly occur, if trends in the magnitude of the variances are correlated to trends in the means, variances were regressed against group means. No significant correlation was observed within this test. However, the post hoc test subsequent to the ANCOVA showed some differences compared to the ANOVA of relative fecundities with the differences between years being more pronounced (Table 5). Corresponding to the analysis of relative fecundity, in 1988 and 1991 the log potential fecundities adjusted for log

fish length were lowest, and showed in 1996 the highest values. In contrast to the relative fecundity, for 1999 and 2000 relatively low length adjusted fecundities were revealed, while for 1990 and 1992 values were comparatively high (Table 5). The magnitude of differences in fecundity values were, nevertheless, the same in both analyses and amounted to 33% between 1988 and 1996 in this analysis.

Table 5: Probability values for Tukey's HSD test for unequal sample sizes for inter-annual comparisons of log potential fecundity with log total length as covariate and common logarithms of length adjusted mean potential fecundity for each sampling year.

Year	1987	1988	1989	1990	1991	1992	1996	1998	1999	2000
Log fecundity	6,06	5,75	5,89	6,18	5,97	6,19	6,23	6,00	5,97	6,04
1987		<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0014</u>	<u>0,0002</u>	<u>0,0000</u>	0,4493	<u>0,0026</u>	0,9665
1988			<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>
1989				<u>0,0000</u>	<u>0,0348</u>	<u>0,0000</u>	<u>0,0000</u>	<u>0,0100</u>	<u>0,0207</u>	<u>0,0000</u>
1990					<u>0,0000</u>	1,0000	0,3148	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>
1991						<u>0,0000</u>	<u>0,0000</u>	0,9874	1,0000	<u>0,0451</u>
1992							0,9753	<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>
1996								<u>0,0000</u>	<u>0,0000</u>	<u>0,0000</u>
1998									0,9948	0,9672
1999										0,1431

3.1.4 Spatial variability in fecundity

The log potential fecundities of cod in the Gdansk Deep and the Bornholm Basin (Polish data set) adjusted for log total weight were compared for 1995 and 1996. ANCOVA results were highly significant ($n = 248$; ANCOVA $p < 0.001$). No significant deviations were observed between the two spawning grounds within a year (Table 6). Significant differences were only detected between years. Length adjusted fecundity comparisons corresponded to the results of the weight adjusted analyses, significant differences were also detected between the two years, but not between the spawning grounds within a year (Table 6). As for both analysis all assumptions of ANCOVA were met and the results unequivocal, data from different areas of the Central Baltic Sea have been applied to establish a time series of observed relative fecundity (ORF, see below).

Table 6: Probability values of Tukey's HSD test for unequal sample sizes for spatial comparisons of log potential fecundities with log total weight or log total length as covariates.

Year / Area	1996 BB		1995 GD		1996 GD	
	W	L	W	L	W	L
1995 BB	<u>0,0001</u>	<u>0,0001</u>	0,9128	0,9110	<u>0,0000</u>	<u>0,0000</u>
1996 BB			<u>0,0000</u>	<u>0,0000</u>	0,3086	0,3019
1995 GD					<u>0,0000</u>	<u>0,0000</u>

Note: BB: Bornholm Basin, GD: Gdansk Deep, W: natural log of total body weight as covariate, L: natural log of total length as covariate.

3.1.5 Explaining variation in fecundity

Figure 5 shows the time trend of ambient water temperatures, the prey availability index, growth anomaly and the average annual condition factor of all females used for fecundity analysis. A multiple linear regression of log transformed potential fecundity as dependent variable and log length, individual condition and ambient water temperature as predictor variables showed that the explained variance in fecundity is dominated by the length (80%). Stepwise inclusion of condition and water temperature yielded 82% and 83% explained variance, respectively. Neither the condition at sampling time nor the ambient water temperatures during the feeding period preceding the investigated spawning season explained a substantial amount of the variability in fecundity, although both factors were significant.

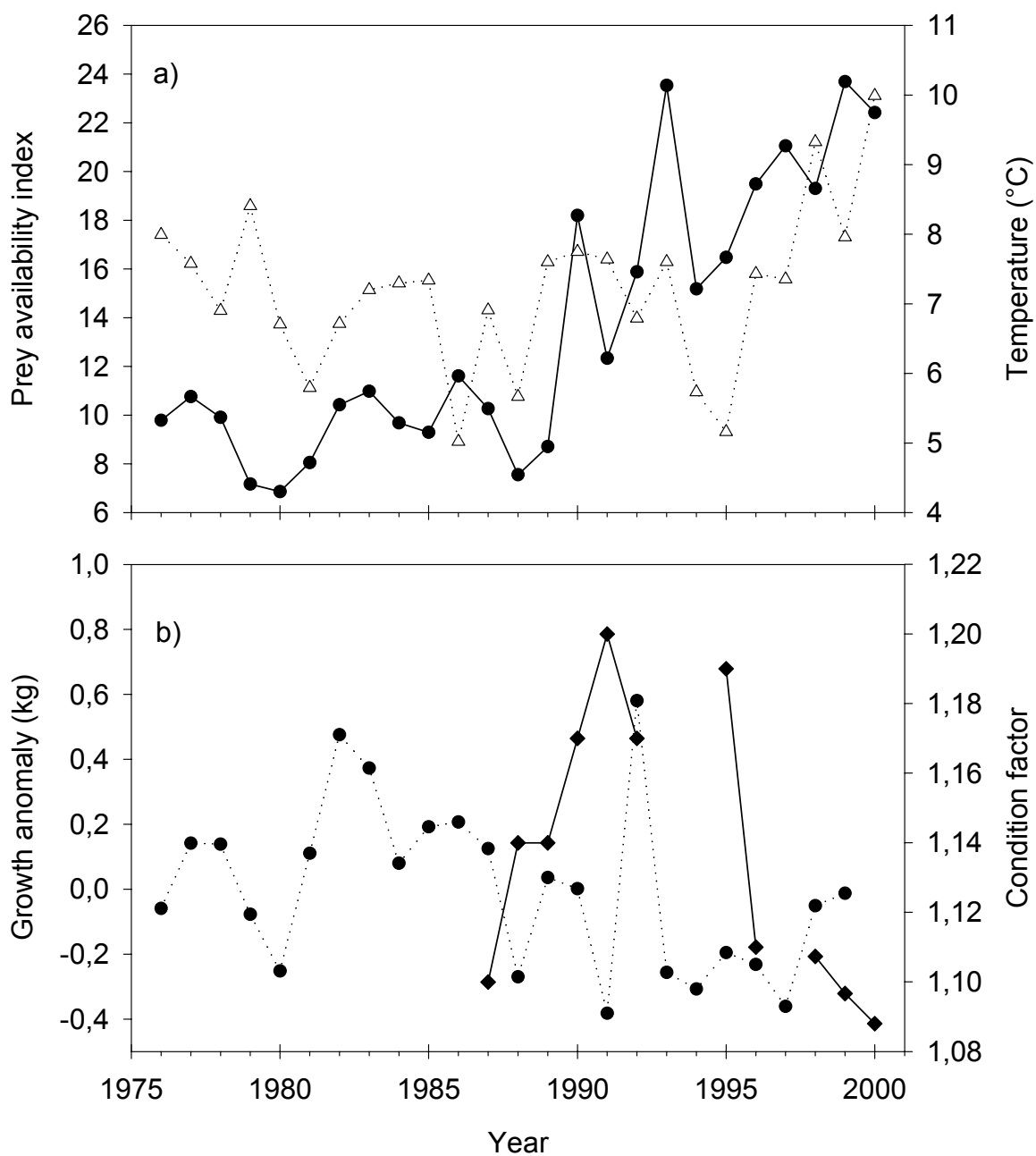


Figure 5: (a) Temporal development of the prey availability index (●), ambient water temperature (Δ), as well as (b) condition (◆) and growth anomaly (●) throughout the covered time period 1976 - 2000. Condition is presented as annual averages of Fulton's condition factor. The full definitions of the prey availability index, growth anomaly and ambient water temperature are given in the text (section 2.1.4).

In contrast to the above, the second analysis was based on annual average relative fecundities of the Bornholm Basin subset of data. Here, a positive highly significant relationship was established between relative fecundity and the prey

availability index using an exponential 2 parameter curve fit ($r^2 = 0.72$; $p = 0.01$; Figure 6). The best fit between water temperature and fecundity was parabolic ($r^2 = 0.21$; $p = 0.18$) with the highest relative fecundities occurring at intermediate water temperatures. This relationship was, however, insignificant ($\alpha = 0.05$), though a significant linear interaction between prey index and water temperature was detected ($r^2 = 0.31$; $p = 0.047$). Similar to water temperature, growth anomaly did not explain a considerable amount of variation in relative fecundity, neither as a single variable nor in a combined model. Consequently, growth anomaly and water temperature were excluded from the prediction model and the above described exponential model was used to establish the time series of PRF:

$$PRF_y = \exp(6.23 + 0.02 * P_{iy})$$

where PRF_y is the annual average relative fecundity and P_{iy} the corresponding prey availability index of year y . The residuals of the model were normally distributed (Kolmogorov-Smirnov test $p > 0.2$) and reflected the ORF including the independent fecundity data from Shapiro (1988) and Bleil and Oeberst (1996) quite well. Except for two years (1978 and 1983), all relative fecundity values estimated by Shapiro (1988) for Eastern Baltic cod in 1976 - 1978, 1983 and 1984 and Bleil and Oeberst (1996) for cod from Sub-division 25 in 1994 and 1995 fell within the prediction limits of above relationship (Figure 6).

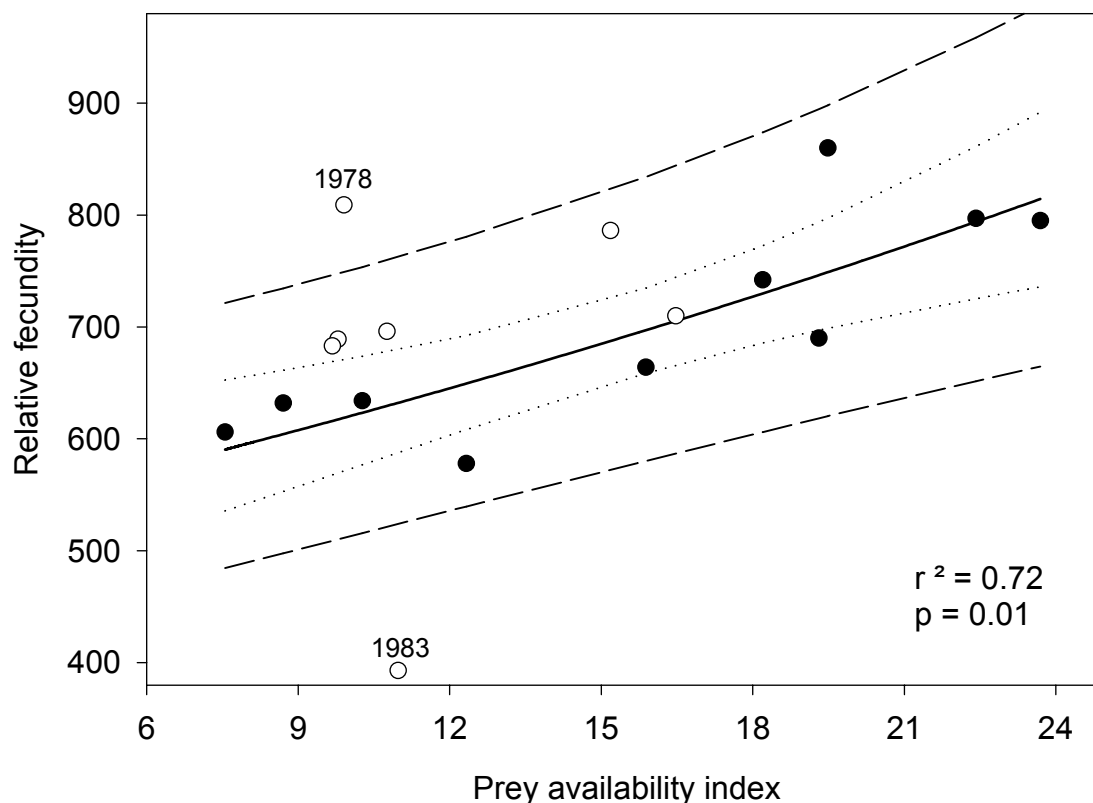


Figure 6: Relative fecundity in relation to the prey availability index, P_i (sprat + herring age 0-2 biomass per unit of mature cod), in ICES Subdivision 25. Dots (●) represent data used to fit the model and circles (○) data from Shapiro (1988) and Bleil and Oeberst (1996). The solid line represents the 2 parameter exponential model curve, the dotted lines the 95% confidence limits and the dashed lines the prediction limits.

