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Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism

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Cod is the top piscivore predator in the Baltic Sea ecosystem. Based on stomach content data from 62 427 cod collected during 1977–1994 and food consumption rates, cannibalism in the Eastern and Western Baltic cod stocks has been quantified using multispecies virtual population analysis. In the Eastern Baltic stock, depending on model assumptions, an average of 25–38% of the 0-group and 11–17% of the 1-group were removed by predation by adults. Thus, between age 0 and age 2 a year class may lose on average about 31% and 44% of the initial number as a result of cannibalism. Cannibalism is lower in the Western Baltic. On average, 19% of the 0-group and 9% of the 1-group are consumed per year, i.e. 24% of the initial cohort is eaten before reaching age 2. Predation was most intense in 1978–1984, a period with high juvenile abundance and large adult stock sizes in both areas. Subsequently, stock, recruitment, and cannibalism declined steadily until the early 1990s and then increased again. Problems identified in relation to data compilation and estimation procedure are discussed with respect to their impact on estimates of cannibalism and stock–recruitment relationships.

Key words: Baltic cod, cannibalism, multispecies VPA, recruitment, suitability coefficients.

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Introduction

Cannibalism has been recorded in 36 out of 410 teleost families, including 4 gadoid species, all of which are marine piscivores and do not guard their fry (Smith and Reay, 1991). In captivity, cannibalism tends to increase with increasing density and decreasing availability of alternative food (e.g. Giles *et al.*, 1986; Hecht and Appelbaum, 1988).

Cod is the top piscivore predator in the Baltic Sea ecosystem (Sparholt, 1994). Genotypic and phenotypic characteristics indicate that two distinct stocks of cod exist in the Baltic Sea (Bagge *et al.*, 1994) occurring east and west of Bornholm (14°30′E), respectively. Therefore, Eastern and Western Baltic cod are generally assessed separately (ICES, 1998).

The main tool utilized for multi-species assessment in the Baltic is multi-species virtual population analysis (MSVPA). Basically, MSVPA integrates the prey–predator suitability concept of Andersen and Ursin (1977) with traditional virtual population analysis. The MSVPA model is described in detail by Sparre (1991). In multi-species assessment of the Central and the Western Baltic, cod is the only predator and herring, sprat, and cod are modelled as prey (ICES, 1999). This simple set-up is justified by the fact that these three species constitute about 95% of the commercial catches in weight (Sparholt, 1994).

The development of the Baltic cod stocks, with the eastern component dominating in terms of both abundance and biomass, is characterized by a dramatic decline in the late 1980s, both stocks reaching historic low levels in 1991/1992 (ICES, 1998). The decline was mainly caused by reduced reproductive success and continued high-fishing effort (Bagge *et al.*, 1994). Recruitment of Eastern Baltic cod is assumed to be largely dependent on environmental conditions in the deep Baltic basins where the cod spawn, particularly at or below the halocline, where the eggs reach neutral buoyancy. Both field (Plikshs *et al.*, 1993; Wieland and Jarre-Teichmann, 1997) and experimental studies (Nissling and Westin, 1991; Westin and Nissling, 1991;

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Wieland *et al*., 1994) show that oxygen concentrations and salinity are important for egg fertilization, development, and survival. Unfavourable oxygen conditions may also affect larval survival, as the eggs hatch in or below the halocline and the larvae have to migrate into the upper layers to ensure suitable feeding conditions (Grønkjær and Wieland, 1997).

Predation on early life stages by clupeids (Köster and Schnack, 1994) as well as cannibalism on juvenile stages (Sparholt, 1994) are also considered to substantially affect cod recruitment. MSVPA runs conducted with cod as prey (Jensen and Sparholt, 1992) suggest that cannibalism may provide a strong self-regulatory mechanism in the Eastern Baltic cod stock and that MSVPA estimates would be appropriate for establishing stock–recruitment relationships (Sparholt, 1996). However, this depends on whether the input data on cod preying on cod are reliable and suitable for use in the MSVPA model. We address this question following three approaches: (1) a description of cannibalism-related signals in the international stomach content database; (2) a summary of cannibalism-related output from MSVPA for both stocks; (3) an attempt to estimate rates of cannibalism for Eastern Baltic cod with alternative suitability sub-models.