The time series of ORF ranged from 383 oocytes per gram body weight in 1983 to 860 in 1996, while the highest value in the PRF series of 813 was detected in 1999 and the lowest value of 582 in 1980 (Figure 7). A significant positive correlation ($r = 0.55$; $p < 0.05$) was revealed between both data sets showing a maximum difference in 1983 with the PRF being 61% higher than ORF (Figure 7), but with an even larger variation between subsequent years in the ORF. A similar pattern is observed for 1978, but less pronounced.

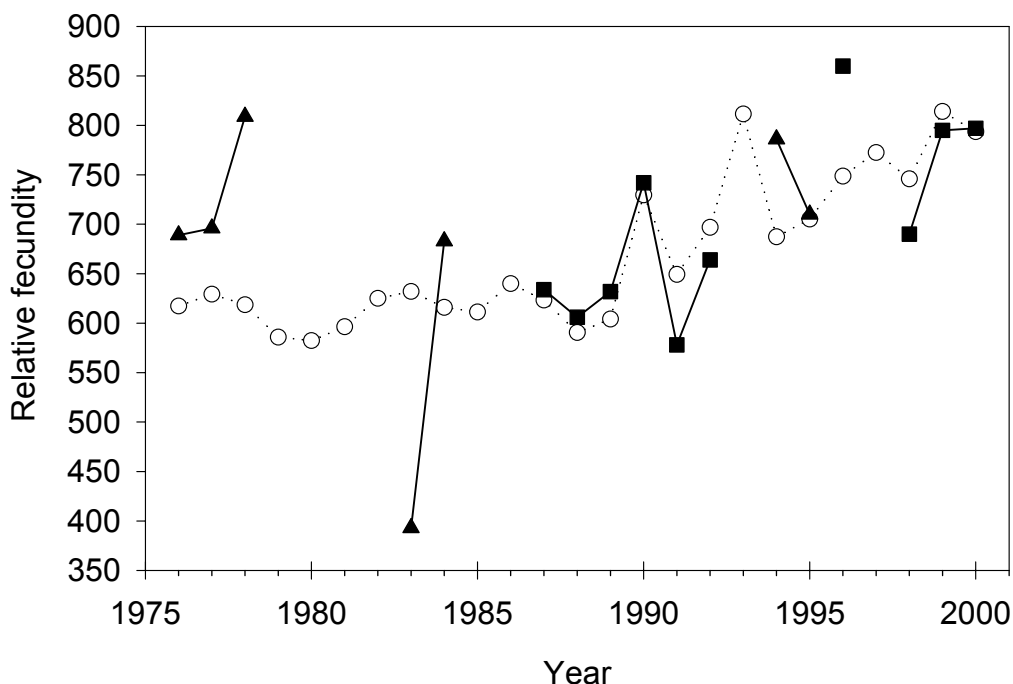


Figure 7: Observed and predicted average relative fecundity in relation to time (ORF: ■ Data from own investigations and ▲ data from Shapiro (1988) and Bleil and Oeberst (1996); PRF: ○ predicted from fecundity model).

3.2 Population egg production

3.2.1 Temporal development of female spawning stock biomass and potential egg production

The FSSB estimates for ICES Subdivision 25 for the period 1976 to 1999 are shown in Figure 8a together with the time series of PEP based on PRF and ORF, respectively. The FSSB and PEP reflect the general stock development with a historic maximum in the early 1980s followed by a pronounced decline from mid 1980s to late 1990s and an intermediate peak in the mid 1990s. The PEP (PRF) ranged from 0.75×10^{13} to 4.41×10^{13} , while PEP (ORF) varied between 0.69×10^{13} and 4.26×10^{13} . The time series showed a good agreement except for the years 1978 and 1983. The deviation corresponds to extreme observed relative

fecundities in these years, which are reflected in the PEP (ORF) series (see section 3.1.5).

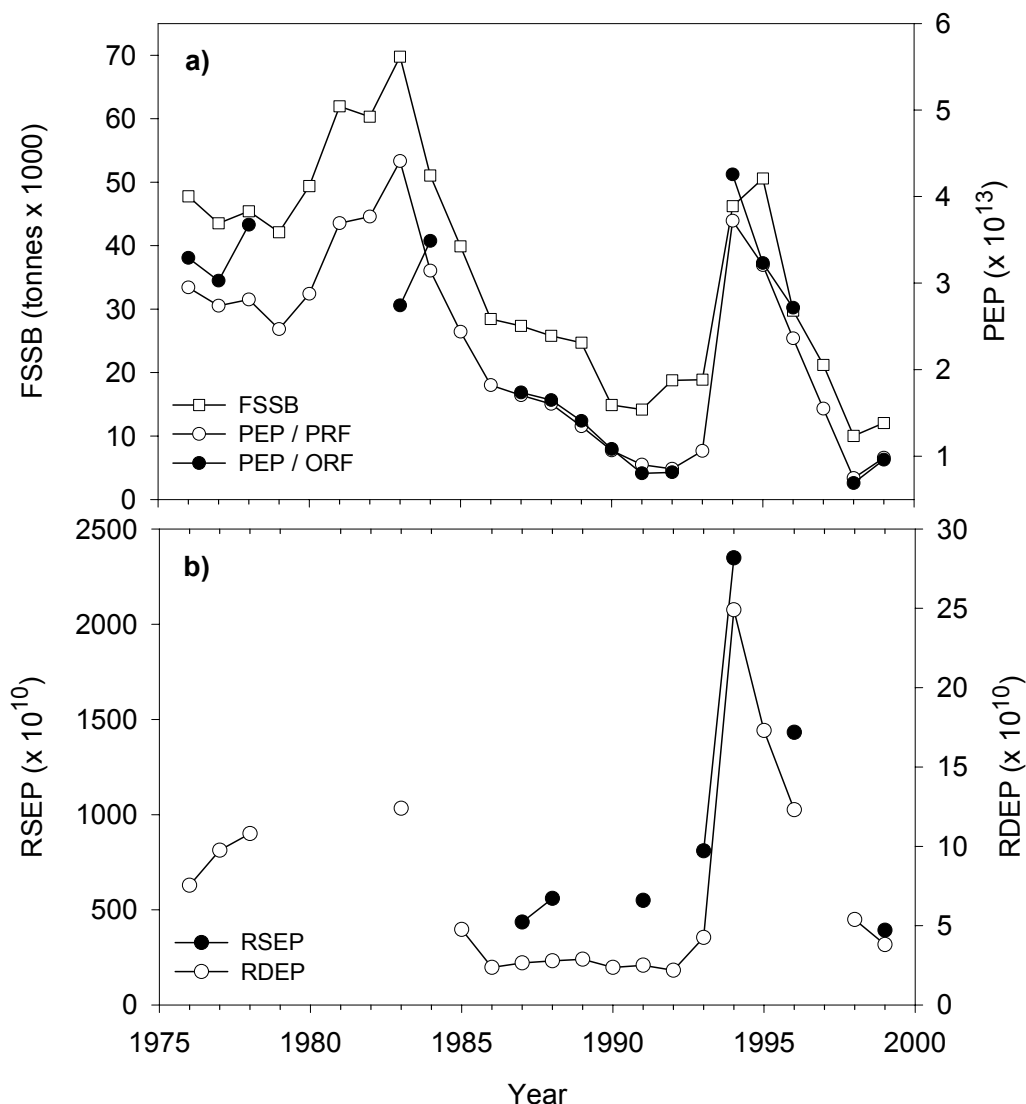


Figure 8: (a) Time series of female spawning stock biomass (FSSB) and potential egg production estimates based on two different fecundity series (PEP (ORF) and PEP (PRF)), as well as (b) realised daily egg production (RDEP) and realised seasonal egg production (RSEP) in ICES Subdivision 25.

3.2.2 Realised egg production

The estimates of RDEP during main spawning time ranged from a minimum of 2.19×10^{10} in 1992 to a maximum 24.9×10^{10} in 1994 (Figure 8b). The pronounced differences in the level of RDEP with low estimates in 1987 and 1999

and a high estimate in 1994 were reflected well by the RSEP with the latter being on average two orders of magnitude higher than daily production values. The underlying relationships to estimate the RSEP were significant ($\alpha = 0.05$) for all included years (Figure 9), with relatively large proportions of the observed variation being explained by the fitted curves ($r^2 = 0.83$ in 1999 to 0.98 in 1996). The correlation between RDEP and RSEP was also highly significant ($r = 0.98$; $p < 0.001$). The RDEP was, therefore, considered a reliable index of the RSEP and used as an extended data series to be compared to time series of PEP.

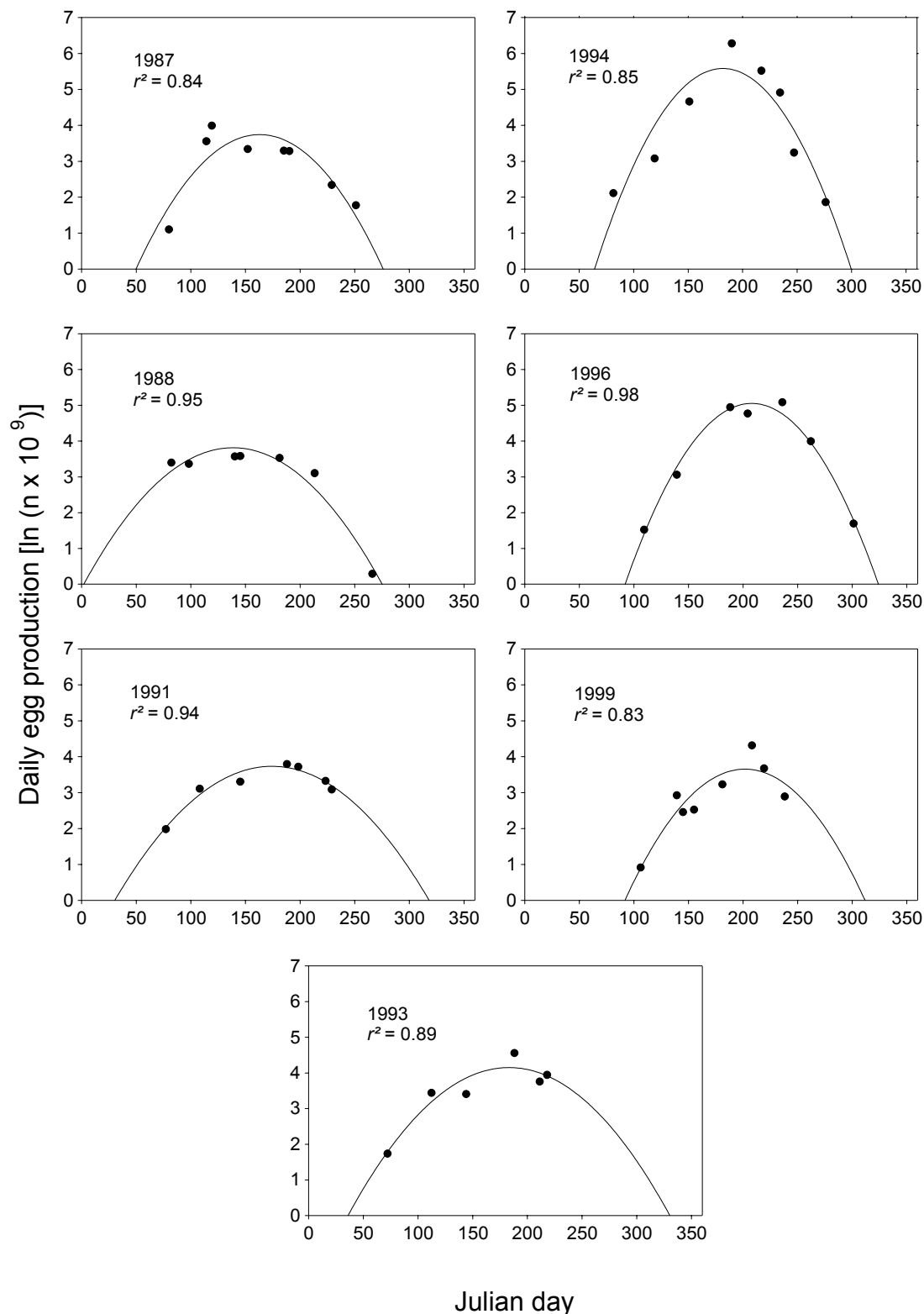


Figure 9: Daily production of youngest egg stage (IA) transformed to natural logarithms over Julian day in different years. The symbols represent the date specific production estimates and the curves second order polynomials fitted to data. The realised seasonal egg production (RSEP) is determined from the area under the curve.

3.2.3 The influence of sex ratio, maturity and fecundity on relationships between potential and realised egg production

The variability of the RDEP and RSEP corresponded well with the variation in the FSSB and both PEP time series (PRF / ORF). FSSB explained 51% of the RDEP, PEP 62% when based on PRF and 72% when based on ORF (Figures 10a, c, e). Applying RSEP instead of RDEP in these relationships resulted in higher coefficients of determination, but due to the reduced degrees of freedom the significance of RSEP relationships were comparatively low. The pattern was however similar for both, RDEP and RSEP. The application of the PEP (ORF) as index of the potential egg production explained the highest proportion of the variability in the RSEP (91%). The use of FSSB in the relationship explained least of the variation (74%), while the coefficient related to PEP (PRF) was at an intermediate level (85%) (Figures 10b, d, f).