The results are compared with respect to time trends in the intensity of cannibalism and the effects of various recruitment estimates on the stock–recruitment relationship.

Material and methods

Estimates of rates of cannibalism are based on an analysis of the International Database on Baltic Cod Stomach Contents (ICES, 1997a), utilizing MSVPA as implemented by ICES (1996). The stock units were largely the same as used in single-species assessments: cod in ICES Subdivisions 25–32 (predator and prey), herring in Subdivisions 25–29+32, including the Gulf of Riga (prey) and sprat in Subdivisions 25–32 (prey).

For the Central Baltic, the MSVPA keyrun (ICES, 1997a) was updated by introducing corrected weight at age and catch at data, maturity ogives, and an improved tuning procedure (ICES, 1997b, 1999). For a description of predation and terminal fishing mortalities derived and applied, see ICES (1997b). For the Western Baltic, MSVPA results were derived directly from ICES (1997a).

In MSVPA, the food composition of a particular predator age group is predicted from the relative abundance of the different prey age groups weighted by their relative suitability as prey. One basic assumption is that suitabilities for each predator-age prey-age combination are constant over time (ICES, 1992a). Suitability coefficients may be interpreted as being proportional to the probability of encounter between prey and predator multiplied by the probability of the predator eating the prey once encountered. The current Baltic MSVPA utilizes a revised suitability submodel (ICES, 1999). The reason for replacing the original suitability submodel (Gislason and Sparre, 1987) was the observation that the suitability coefficients derived were underestimating observed stomach contents in simulations (ICES, 1992b). We used both submodels for comparison.

The extensive output has been summarized as follows. Predation mortalities per year and prey age group and corresponding number of cod consumed were obtained by adding quarterly values (0-group: quarters 3 and 4; 1- and 2-group: quarters 1–4). Predator stock sizes were computed on the basis of mean stock numbers within a quarter averaged over quarters and summed over age 2+. For calculating spawning stock biomass (SSB), weight at age and maturity ogives were applied to the age-specific stock numbers. Recruitment refers to the beginning of the 3rd quarter (0-group) or to the 1st of January (1- and 2-group). Recruitment estimates for the last year in the analysis (1996) were omitted as being too sensitive to the tuning procedure.

For an independent analysis of the stomach content data, the average contribution of cod in the diet (in g wet weight or as % weight of the total stomach content) was computed for 1977–1993 by averaging data over all predator length groups, Subdivisions and quarters, weighted by the square root of the number of stomachs analysed. Missing data for length groups and Subdivisions were substituted according to Sparholt (1993). Missing quarterly values were ignored. The length frequencies of ingested cod are based partly on items which could be measured directly, and partly on estimates based on a length–weight relationship or on back-calculations from the size of vertebrae (or the entire vertebral column).

As a test of the suitability submodels, the yearly predation on 1-group (P) by the Eastern Baltic cod stock was estimated independently of any suitability submodel by:

$$P_{y,a=1} = \sum_{j=2}^{J=9} \bar{N}_{y,j} \cdot R_{y,j} \cdot S_{y,a=1} \qquad (1)$$

where N is mean abundance of cod by year y and age group j, R is yearly food intake (in weight) by individual cod, and S is the relative stomach content of 1-group cod in the diet.

Stock sizes of age 2+ cod were taken from MSVPA, because these age groups are virtually unaffected by predation. This also means that deviations in the output for recruitment and consumption are largely caused by the suitability submodel. Applying residual mortalities (M1) and catch in numbers at age 1 (C) to the estimated stock size of age group 2 at the beginning of the year,

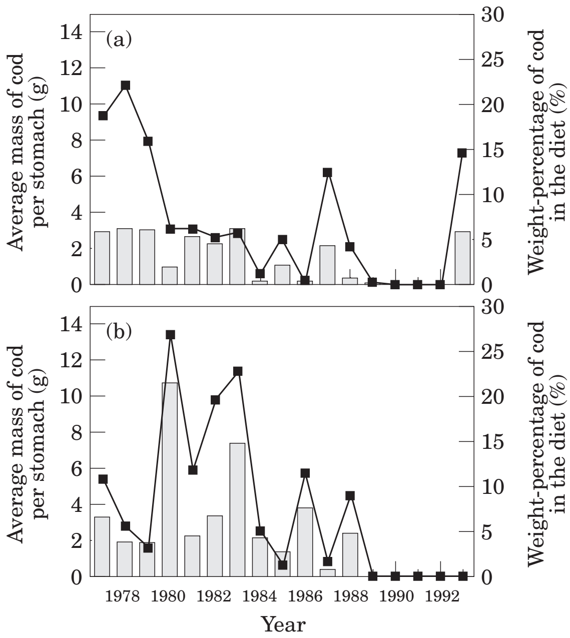

Figure 1. Average weight of cod per cod stomach in gram wet weight (bars) and percentage contribution to the total diet (lines) in the Central Baltic (a) and Western Baltic (b).