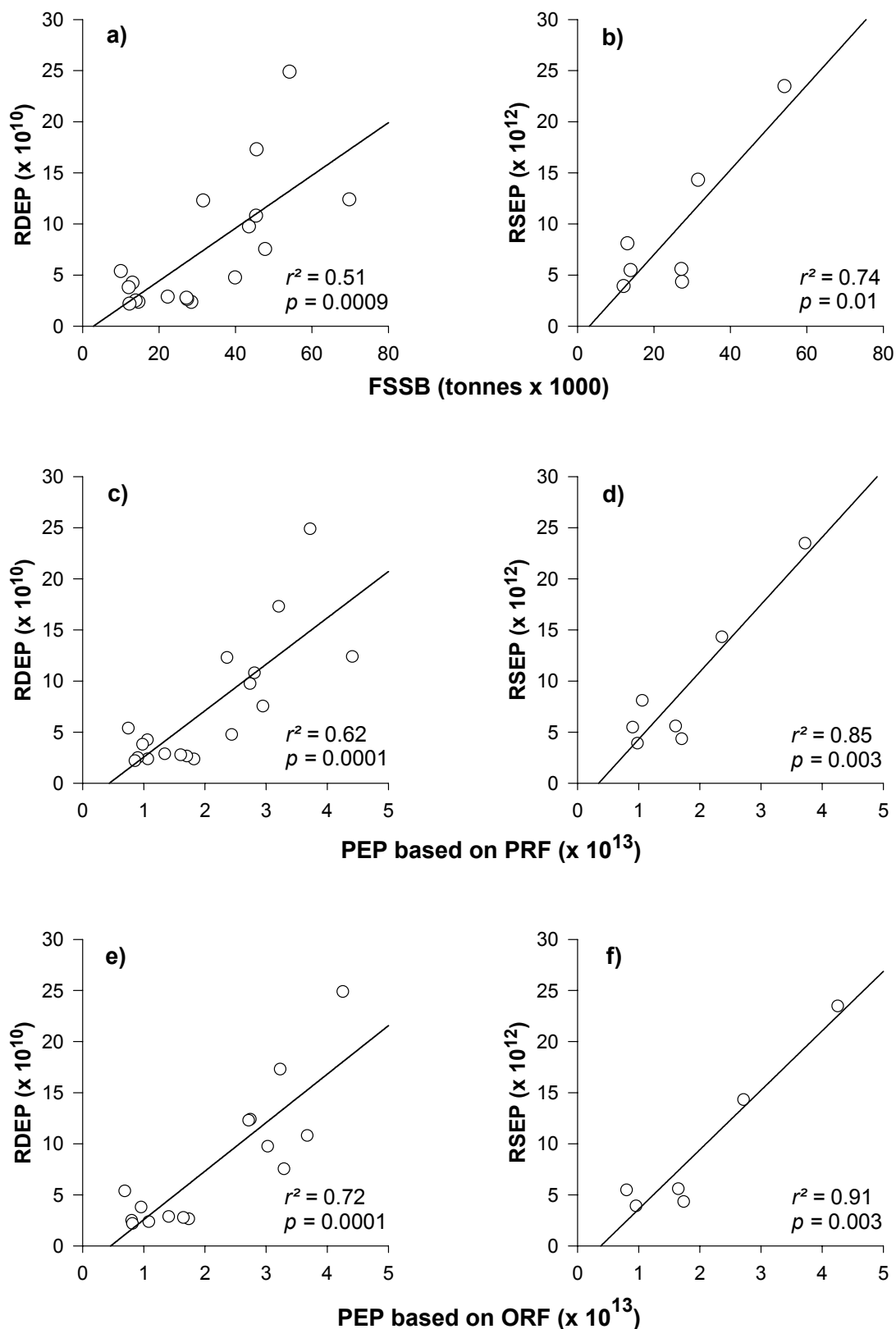


Figure 10: Relationships between the realised egg production (RDEP and RSEP) and different indices of the reproductive potential, as well as explained variation and significance levels for linear regressions. The RDEP and RSEP are plotted versus (a) and (b) FSSB; (c) and (d) PEP based on PRF; (e) and (f) PEP based on ORF.

Removal of the variability in sex ratio, maturity and relative fecundity from PEP deteriorated the relationships to the realised egg production (Figure 11). The coefficients of determination of the linear relationships between the three manipulated PEP series and the RDEP as well as RSEP were substantially lower than coefficients of the corresponding relationships with the un-manipulated PEP (ORF) time series (Table 7). The highest impact on the relationship with the RDEP and RSEP was observed when removing the temporal variability in female maturity. The application of a constant maturity ogive reduced the r^2 by 34% for RDEP and by 44% for RSEP, the latter with a loss of significance ($\alpha = 0.05$). Keeping the relative fecundity constant, reduced the per cent explained variation by 17% and 10% for RDEP and RSEP, respectively, while constant sex ratios resulted in a reduction of 5% in the explained variation for both relationships.

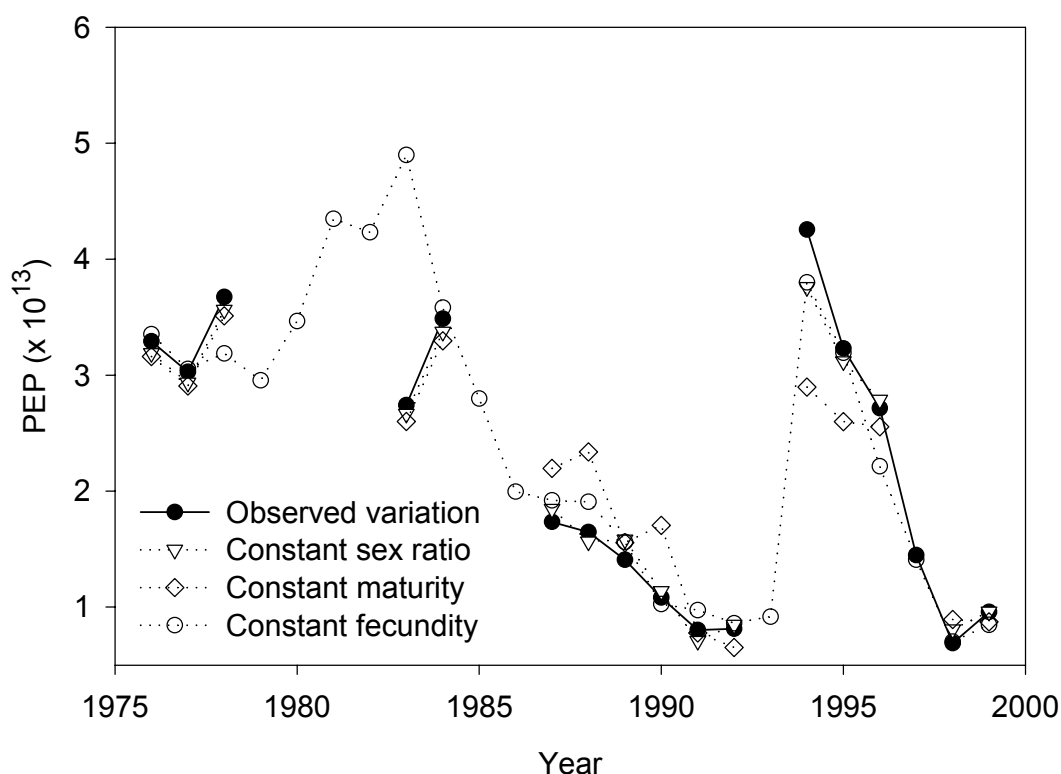


Figure 11: Time series of potential egg production (PEP) with constant sex ratio, maturity ogive and fecundity in comparison to the PEP (ORF) series. For constant sex ratio and maturity the age specific means of the time series were applied, while for constant fecundity the long term average relative fecundity was used.

Table 7: Coefficients of determination and corresponding probability values for relationships of potential egg production (PEP) with constant maturity, fecundity and sex ratio versus realised daily (RDEP) and seasonal egg production (RSEP). In addition reference relationships of PEP (ORF) versus RDEP and RSEP are given.

PEP		RDEP	RSEP
Observed data	r^2	0.72	0.91
	p	< 0.001	< 0.005
Constant maturity ogive	r^2	0.38	0.47
	p	< 0.05	0.13
Constant relative fecundity	r^2	0.55	0.81
	p	< 0.005	< 0.05
Constant sex ratio	r^2	0.67	0.86
	p	< 0.001	< 0.01

The difference between PEP (ORF) and RSEP was estimated as an index for the loss of eggs from the final maturation stage (at which fecundity is analysed) to earliest embryonic phase (egg stage IA) using two different approaches. The ratio between RSEP and PEP (ORF) was on average 0.46 corresponding to an egg loss of 54%. Determining the loss from the slope of the regression between RSEP and PEP (ORF) (Fig. 10f) resulted in a reduction of potential fecundity of 58 %. As the intercept of the relationship was not significantly different from zero ($p = 0.16$), it was set equal to zero resulting in an egg loss due to atresia, fertilisation failure and early egg mortality of 50% ($RSEP = 0.5 * PEP (ORF)$).

3.3 Atresia

3.3.1 Morphology of atresia

A first visible sign of atresia for all oocyte stages occurred in the zona pellucida, which became pitted, thickened and showed a wavy outline (Figure 12a). Later, the zona pellucida broke down and shrank towards the centre of the structure in cortical alveoli (Figure 12b) and vitellogenic oocytes (Figure 12c, d), while the breakdown in final maturation and hydrated oocytes was often hampered (Figure 12e-g). Atretic oocytes of this type often occurred as an extremely folded structure in the centre of the atretic follicle (Figure 12g). As atresia progressed, follicle cells got hypertrophied (Figure 11f, h) and the disorganised ooplasm of previtellogenic, cortical alveoli (Figure 12, i) and vitellogenic (Figure 12 d) oocytes appeared as a homogenous esinophilic area. At late alpha atretic phases the resorption of the yolk was completed and the atretic follicle could hardly be distinguished from degenerating empty follicles (Figure 12f).

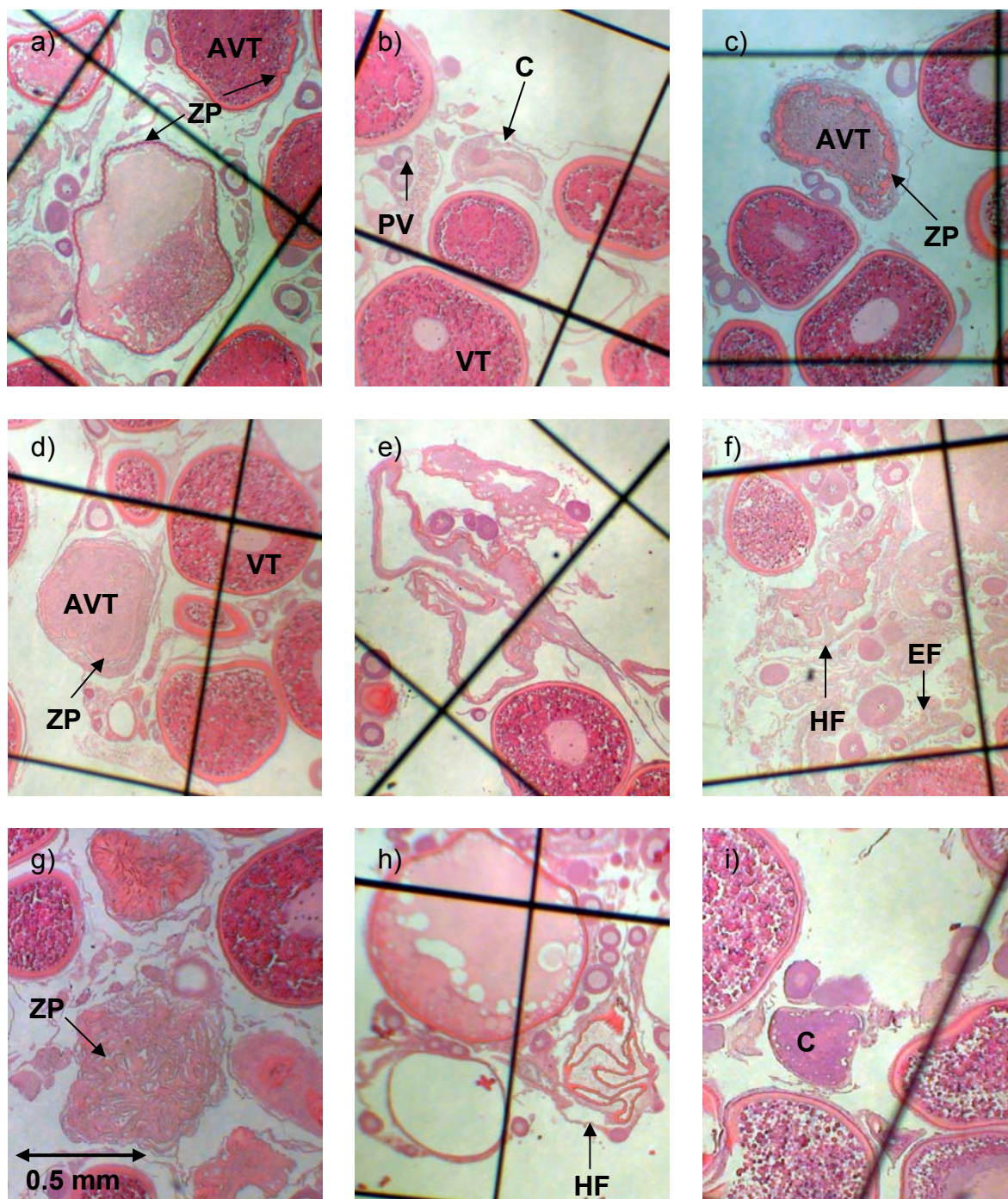


Figure 12: Different types of atretic and normally developing oocytes: (a) First signs of atresia in early hydration (AHY) and vitellogenic oocytes (AVT) with pitted, wavy zona pellucida (ZP); break down and shrinking ZP in cortical alveoli (CA) (b) and vitellogenic oocytes (c,d), as well as atretic phases in hydrated oocytes from beginning to early encapsulation (e-g). Hypertrophied follicle cells (HF) (f, h) and homogenous eosinophilic staining in CA (i) and vitellogenic oocytes (d) characterise the progress of atresia. Additionally, normally developing pre-vitellogenic (PVT), vitellogenic (VT) and early hydration (HY) oocytes as well as empty follicles (EF) are indicated (b, c, f, h).

3.3.2 Prevalence and intensity of atresia

The prevalence of atresia (P_a) did not differ significantly between the five fish size categories ($\chi^2 p > 0.05$; Table 8), although the largest P_a 's were observed for females larger than 50 cm within most maturity stages. Exceptions from this pattern were detected for stage 4, where the highest proportion of individuals with atresia (50%) were found in the size class of 31 to 40 cm (but based on two samples only) and for stage 2, where the largest present size category was 41-50 cm. In the latter stage, atretic oocytes were observed only for fish from 31 to 40 cm with P_a at an extremely low level (Table 8). No atresia was observed in maturity stage 1 and 100% of stage 8 ovaries contained atretic oocytes. Excluding maturity stages 1 to 3 from the analysis, i.e., maturity stages not relevant for the determination of the atretic loss of eggs between potential and realised fecundity, revealed the same picture; P_a did not differ between length categories ($\chi^2 p > 0.05$).

Table 8: Prevalence (as proportions from one) of individuals with alpha atretic oocytes (P_a) in length categories and maturity stages as well as corresponding sample sizes (n).

Length (cm)	Maturity stage															
	1		2		3		4		5		6		7		8	
	n	P_a	n	P_a	n	P_a	n	P_a	n	P_a	n	P_a	n	P_a	n	P_a
<= 30	5	0	4	0	2	0	1	0	0	0	0	0	0	0	4	1,00
31 - 40	6	0	11	0,09	11	0,09	2	0,50	10	0,10	11	0,36	10	0,70	1	1,00
41 - 50	2	0	2	0	19	0,16	42	0,21	35	0,23	27	0,33	35	0,37	1	1,00
51 - 60	0		0		4	0	17	0,24	10	0,40	4	0,50	8	0,38	1	1,00
> 60	0		0		0		2	0	8	0,50	5	0,40	7	0,71	0	

In contrast to length, P_a combined for all length categories showed highly significant differences between maturity stages ($\chi^2 p < 0.001$) with increasing values of P_a as maturity progressed. Within length categories, this trend was visible in all four length categories, but most pronounced and continuous for 41 to 50 cm fish, the group which contained also the largest numbers of samples (Table 8). The exclusion of stage 1 to 3 females from the analysis again did not change

the picture with significant differences between maturity stages (χ^2 $p < 0.001$) and increasing P_a values in later maturity stages.

Fulton's condition factor was significantly lower for females with atresia than for individuals without atresia (t-test $p < 0.001$) with average K 's of 0.86 and 0.94, respectively. However, K was also related to maturity stage (Figure 13) and differences in condition between stages were significant (ANOVA $p < 0.001$). Thus, differences in K between fish with and without atresia were tested separately for each maturity stage (excluding stages 1 and 8, where P_a was zero and one, respectively). For maturity stages 2 to 5 no significant differences in K were found (all t-test $p > 0.05$), while for the later stages 6 and 7 tests revealed significantly lower values for individuals with atresia (t-test $p = 0.02$ and 0.04 , respectively). In stage 8, where all females had atretic ovaries, the lowest condition factor was observed (Figure 13).

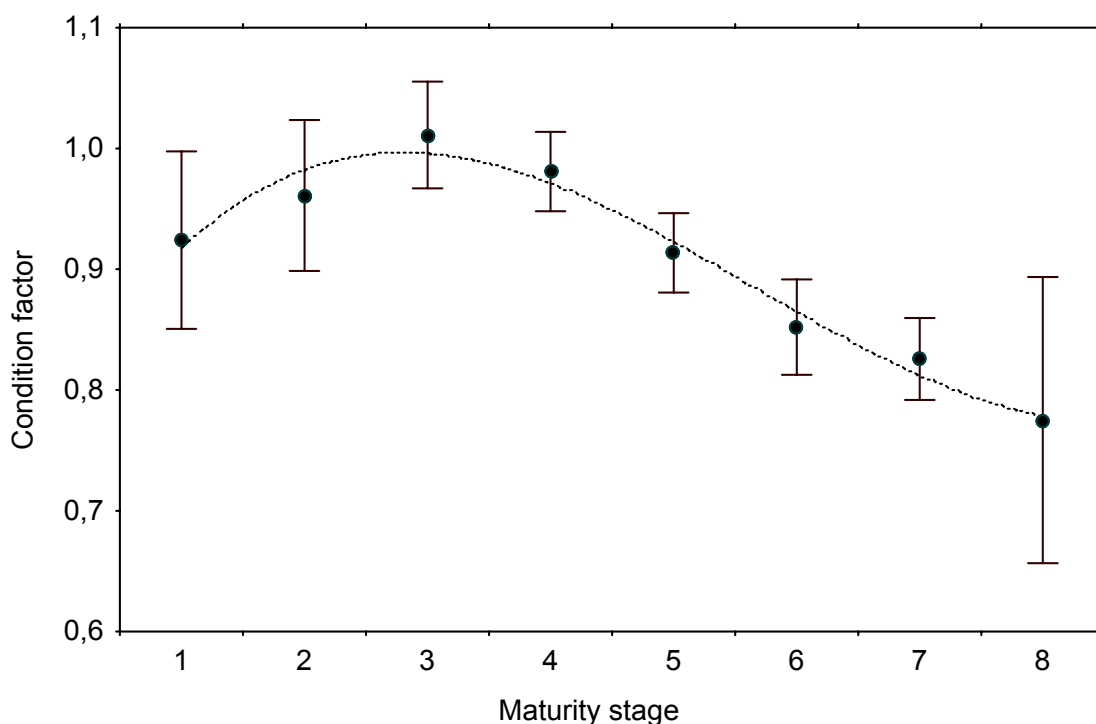


Figure 13: Averages of Fulton's condition factor (K) in relation to maturity stages and a fitted 3rd order polynomial curve. Bars indicate significance levels for Tukey's honest significant difference test for unequal sample sizes.

The liver index (HSI) was in contrast to Fulton's condition factor not significantly different between atretic and non-atretic specimens (t – test $p = 0.41$), but varied similar to K significantly with maturity stages (ANOVA $p < 0.001$; Figure 14). Separate tests for maturity stages (excluding stages 1 and 8, where P_a was zero and one, respectively) did not reveal significant differences in HSI in any of the stages included (all t -tests $p > 0.05$). Corresponding to Fulton's K , in stage 8 the lowest average HSI value was observed (Figure 14). However, a low reliability of the average is indicated by the small sample size and comparatively large variance in HSI values in stage 8.

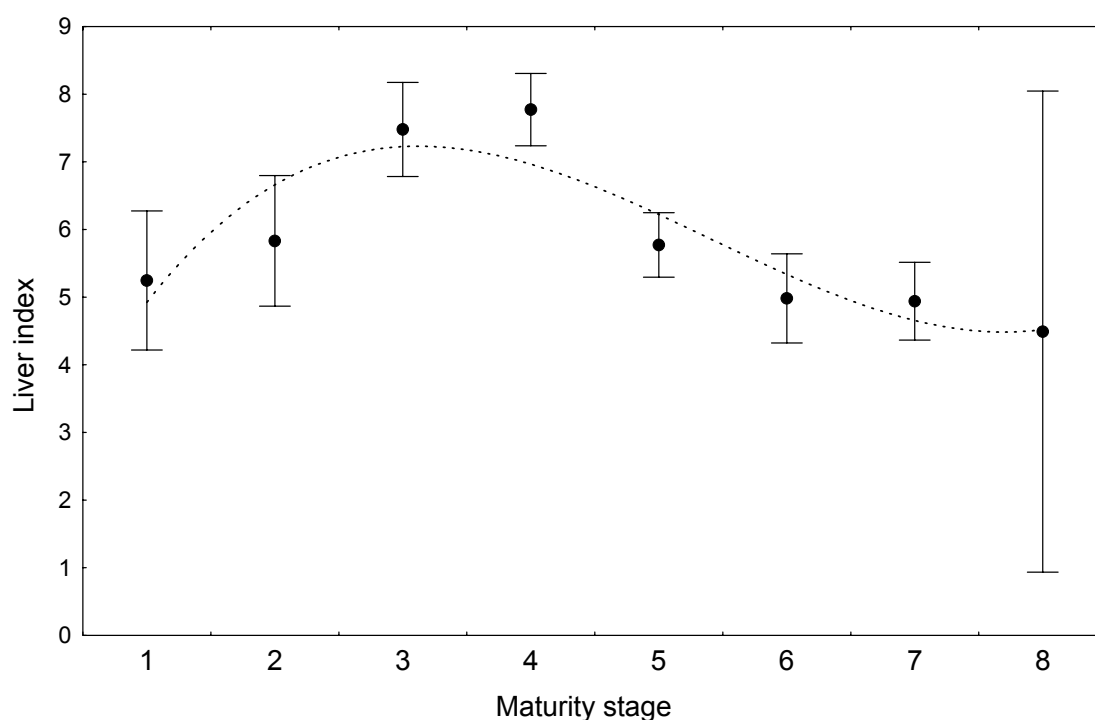


Figure 14: Average liver index (HSI) in relation to maturity stages and a fitted 3rd order polynomial curve. Bars indicate significance levels for Tukey's honest significant difference test for unequal sample sizes.

In contrast to prevalence, the total (I_a) and relative intensities of atresia (RI_a) excluding the specimens without atresia did not differ significantly between maturity stages 2 to 8 (Kruskal - Wallis H-tests $p = 0.21$ and 0.32 ; Figure 15). When restricting the same analysis to stages 4 to 8 (see above) the significance level further decreased in both cases (Kruskal - Wallis H-test $p = 0.66$ and 0.45).

Consequently, varying maturity stages were not considered in the following analysis.

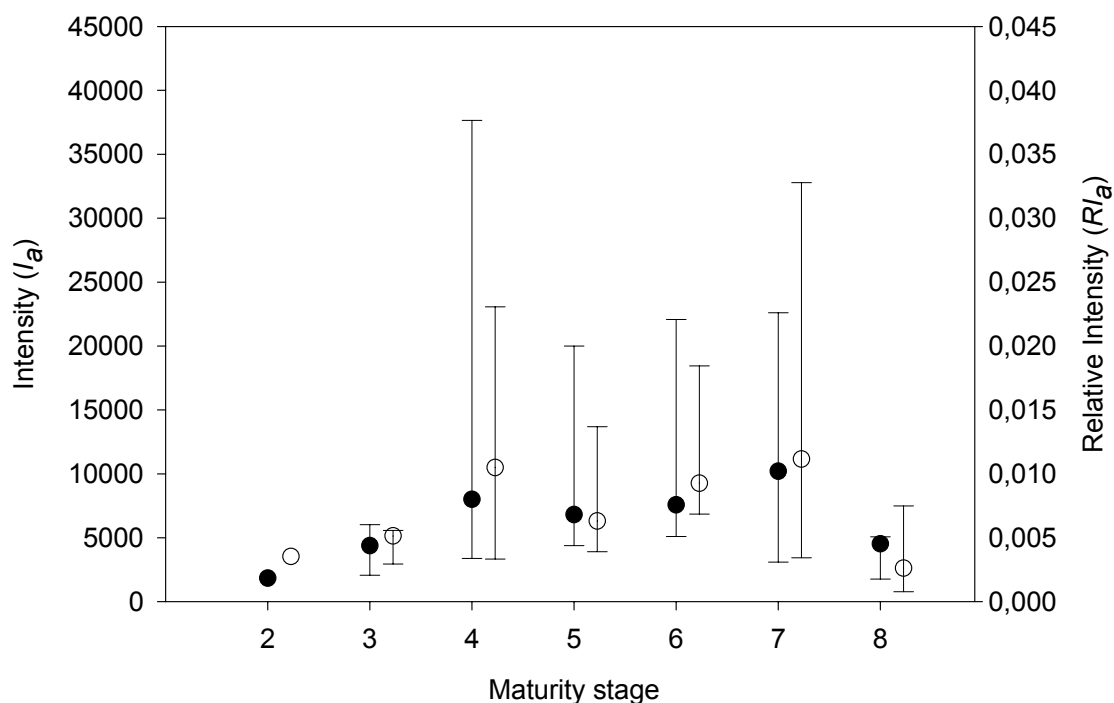


Figure 15: Total (I_a) and relative (RI_a) intensities of atresia according to maturity stage. Dots (●) represent the medians of I_a , and circles (○) medians of RI_a ; the bars indicate the 25% and 75% percentiles.