stock sizes of 1-group at the beginning of the preceding year and corresponding predation mortalities (M2) were computed by a recursive cohort analysis, starting with M2=0:

$$N_{y,a=1}=(N_{y+1,a=2}*e^{((M1_{y,a=1}+M2_{y,a=1})/2)}+C_{y,a=1})*e^{((M1_{y,a=1}+M2_{y,a=1})/2)} \quad (2)$$

The mean stock size of age group 1 within a given year is then calculated as

$$\bar{N}_{y,a=1}=N_{y,a=1}*(1-e^{-Z_{y,a=1}})/Z_{y,a=1} \quad (3)$$

where $Z_{y,a=1}$ is the total mortality coefficient. Finally, M2 is estimated utilizing average weight of the 1-group in the stock (W) by

$$M2_{y,a=1}=P_{y,a=1}/(\bar{N}_{y,a=1}*W_{y,a=1}) \quad (4)$$

Restart with the M2 estimate in Equation (2) until convergence is achieved.

Results

Cod in cod stomachs

The average weight of cod in cod stomachs and the percentage contribution to the total diet for the two areas are presented in Figure 1. In the Central Baltic, the highest quantities were found in 1977–1983 (1.5–2.7 g per stomach), whereas in later years only occasionally similar amounts were encountered (1987, 1993). The percentage contribution to the diet showed a similar trend, but with a more pronounced maximum in 1977–1979. Western Baltic cod had on average comparable quantities of cod in their diet, with relatively high values in 1981 and 1984. Cannibalism remained high until 1989, but was virtually absent subsequently. The relative contribution to the total stomach content was highest in 1981–1984.

Although the relative diet contributions are substantial, the incidence of cannibalism is fairly low (on average <1%), indicating that cod prey are much larger than most other prey. The length frequencies (Fig. 2) of cod found in cod stomachs show the majority to be <30 cm in both areas. In the Western Baltic, the cod consumed were slightly larger. Size classes below 8 cm in particular were almost absent, while cod >20 cm were ingested more frequently. Clearly, mainly 0- and 1-group cod are affected by cannibalism.

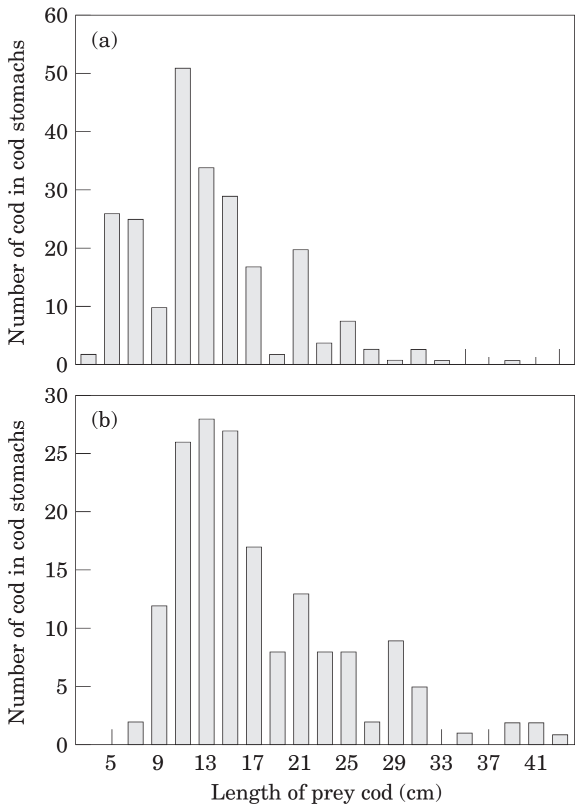

Figure 2. Length distributions of cod as prey (2 cm length groups) in the Central Baltic (a) and Western Baltic (b). Sample sizes are 237 and 171, respectively.