For an exploratory correlation analysis of total and relative intensity of atresia (Figure 16), both variables were transformed to natural logarithms. Major deviations from normal distribution were neither revealed for $\text{Log } I_a$ nor for $\text{Log } RI_a$ (Kolmogorov – Smirnov test $0.05 < p < 0.1$ and $p > 0.2$, respectively), whereas for fish length as well as weight even after logarithmic transformation severe deviations from normal distribution were observed (Kolmogorov – Smirnov test $p < 0.01$). Fulton's condition factor (K) and liver index (HSI), of which the former has been shown to differ between females with and without atresia, were normally distributed (Kolmogorov–Smirnov test $p > 0.2$) and could be used without transformation in the correlation analysis.

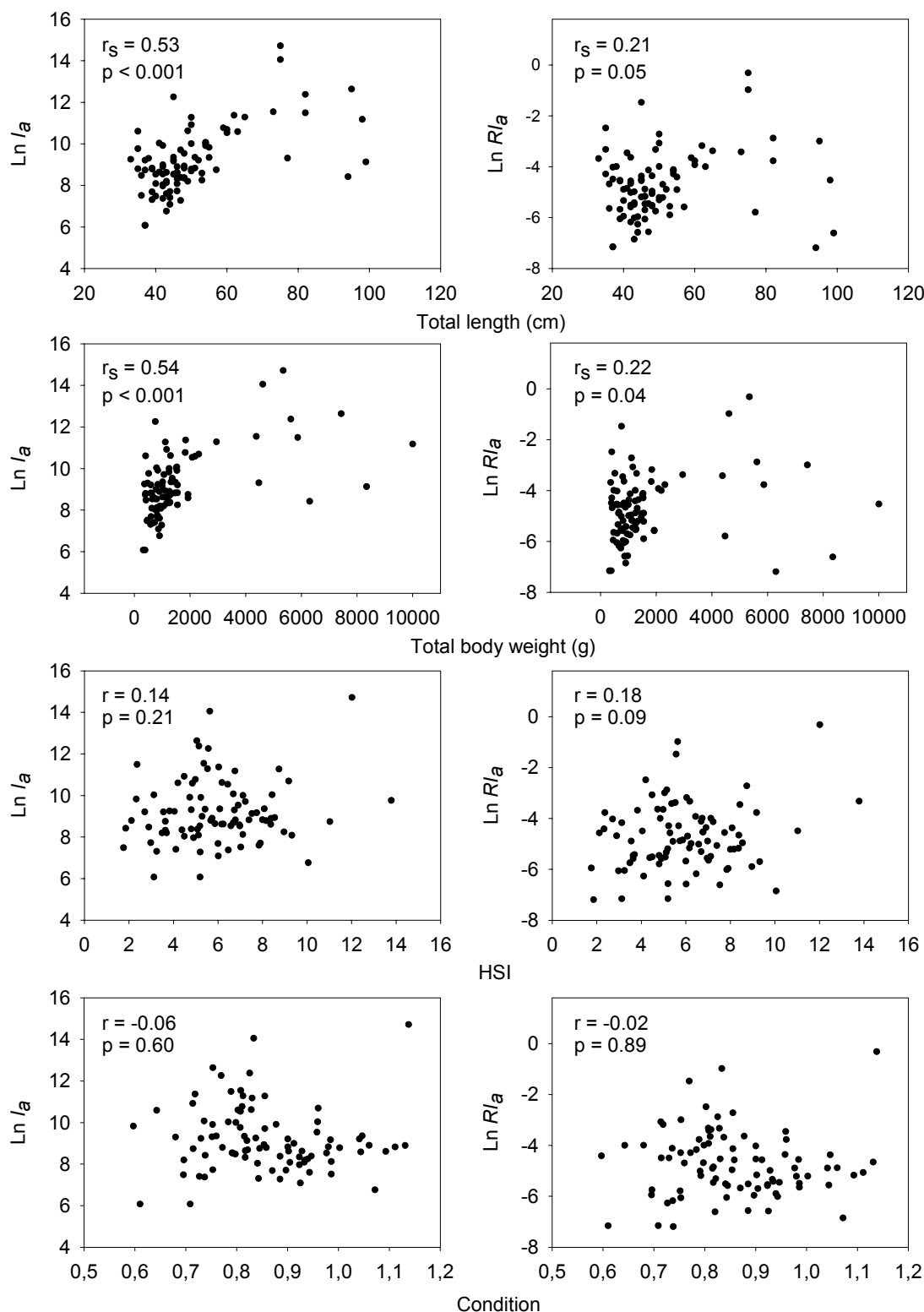


Figure 16: Total (I_a) and relative ($R I_a$) intensity of atresia in relation to fish length, weight, liver index (HSI) and Fulton's condition factor (K). For total fish length and weight Spearman's rank correlation coefficients (r_s) are given, while for condition and HSI Pearson's product moment coefficients (r) are displayed with corresponding probability values.

Highly significant correlations between the log transformed intensities of atresia and fish length and weight were found by rank correlation analysis (Figure 16), which was also to be expected as an effect of larger ovary sizes of larger compared to smaller fish. In contrast, the log transformed relative intensities of atresia were independent of length and rank correlation with fish weight was only weak ($p = 0.04$). RI_a was, thus, considered to be independent of fish size (Figure 16). Similarly, both measures of condition, i.e., the HSI and Fulton's K, were unrelated to fish size (Spearman rank correlation, K: r_s (length) = -0.09, $p = 0.40$; r_s (weight) = 0.07, $p = 0.52$; HSI: r_s (length) = 0.02, $p = 0.86$; r_s (weight) = 0.08, $p = 0.45$). A negative correlation coefficient between either I_a or RI_a and K was found, while for HSI positive coefficients were detected. The association between both indices of nutritional condition with atresia was, nevertheless, insignificant (Figure 16).

For a limited number of females, i.e. those in maturity stage 4, data on potential fecundity were available in addition to atresia estimates (see section 2.1). A tendency towards higher RI_a values in specimens with lower fecundity values than predicted by the annual fecundity - weight or length relationship (section 3.1.1) was observed (Figure 17). This negative trend was more pronounced for the fecundity - weight residuals ($p = 0.08$) than for the fecundity - length residuals ($p = 0.14$). However, both relationships were not significant at the 95% confidence level.

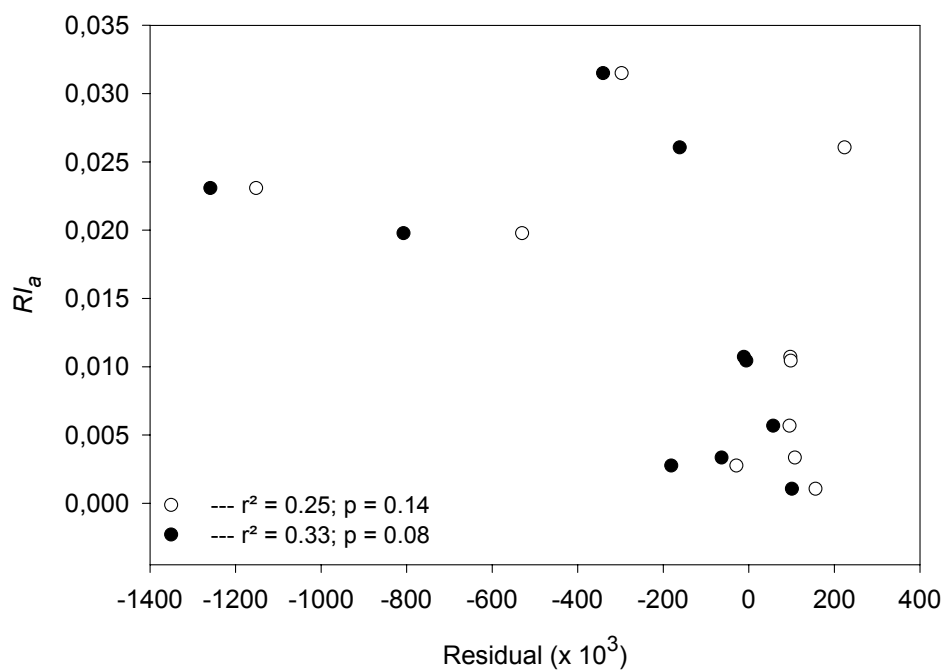


Figure 17: Residuals of the fecundity – length and weight relationships versus the relative intensity of atresia (RI_a) of the same females. Dots (●) represent the residuals of the fecundity – weight relationship and circles (○) of the fecundity - length relationship.

4 Discussion

4.1 Fecundity

In determinate batch spawning fish species such as cod, the number of developing oocytes is fixed well before spawning is initiated and assumed to represent the number of eggs to be spawned in a given season (e.g. Kjesbu et al 1990). An estimate of the individual annual egg production could, thus, easily be obtained by counting the number of developing oocytes prior to spawning. However, environmental conditions and nutritional status are known to potentially have strong modifying influences on fecundity. Inter-individual, inter-annual and geographical variation in fecundity might all be indications of genetic and environmental effects on fecundity (Wootton, 1979). Various factors that reflect the level of an individual's energy reserves and food intake, as well as some environmental factors, have been related to fecundity (see review by Lambert et al. 2002). In this framework, variations in fecundity of Eastern Baltic cod are discussed in the following sections.

4.1.1 Spatial and seasonal variability in fecundity

Spatial variability in fecundity was investigated in 1995 and 1996 and intra-annual variation in 1996. There was evidence neither of significant spatial variability in fecundity between cod spawning sites in the Central Baltic nor an indication for intra-annual variation. Spatial fluctuations in fecundity of cod between different components of one stock have only been reported by Pinhorn (1984) from the Newfoundland region. He related significant differences in the slopes of the fecundity - length and fecundity - age relationships between sampling areas to bottom water temperature, as the investigated areas were characterised by varying hydrographic conditions. Temperature deviations in the Central Baltic are

most pronounced between the Gotland and the Bornholm Basin (ICES 1999), with the spawning component in the former area being close to extinction (Köster et al. 2001b). Hence, sufficient sample sizes to include the Gotland Basin into the present study could not be obtained (CORE 1998). The Gdansk Deep and the Bornholm Basin are characterised by a similar temperature regime and spatial variability in fecundity induced by different water temperatures would not be expected.

Apart from temperature, feeding conditions may result in variable fecundity. In an experimental study, Kjesbu et al. (1991) observed that a reduction in potential fecundity due to atresia in the pre-spawning ovary of Atlantic cod is uncommon except for fish in poor condition, while the realised fecundity depended on pre-spawning feeding opportunities. For Northeast Arctic cod, Marshall et al. (1998) showed that in years where condition was poor a considerable amount of repeat spawning females skipped spawning, though a higher proportion of mature specimens initiated gonadal maturation. Omitted spawning was also found in Northwest Atlantic cod by Burton et al. (1997) for individual females and by Rideout et al. (2000) for both sexes. Food limitation to the Eastern Baltic cod appears to be unlikely for the investigated years, as the most important prey species in pre-spawning time, i.e. sprat (Sparholt 1994), was at the highest stock level on record in 1995 / 1996 in all studied areas (ICES 1999). In contrast, stock sizes of cod were on a relatively low level in these years (ICES 1999). Thus, intensive atresia as well as pronounced differences in fecundity caused by variable food availability were not expected.

Seasonal trends in fecundity may be masked by low condition females appearing late in the season on the spawning grounds (Kjesbu et al 1998; Arcto-Norwegian cod) affecting relative fecundity through a change in weight. This was not observed in the present study. Average relative fecundities in 1996 showed a minor decrease from April to July concurrent with an increasing trend in condition factors stabilising the fecundity (Figure 3). Kjesbu et al. (1998) did not only find

that later spawning Arcto-Norwegian cod were in poorer condition than early spawners, but also produced fewer eggs. The reasons for this remained unclear; one proposed explanation was that the two categories belonged to different sub-populations. Aro (1989) reviewed the migration patterns of common fish stocks in the Baltic and stated that homing behaviour of the Eastern Baltic cod is not pronounced and individuals may use different spawning grounds in successive years. Given this permanent mixing of the stock, it is not likely that distinct sub-components of the spawning stock using different spawning grounds or time windows have established in the Central Baltic Sea. The lack of intra-annual and spatial variability in fecundity could, therefore, be explained by a combination of the latter with sufficient food supply and similar temperature regimes.

4.1.2 Annual variability in fecundity

In contrast to insignificant spatial and intra-annual variability in fecundity, a significant variability in fecundity did exist between years in the time series from 1987-2000. In the literature, annual deviations in fecundity are considered of varying importance and were mainly detected in studies examining extensive time series data. For example, Bleil and Oeberst (1996) did not detect significant differences in Eastern Baltic cod between 1993 and 1994. Oosthuizen and Daan (1974), who tested fecundity – weight relationships of North Sea cod in the years 1970 to 1972, similarly found no significant annual variation. Kjesbu (1988) compared fecundity of Arcto-Norwegian cod in 1986 and 1987 with data from Botros (1962) obtained in 1959 and also found no deviations. As only few or widely spaced years were inspected, inter-annual variability in fecundity of cod could not be generally rejected by these studies.

Other investigations described annual changes in fecundity for cod and other species. In fact, Kjesbu et al. (1998) applying a prolonged time series on Arcto Norwegian cod compared to the data used in Kjesbu (1988) found significant differences in fecundity within a time period of varying environmental and feeding

conditions. Pinhorn (1984) detected significant differences for Newfoundland cod not only between different sampling places, but also between sampling years. Rijnsdorp et al. (1991) found that relative fecundity of North Sea cod varied between years. Inter-annual changes in absolute and relative fecundity for several North Sea species, e.g. haddock (*Melanogrammus aeglefinus*), long rough dab (*Hippoglossoides platessoides*), herring (*Clupea harengus*), witch (*Glyptocephalus cynoglossus*), plaice and Norway pout (*Trisopterus esmakii*) were reported by Bagenal (1973), who was able to relate variations in the latter three species to stock density.

The maximum difference in relative fecundity observed within this study amounted to 33% between years. Evidence is strong that relative fecundity of Eastern Baltic cod varies between years, as this is a substantial variation based on a relatively large number of investigated specimens. The same amount of variation was found for potential fecundity corrected for fish length, although there were differences in the magnitude of variability and their statistical significance between some years. These deviations between length and weight based methods might be due to the variability in growth according to length and weight. The fact that the Eastern Baltic cod stock had undergone large changes in abundance and size structure in the covered period with the Central Baltic Sea ecosystem having changed from a sprat to a cod dominated system (Köster et al. 2001b) may be an indicator that the observed variation in fecundity reflects the full natural range.

4.1.3 Explaining variation in fecundity

Processes regulating the number of vitellogenic oocytes prior to spawning were studied in detail by Woodhead and Woodhead (1965) for Barents Sea cod. A more general picture for Atlantic cod was developed by Kjesbu et al. (1991). The number of developing oocytes is partly determined during the post-spawning period by the number of previtellogenic oocytes entering the circumnuclear ring phase (Woodhead and Woodhead 1965). As little energy is required for their

production, the number of these oocytes is more a function of fish size and, hence, ovary size, than it is dependent on the nutritional status of the fish (Kjesbu et al. 1991). A second process controlling the annual fecundity is the number of extra oocytes entering the circumnuclear ring phase during the feeding period that follows the post-spawning phase until vitellogenesis becomes well established. The number of the latter oocytes is linked to the nutritional status of the fish achieved during the feeding period (Kjesbu et al. 1991) and is most likely to provide the major contribution to the yearly variability in potential fecundity of similar sized fish. Although the relation between food availability, condition or growth and fecundity in cod was studied by several authors (e.g. Waiwood 1982; Kjesbu and Holm 1994; Kjesbu et al. 1998; Lambert and Dutil 2000), it is still unclear whether the energy needed for oocyte production is directly allocated from food intake or if their production is related to the growth rate. As both, food intake and growth, are related to temperature (e.g. Kohler 1964; Pedersen and Jobling 1989; Temming and Andersen 1994) the mean ambient temperature during the feeding period (fourth quarter) was tested in this study as a possible explaining factor of variability in potential and relative fecundity. In the individual based analysis, neither the temperature nor the individual condition factor at sampling time explained a considerable amount in the observed variability in potential fecundity. Fish length was the main variable responsible for the determination of potential fecundity. It is most likely that other factors responsible for variations in size-specific fecundity as, for example, an individual's condition could not be identified due to the fact that the determination of developing oocytes was settled prior to sampling. Hence, in a second approach, annual average relative fecundity was applied as a dependent variable. As this second analysis was not dependent on data measured on the same individual, possible predictor variables were chosen so that they could be measured as population averages in an appropriate time window. However, it has in general proven difficult to transfer individual based relationships to the population level to explain or predict inter-annual variation in

average relative- or size-specific fecundity. Seasonal variation in the influencing parameters and the associated problem to identify the right time of sampling in the field seems to be the main difficulty. Consequently, factors influencing or co-varying with fecundity (e.g., water temperature and prey biomass: Kjesbu et al. 1998) or total egg production (e.g., total lipid energy: Marshall et al. 1999) were used as indices.

In the present study, the relationships between relative fecundity and possible predictors including prey availability, temperature and growth anomaly were tested to establish a prediction model of relative fecundity. The final model was solely based on the relative prey availability during the early period of gonad ripening (fourth quarter) as the ambient water temperature and growth did not contribute significantly to the explained variation in relative fecundity. This observation differed to a certain degree from the results of Kjesbu et al. (1998) and Kraus et al. (2000). Relative fecundity in the present investigation also tended to increase with increasing temperatures in the lower temperature range, but the historically high ambient temperatures in most recent years (ICES 2001a, b) changed the relationship and indicated a dome shaped fecundity-temperature curve. However, as co-variation between prey biomass and temperature were found in both, Kjesbu et al. (1998) and the present study, it might be questioned whether temperature had a direct effect on fecundity or was rather manifested through food availability and metabolic rate. The ability of the fecundity model to predict relative fecundity was, however, convincing also for years not used to establish the model except for two years, i.e. 1978 and 1983, originating from Shapiro (1988). Sample sizes in the study of Shapiro (1988) were generally low and anomalies in prey availability, water temperature or FSSB could not explain these deviations. The limited capability of the fecundity model to predict these years may, thus, be ascribed to large individual variation in fecundity at low sample sizes biasing Shapiro's (1988) estimates and not to a mis-specification of the model.

4.2 Population egg production

For batch spawning fish species, the realised egg production derived from egg surveys in combination with information on individual fecundity has commonly been used to estimate spawning stock biomass applying egg production methods (e.g., Alheit 1993). In the present study, the potential egg production estimated from the female spawning stock biomass and relative fecundity was compared to the realised egg production derived from egg abundance data. The data applied to scale the MSVPA stock abundances to the PEP (see Table 2 for definitions of acronyms) represent the best available time series data on reproductive potential of Eastern Baltic cod reflecting to a large degree natural variability. The degree to which the estimates of potential and realised egg production corresponded, thus, depended on the loss of eggs from late vitellogenesis to early embryogenesis, i.e., due to atresia, fertilisation failure and early egg mortality, as well as the accuracy of the estimates.

The variability imposed on the relationship between PEP and the realised egg production was limited compared with a traditional stock-recruitment relationship. With this in mind, the RSEP was used as an independent estimate of the egg production to evaluate the applicability of different PEP time series. As the RSEP data points were few, the complementing RDEP was used as an index to extend the number of observations and, thereby, ascertain the agreement of the PEP and the realised egg production.

4.2.1 Reliability of female spawning stock biomass and egg production

The comparison of RSEP and RDEP with the FSSB, PEP (PRF) and PEP (ORF) showed good agreement with highly significant relationships between the stock based estimates and both data sets of the realised egg production. In these relationships the PEP (PRF) performed better than the FSSB, but the best performance was observed for PEP (ORF), which was therefore considered the

most accurate PEP estimate. This confirms a study of Köster et al. (2002) on Baltic cod, which showed a better accordance between RDEP and FSSB ($r^2 = 0.61$; $p < 0.001$) than between RDEP and the SSB applied in standard assessments ($r^2 = 0.30$; $p < 0.03$). However, their analyses were based on shorter time series and egg stage IA production. In addition, the potential egg production based on observed and interpolated relative fecundity ($r^2 = 0.63$; $p < 0.001$) instead of FSSB showed in Köster et al. (2002) only a limited improvement of the relationship. In the present study, relating a revised and updated RDEP to PEP (ORF) without interpolation increased the explained variation by 21% and by 17% when using the RSEP. Although the data points especially for the RSEP are relatively few, these results clearly show the scope for improving indices of the reproductive potential in stock - recruitment relationships as also evidenced by Marshall et al. (1999). A frequent limitation to the estimation of PEP is the lack of fecundity time series. However, the predicted relative fecundity reflected convincingly the observed variation in fecundity. Furthermore, the PEP based on PRF considerably improved the FSSB as a measure of the reproductive potential. At the same time the fecundity model can be applied to hindcast as well as to forecast fecundity.

The RSEP is expected to estimate the total realised egg production quite accurately. The Bornholm Basin is a well defined spawning area due to its unique topography and the fact that cod eggs can only float within and below the halocline (Wieland 1995). A simulation study performed with a three-dimensional hydrodynamic model has demonstrated that advection, one of the major problems in egg surveys, is hardly any source of error (STORE 2001) enabling a quasi-synoptic sampling of a large number of stations over the entire spawning area. Furthermore, additional information necessary to quantify egg production from abundance data is available, e.g., temperature - stage duration relationships (Wieland 1995). As a high frequency of egg surveys is necessary to estimate the RSEP, the number of years for which the RSEP could be determined was limited.

These years, nevertheless, represent years from the 1980's with high FSSB as well as recent years with low FSSB. The shape of RSEP curves, the peak of daily egg production, as well as the total egg production changed over the period. Changes were at least partially related to the altered FSSB structure from being dominated by older specimens to younger ones.

In the relationship to the PEP, RSEP data points were relatively few with rather clustered observations at low production indicating that additional factors not incorporated into the present PEP modelling approach influenced the relationship. Thus, the RDEP available for considerably more years was used as an alternative index. The RDEP confirmed the trends in the RSEP relationships to the FSSB and PEP, but RSEP explained a larger amount of the variance compared to RDEP. This was also expected, as RSEP was only calculated for years that were covered best with egg surveys and the impact of egg mortality was minimised using the youngest egg stage IA. Although the scatter of the RDEP was larger, the data showed a more even distribution over the range of the independent variable confirming continuous relationships between both measures of the realised egg production and PEP. The extreme changes in cod stock size and prey availability were clearly an advantage in establishing the relationships used in this analysis. The availability of reliable, independent sources of egg production to evaluate the quality of data used to estimate reproductive potential has also been fortunate, as the recruitment variability of Baltic cod largely is caused by environmentally induced mortality of eggs and larvae (Köster et al. 2001a). Thus, a comparison to recruitment success may have been inconclusive.

4.2.2 The influence of sex ratio, maturity and fecundity on relationships between potential and realised egg production

The agreement of the relationships between potential and realised egg production indicated that the variability in the time series reflected natural fluctuations rather than sampling noise. The decrease in explained variation and lower significance

levels of the relationship between RSEP / RDEP and the manipulated PEP time series with constant sex ratios, maturity or fecundity further confirmed that the observed variation in these data represents natural variability and that the variation is substantial. This effect was most pronounced, when a constant female maturity ogive was applied and the PEP to RSEP relationship lost significance at the 95% confidence level. This again parallels the study of Köster et al. (2002), who related the RDEP of stage IA to various measures of Baltic cod SSB. The analysis showed a significant correlation between the RDEP and SSB when estimated from variable maturity ogives ($r^2 = 0.30$; $p < 0.03$), but no correlation if SSB was based on a constant maturity ogive formerly used in standard assessments ($r^2 = 0.03$; $p = 0.49$). On the contrary, a sensitivity analysis to test the effects of different published maturity, sex ratio and fecundity time series on Baltic cod egg production estimates (MacKenzie et al. 1998) showed the largest impact for fecundity. The fecundity estimates used in these simulations were generated from various published and historic fecundity - size relationships, which in combination resulted in higher variation than in this study, most likely due to differences in methodology. The results emphasise the importance of high quality data to accurately estimate the reproductive potential of a stock.

Maturation rates in fish are highly variable owing to a number of factors. Being a poikilothermous animal, fish more than other animals are influenced by environmental temperature with direct impacts on metabolism and growth. The variability in the maturity time series reflects substantial changes in growth and maturation related to substantial changes in stock size and prey availability that occurred within the year range covered by the present study (Köster et al. 2001b). Thus, the proportions of mature cod within the age groups 2 - 5 were substantially higher in the 1990's than in the 1980's (Tomkiewicz et al. 1997; Cardinale and Modin 1999). Similarly, the relative fecundity tended to be lower in the early period of the study than in the latter, and the fecundity model showed that these changes were related to relative prey availability. The effect of removing the variability in

sex ratio at age on the PEP to RSEP / RDEP relationships was less pronounced than for constant maturity and fecundity. Reasons might be that the longevity of males in the stock is shorter than of females and that males mature earlier compared to females (Joergensen 1990; Tomkiewicz et al. 1997). If the age-specific differences in the sex ratio are not considered, the combined effect of these two causes will lead to underestimation of the PEP in a stock dominated by older age classes (1980's) and to overestimation of the PEP in a stock consisting mainly of young age classes (1990's).

4.3 Atresia

Systematic differences were revealed between potential and realised egg production. The difference between PEP (ORF) and the RSEP corresponds in principle to the loss of eggs due to atresia, fertilisation failure and mortality of eggs during early embryogenesis. In the following, the role of atresia among these processes is discussed.

In Eastern Baltic cod, atresia appeared to be a common phenomenon, although the number of oocytes affected by atresia was generally low. During the 2000 spawning season on average 32% of the mature females showed atretic oocytes with a mean relative intensity of 2.8%. Similar observations were made for other cod stocks. Kjesbu et al. (1998) observed atresia in 30% of Arcto-Norwegian cod ovaries with an average relative intensity of 2.5% and Hardardottir et al. (2001) found 24.5% of Icelandic cod ovaries to be atretic with, however, a large variation in relative intensity (1-29%). Very similar patterns to the ones observed for cod were also reported for other determinate batch spawning species (sole: prevalence 4-69%, relative intensity 1.7-7.6%, Witthames and Greer Walker 1995; turbot: prevalence 33%, relative intensity <5%, Bromley et al. 2000). Atresia in species of this spawning type seems to be a mechanism to fine tune batch sizes or to remove damaged or abnormally developing oocytes (Bromley et al. 2000). The relative intensities of atresia observed in this study were not related to

condition with the low intensities observed in the majority of the individuals being probably a matter of the regulatory mechanisms described by Bromley et al. (2000). This was also expected, as condition indices of cod were above the long-term average and the sprat stock, the major prey item of cod in the Central Baltic, was at high and the cod stock at an extremely low level (ICES 2001a) making food limitation to cod in the year 2000 rather unlikely.

Mass resorption of oocytes leading to cessation of spawning activities or skipped spawning seasons was mainly described for species with an indeterminate annual fecundity under food limitation (e.g. Hunter & Macewicz 1985), but was also reported for cod in poor condition (Burton et al. 1997; Rideout et al. 2000). In the present study massive atresia was observed only in three specimens of 87 reproductively active atretic females. As the condition indices of these individuals were nearly equal to or above the average, it was suspected that they suffered from diseases or atypical reproductive disturbances. Massive atresia due to parasite infection was reported for example by Luksiene et al. (2000) for roach in the coastal areas of the Bothnian Sea.

However, Fulton's condition indices of non-atretic specimens were significantly higher than those of females with atretic ovaries. This might be an effect of declining condition in the later maturity stages in combination with higher prevalences of atresia in these stages. No differences in the proportion of females with atresia were found between size groups, while the total number of atretic oocytes per ovary increased with the size of fish presumably as an effect of increasing ovary volume. The size effect could largely be removed by introducing the relative intensity of atresia. RI_a was assumed to be independent of size, because the relationship to length was not significant at the 95% confidence level and was only weak to weight. Size independency of prevalence and relative intensity of atresia was correspondingly observed in Icelandic cod (Hardardottir et al. 2001).

The prevalence of atresia was increasing with progressing maturity stages. Hardardottir et al. (2001) observed a contrary trend for Icelandic cod, while Witthames and Greer Walker (1995) confirmed the increasing trend in the number of atretic individuals in sole. No seasonal trend, though not resolved for maturity stages, was observed in P_a , as well as in RI_a in Atlanto-Iberian sardines (Zwolinski et al. 2001). Correspondingly, the relative intensities of atresia in Eastern Baltic cod as well as in Icelandic cod (Hardardottir et al. 2001) did not differ between maturity stages, while a distinct pattern in RI_a was found for sole with a peak in intensity when the fish entered the second half of the spawning period (Witthames and Greer Walker 1995). The RI_a tended to increase in specimens with a potential fecundity lower than predicted by the year specific fecundity-size relationship. From this observation two conclusions could be drawn. First, atresia in these fish has already removed a considerable part of the vitellogenic oocytes by the time of fecundity sampling and/ or secondly, the processes determining the number of developing oocytes and atresia have common causes. It is not very likely that the nutritional status was one of the latter causes, as the condition of the fish was not related to RI_a and the explained variation in fecundity by condition was negligible. Hence, the first point possibly in combination with other common reasons as for example genetically or contamination induced reproductive disturbances are likely to be responsible for this observation.

Little attention has been paid in former times to study atresia as a mechanism to regulate fecundity, although follicular atresia has been described in a wide range of species (Guaraya 1986). So far, only a few attempts have been made to quantify the loss of eggs due to atresia, as large efforts including laboratory studies are required (e.g. Withames et al. 2000). The most simple but indirect method would be the comparison of potential fecundity with realized fecundity collecting spawned eggs in tank experiments as described in Kjesbu et al. (1991) and Bleil and Oeberst (1998). A major problem associated with this method is that the potential fecundity could hardly be measured on the same fish used to

determine the realized fecundity as these methods require the sacrificing of fish to obtain the ovary. To avoid this problem the potential fecundity of reference fish of a similar size and condition have been applied (Witthames et al. 2000) and ultrasound techniques in combination with ovarian biopsy to estimate fecundity have been suggested (Kjesbu et al. 1991). Nevertheless, the accuracy of the latter method has to be validated.

In order to measure the total atretic loss of oocytes directly, it is necessary to know the number of atretic oocytes, to estimate the rate of turnover for the atretic stage recorded, and to know the time elapsed from the determination of potential fecundity to the end of spawning. Turnover rates for alpha atresia were for example estimated by Kjesbu et al. (1991) by combining the experimentally determined egg loss (see above) with atretic intensity estimates from histological sections. Their investigations resulted in turnover rates of on average 10 days for Atlantic cod. Recent work by Witthames et al. (2000) applied a different approach. Frequent ovarian biopsies covering the pre-spawning and spawning period of individual captive Northeast Arctic cod were used to obtain quantitative estimates of atresia. Histological investigations of these biopsy samples provided progressive series of alpha atretic rates, which were used in combination with information on residual fecundity to estimate the stage duration of alpha atresia, which was estimated to be on average 8.2 days.

From the results of the present study it was assumed that the relative intensity of atresia is stable over maturity stages and that the observed increase in P_a with maturity stages is representative of the population. Thus, for a quantification of the total, seasonal atretic loss only the changing P_a has to be considered, while an average RI_a value could be applied. RI_a was defined as the proportion of total alpha atretic oocytes per ovary in relation to the predicted potential fecundity (Witthames and Greer Walker 1995). This definition enables the application of RI_a to estimate the total atretic loss of eggs for all pre-spawning and spawning stages (Witthames and Greer Walker 1995). In contrast, the frequently used definition of

relative intensity of atresia as the number of atretic oocytes in relation to the number of normally developing oocytes (Kjesbu et al 1991, 1998) could only be used in pre-spawning individuals, because during spawning the number of developing oocytes are successively reduced.

Information on duration of the average individual maturation and spawning season of female cod in the Bornholm Basin are provided by Tomkiewicz and Köster (1999). Maturation of oocytes lasted on average 2.5 months. As the potential fecundity is determined at an advanced stage of oocyte maturation and the growth rate of oocytes accelerates during maturation (Witthames and Greer Walker 1995) the assumption of a period of one month from fecundity sampling to the start of spawning is used in this study as a conservative approach. The duration of the female spawning season was also estimated to be 2.5 months (Köster and Tomkiewicz 1999). As no finer resolution into spawning stages was provided, the overall spawning days were partitioned into three phases of equal length for the calculation of the atretic loss of oocytes, i.e. early, peak and late spawning of 25 days corresponding to maturity stages 5, 6 and 7, while for the truncated maturity stage 4 a period of 30 days was presumed.

Assuming that an average stage duration for alpha atresia of 9 days (Kjesbu et al. 1991; Witthames et al. 2000) would also apply to Baltic cod, a rough estimate of the atretic loss in each stage could be calculated by multiplication of P_a , RI_a , turnover rates and the duration of spawning or maturation phases, respectively:

$$L_i = P_{ai} \times RI_a \times (D_i / T),$$

where L_i is the proportion of oocytes lost in stage i , P_{ai} is the prevalence of atresia in stage i , RI_a the average intensity over all fish size groups and maturity stages, D_i the number of days in the maturation/spawning phase corresponding to maturity stage i and T the average turnover rate of 9 days. Combining the above formula for all phases, the average total loss of oocytes for the entire period from the

fecundity determination at maturity stage 4 through the spawning process amounted to 3.6% in Eastern Baltic cod.

A quantification of the duration of atretic stages as well as the experimental validation of the length of individual spawning seasons and maturity stages had, so far, not been done for Eastern Baltic cod. The necessary effort would be tremendous and was beyond the scope of this thesis. Moreover, the degeneration of oocytes in the field may be subjected to spatial and temporal variations and for the understanding of these processes it would be required to investigate a broad scale of environmental scenarios. For the estimate of the total, seasonal atretic loss of eggs of Eastern Baltic cod presented here, information from different sources, stocks and years had to be combined. Although the assumptions inherent with the input variables are considered to be conservative, this estimate should only be treated as an indicator for the magnitude of the impact of atresia on egg production.

The loss of eggs from potential egg production to the realised egg production in the field was estimated to be 50 - 58% or 54% of the PEP based on regression slopes or the average ratio, respectively. Fertilisation success and mortality of cod eggs in the Bornholm Basin are well studied. Vallin and Nissling (1998) reported high average fertilisation rates (85%) for salinity above 11psu, which is normal for the spawning layers in the Bornholm Basin. Wieland (1995) estimated daily mortality rates for egg stage IA to range from 10 to 30% and a maximum duration of this stage of three days at 5 °C. Thus, the mortality throughout the half stage duration, assumed as catch date, would than range between ~14 - 40%. Combining this information with the estimate for the atretic loss of approximately 3.6%, the integrated loss of eggs due to fertilisation failure, early egg mortality and atresia would be in the range from 33% to 59% with atresia playing only a minor role compared to fertilisation success and egg mortality. This corresponds well to the egg loss estimated as the difference between PEP (ORF) and RSEP in the present study.

5 Conclusions

During the previous several years, the reproductive biology of commercially important fish species has received plenty of attention. Recent findings indicate that the reproductive potential of exploited fish stocks exhibits considerable variation at given stock sizes, which influences interpretations of the relationship between stock size and recruitment.

The present study demonstrated that individual fecundity of Eastern Baltic cod varied strongly among years. The availability of prey during ovarian maturation was related to fluctuations in fecundity giving rise to the conclusion that the variability is driven by nutritional condition or growth rates. Considerable temporal variation also existed in age-specific sex ratios and in the proportion of mature females. The potential egg production of cod in the Bornholm Basin calculated on the basis of these data was well reflected by the realised egg production in the field. This indicated that the observed patterns in sex ratio, maturity as well as fecundity represent natural variations and that the potential egg production is a reliable measure of the reproductive potential. Rates of ovarian atresia were low and, hence, considered to be of minor importance as a regulatory mechanism of the individual egg production. However, this interpretation should not be generalised as the importance of atresia may increase under food limitation.

In the management of Eastern Baltic cod, biological reference points are based on relationships between spawning stock biomass derived from combined female and male maturity data and corresponding recruitment estimates. Due to the substantial temporal variation in reproductive parameters revealed within the present study, large differences in the egg production at a given size of spawning stock biomass could occur. Applying egg production instead of spawning stock biomass could potentially reduce the variance in stock-recruitment relationships. Consequently, the uncertainty in forecasts of future stock size from these

relationships would be reduced and the quality of derived biological reference points enhanced.

However, the effort required to estimate egg production is large and would for many stocks be beyond the scope of routine survey programs. Exploratory analysis as applied in this study to identify predictors of fecundity could be a valuable approach useful to develop easy to measure proxies of reproductive potential that in turn can be applied to stock recruitment relationships.

6 Summary

In the management of exploited marine fish populations, stock – recruitment relationships are frequently used to determine biological reference points. However, stock – recruitment relationships for many highly fecund marine fish species are not well determined. The main reasons for the large scatter in these relationships were assumed to be environmentally-induced high mortality rates of pelagic eggs, larvae and juveniles, as well as uncertainties in stock and recruitment estimates. Recent findings also indicated that stock size or stock biomass does not reflect the true reproductive potential of a population. An explanation could be that the inherent proportionality assumption between stock size and viable egg production is invalid. For example, a number of studies showed that age of first maturity and sex ratio were subjected to temporal variation within a stock. In addition, fecundity and egg quality are related to parental condition and, thus, vary in space and time depending on adult food availability.

Using Eastern Baltic cod as a test species, the present study, thus, focused on individual and population egg production in the Bornholm Basin, presently the only important spawning ground in the Central Baltic Sea. One major aim was the investigation of individual fecundity, its spatial and temporal variation and the underlying processes responsible for its variability. Another focus was the population egg production in the Bornholm Basin, which is addressed with special emphasis on the causes of its fluctuations over the last 25 years. Ovarian atresia was investigated as a regulatory mechanism of fecundity, and hence, the population egg production.

The potential fecundity, defined as the number of developing oocytes per spawning season, was dependent on length and weight with high coefficients of determination. Fish weight was linearly related to fecundity and fecundity relative to weight was constant over the whole size range covered in the analyses. Relative, as well as size-specific fecundity showed neither spatial nor seasonal

differences within a year, but pronounced differences amounting to a maximum of 33% were observed between years. The availability of sprat and herring, the most important prey species of cod in the Central Baltic Sea, explained 72% of this inter-annual variability in relative fecundity and was used for fecundity predictions. The female spawning stock biomass was calculated as one measure of the stock's reproductive potential. Scenarios of the potential egg production were then developed by combining the female spawning stock biomass with the predicted and observed fecundity data. Estimates of the potential egg production were complemented by data sets on the realised egg production derived from cod egg abundance in the Bornholm Basin.

The relationships between potential and realised egg production were highly significant. The potential egg production based on observed fecundity data explained the largest amount of the inter-annual variation in the realised egg production. Potential egg production based on predicted fecundity explained ~10% and the female spawning stock biomass ~20% less of this variation, respectively.

The application of constant values of sex ratio, proportion of mature females and fecundity in the calculation of the potential egg production deteriorated the relationships to the realised egg production in all three cases. A large reduction of 30-40% in the explained variation of the realised egg production was observed for constant proportions of mature females. The effects of constant fecundity and constant sex ratio on the relationships between potential and realised egg production were less pronounced. Removal of the inter-annual variability in fecundity reduced the explained variation in realised egg production by 10 to 20% and a constant sex ratio by approximately 5%. These results indicate a considerable sensitivity of the egg production to fluctuations in the underlying parameters and, thus, emphasise the importance of regularly obtained survey data to improve models of population dynamics.

The difference between potential and realised seasonal egg production amounted to approximately 50%. Assuming reliability of both egg production estimates, this

value should reflect the loss of eggs due to atresia, fertilisation failure and early egg mortality. Results obtained within the present study indicated a rather low importance of atresia among the above processes. On average, 32% of female cod showed signs of atresia with a mean relative intensity of 2.8% of the annual potential fecundity. Based on these data, a total, annual atretic egg loss of 3.6% was estimated for the stock. The loss of eggs expected due to fertilisation failure and early egg mortality in Baltic cod plus the estimated value for atresia was of a magnitude corresponding to the difference between potential and realised seasonal egg production and confirmed the reliability of the estimates.

7 Zusammenfassung

Bestands-Nachwuchs Beziehungen genutzter Fischbestände werden häufig als Grundlage für die Bestimmung biologischer Referenzpunkte im Fischereimanagement verwandt. Für viele marine Populationen mit hoher Fruchtbarkeit weisen diese Beziehungen allerdings eine sehr hohe Streuung auf. Als Hauptursachen dafür gelten hohe, umweltbedingte Sterblichkeit pelagischer Ei- und Larvalstadien, sowie Ungenauigkeiten in den Abschätzungen des Bestandes und des daraus rekrutierenden Nachwuchses. Neuere Erkenntnisse lassen darauf schließen, daß auch die Bestandsgröße oder Biomasse als Maß für das Reproduktionspotential einer Population ungeeignet ist. Begründet wird diese Beobachtung damit, daß die inhärente Proportionalitätsannahme zwischen Bestandsgröße und der Anzahl lebensfähiger Eier falsch ist. In einer Reihe von Studien wurde gezeigt, daß das Alter des Eintritts der ersten Geschlechtsreife innerhalb einer Population und das Geschlechterverhältnis zeitlicher Variabilität unterliegen. Zusätzlich sind die Fruchtbarkeit von Fischen gleicher Größe, sowie die Qualität und die Lebensfähigkeit der Eier abhängig von dem Ernährungszustand der Elterntiere. Sie weisen damit räumliche und zeitliche Schwankungen im Bestand auf, die die Proportionalität von Bestandsgröße und Reproduktionspotential in Frage stellen.

Ausgehend von diesen Ergebnissen fokussierte die vorliegende Arbeit am Beispiel des Dorsches in der zentralen Ostsee (*Gadus morhua callarias* L.) auf die Beziehungen zwischen Adulten und deren Eiproduktion auf individueller Ebene, sowie den sich daraus ergebenden Auswirkungen auf die Eiproduktion des Gesamtbestandes. Zunächst wurde auf die individuelle Fruchtbarkeit, ihre räumliche und zeitliche Variabilität, sowie die für Schwankungen verantwortlichen Faktoren eingegangen. Im Weiteren wurde die Eiproduktion des Bestandes im Bornholm Becken, des derzeit einzigen für die Bestandserhaltung wichtigen Laichgebietes, und die Ursachen für deren Variabilität über die letzten 25 Jahre

untersucht. Atresie als Regulationsmechanismus der Fruchtbarkeit und damit der gesamt Eiproduktion bildete einen weiteren Fokus.

Die Analyse der potentiellen Fruchtbarkeit als Anzahl heranreifender Oozyten pro Laichsaison zeigte eine klare, durch geringe Streuung gekennzeichnete Abhängigkeit von Länge und Gewicht der untersuchten Tiere. Das Gewicht stand in einem linearen funktionalen Zusammenhang mit der Fruchtbarkeit, wobei die Fruchtbarkeit relativ zum Fischgewicht Konstanz über den gesamten Größenbereich der untersuchten Tiere aufwies. Relative, als auch größenspezifische Fruchtbarkeit wiesen weder einen saisonalen noch räumlichen Trend auf, waren jedoch durch deutliche Unterschiede zwischen Jahren gekennzeichnet, die sich auf maximal 33% beliefen. In einem Vorhersagemodell konnten 72% der zwischenjährlichen Variabilität in der relativen Fruchtbarkeit durch Beuteverfügbarkeit erklärt werden.

Anhand von vorhergesagten Bestandsgrößen aus einem Mehrartenmodell (**Multi-Species-Virtual-Population-Analysis**), altersspezifischen Zeitseriendaten über Geschlechterverhältnis und geschlechtsspezifische Anteile an der Reproduktion beteiligter Individuen, sowie mittleren Gewichten wurde die Laicherbestandsbiomasse an Weibchen berechnet. In Kombination mit beobachteter oder vorhergesagter Fruchtbarkeit konnten verschiedene Szenarien der potentiellen Eiproduktion als Maß für das Reproduktionspotential des Bestandes im Bornholm Becken entwickelt werden. Die Zeitserien der potentiellen Eiproduktion wurden komplettiert durch zwei Datensätze der beobachteten Eiproduktion aus Planktonfängen, einer mittleren täglichen- und der Saison-Eiproduktion.

Die Ergebnisse zeigten, daß die potentielle Eiproduktion berechnet mit beobachteten Fruchtbarkeiten 72% der Variabilität in der beobachteten mittleren täglichen Eiproduktion beziehungsweise 91% der Saison-Eiproduktion erklärte. Im Vergleich dazu trugen potentielle Produktion basierend auf vorhergesagter Fruchtbarkeit und weiblicher Laicherbestandsbiomasse etwa 10 bzw. 20% weniger zur Erklärung der Varianz für beide Abschätzungen der beobachteten Eiproduktion

bei. Die Vernachlässigung der zwischenjährlichen Variabilität in den Anteilen geschlechtsreifer Weibchen übte mit einer Reduktion in der erklärten Varianz von etwa 30-40% einen besonders starken Einfluß auf die Beziehung zwischen potentieller und beobachteter Eiproduktion aus. Weniger starke Auswirkungen konnten für den Einfluß jährlicher Fluktuationen in der Fruchtbarkeit nachgewiesen werden (~10-20%), während ein konstantes Geschlechterverhältnisses die geringsten Auswirkungen zeigte (~5%).

Die Differenz zwischen den repräsentativsten Datensätzen potentieller und beobachteter Eiproduktion spiegelt den Verlust an Oozyten bzw. Eiern durch Atresie, Misserfolg in der Befruchtung und frühe Eisterblichkeit wider. In dieser Arbeit belief sich die Differenz auf 50-58% in Abhängigkeit von der angewandten Berechnungsmethode. Exemplarisch wurde für das Jahr 2000 der Gesamtverlust an Eiern durch Atresie bestimmt. Im Mittel zeigten 32% der weiblichen Dorsche Anzeichen für Atresie mit einer Resorptionsrate von 2.8% der potentiellen Fruchtbarkeit. Für den Bestand wurde ein Gesamtverlust durch Atresie von ~3.6% ermittelt. Die Rolle von Atresie als Regulationsmechanismus der Eiproduktion unter den oben angesprochenen Prozessen wurde daher als gering bewertet. Die in der vorliegenden Untersuchung ermittelte Differenz zwischen potenzieller und beobachteter Eiproduktion entsprach jedoch der erwarteten Größenordnung unter Berücksichtigung realistischer Annahmen für Befruchtungserfolg und Sterblichkeit.

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9. Appendix

Annex Table 1: Macroscopic maturity scale by Maier (1908) revised by Tomkiewicz et al. (2002).

Stage	Macroscopic characteristics of maturity stages and phases
I	Juvenile Ovary tiny, attached to the air bladder posterior in the body cavity. Elongated and soft with smooth walls. From glassy transparent in very, small specimens to orange-reddish translucent in larger specimens. Rarely females > 30 cm ¹ ; $I_G < 1^2$.
II	Preparation Ovary small, but clearly distinguishable posterior in the body cavity. Soft with even surface and smooth walls, flattens on a solid sheet. Blurred translucent, reddish-orange. Female size range: 25-60cm; $I_G < 1.5$.
III	Ripening 1: Early vitellogenesis Ovary still relatively small and restricted to the posterior part of the body cavity. Firm and roe shaped (keeps the form on a solid sheet) with uneven surface and distinct blood vessels. Opaque orange-red to dark orange often with a greyish cast in large females. Towards the end of the stage, eggs become visible as small, light dots in the ovarian tissue. Rarely females < 30 cm; I_G 1-7.5.
IV	Ripening 2: Late vitellogenesis Ovary enlarged, extending to around the middle of the body cavity. Plump and firm with tight walls and prominent blood vessels. Completely opaque, orange to creamy yellow. The individual eggs are clearly visible. I_G range: 3-14.
V	Spawning 1: Initiation Ovary fully developed, extending into the anterior part of the body cavity. Soft with smooth, distended walls; lumen with viscous fluid. Opaque, orange to creamy yellow. Single glassy, hydrated eggs normally present, but the majority of eggs are as in IV, but round. Ripe eggs in lumen may occur. I_G range: 12-25.
VI	Spawning 2: Main period Ovary filling most of the body cavity. Very soft with distended walls; lumen filled with viscous fluid in excess, which may contain hydrated eggs that flow at pressure. The mixture of glassy and opaque eggs is more even than in V giving the ovary a granulated orange- to reddish-grey appearance. I_G range: 15 to 60.
VII	Spawning 3: Ending Ovary restricted to the posterior part of the body cavity. Shrunken with wrinkled walls and prominent blood vessels; lumen large with excess fluid. Unclear red-orange with a slight greyish cast. Often with hydrated eggs that flow at pressure, while no or very few opaque eggs are left. I_G range: 3 to 8.
VIII	Regeneration 1: Spent Ovary contracted to the posterior body cavity. Slack walls with a greyish cast, rich in blood vessels. Partly transparent reddish-grey. Single hydrated eggs may occur, but no developing eggs are present. Degenerating eggs (atresia) may appear as white, irregular granules. I_G normally 2 to 3; in case of atresia up to 10.
IX	Regeneration 2: Resting and skip of spawning Ovary small, as in Stage II with signs of previous reproduction. Soft with a greyish cast and often uneven walls. The ovary is blurred translucent, reddish-grey, but appears more opaque and granulated than in II. I_G range: 1-3.
X	Degeneration Ovary abnormalities significantly reducing fecundity: a) Fibrous tissue: affected areas compact and hard, opaque of brownish-yellow colour, non-affected parts show normal development; b) Other abnormalities, e.g. significantly increased gonad weight (app. 5-10 x). Observed in females above 65 cm.

¹ length and ² gonadisomatic index, I_G , given as observed minimum and maximum values.

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