Standard MSVPA runs

Recruitment of Eastern Baltic cod, along with the corresponding annual removal by cannibalism as estimated

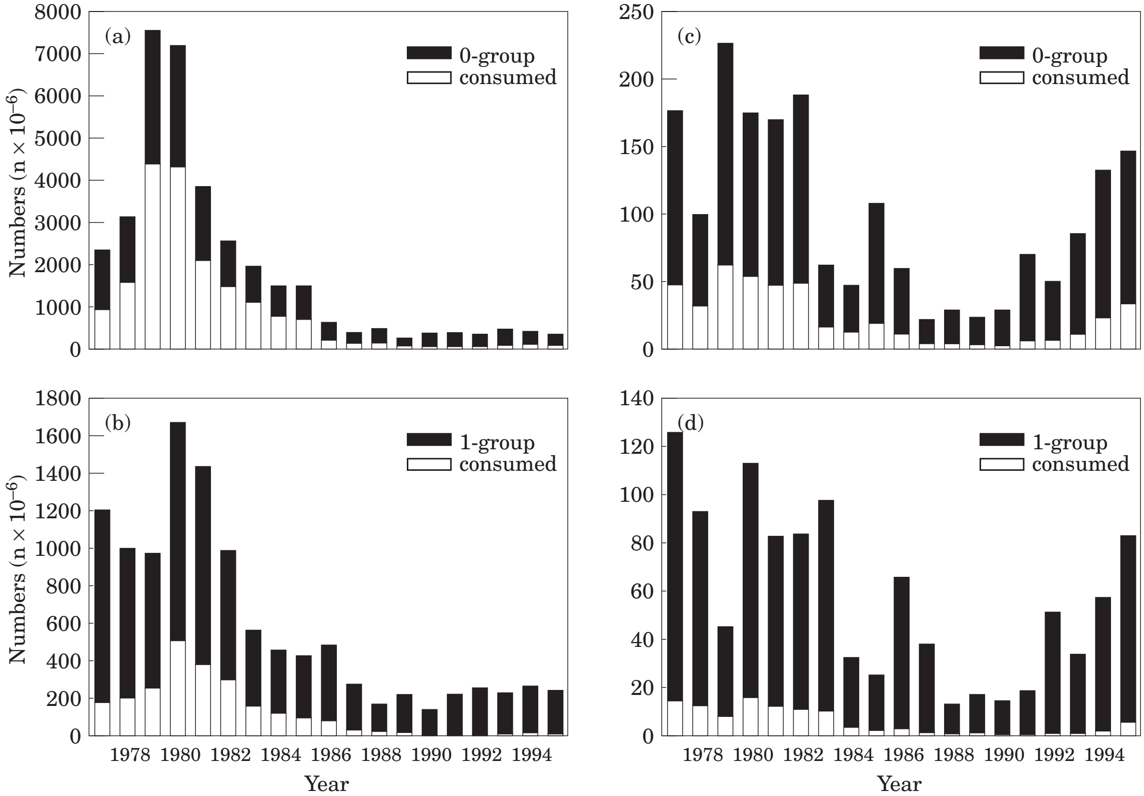

Figure 3. Abundance of recruits and numbers consumed by cod estimated by standard MSVPA for (a) 0-group in the Central Baltic, (b) 1-group in the Central Baltic, (c) 0-group in the Western Baltic, and (d) 1-group in the Western Baltic.

by standard MSVPA, shows a clear peak for the 0-group in 1979/1980, followed by a dramatic decline until 1987 to about 5% of the maximum level (Fig. 3a). After reaching the lowest value on record in 1989, there has been a slight increase. Estimated cannibalism in the 3rd and 4th quarters was a major cause of mortality until 1988, i.e. responsible for removing 32–60% of the initial abundance. Since 1989, predation pressure has declined to 14–25% removal during the 2nd half of the year. For age 1, a similar decreasing trend in abundance and cannibalism is observed between 1980 and 1988 (Fig. 3b). In contrast to age 0, however, high recruitment levels were already reached in 1977–1978, which may be explained by the relatively low predation on 0-group during these years. Cannibalism on age 1 accounted for 14–31% of the initial abundance, with highest values also in the first half of the 1980s and a decline to <10% in recent years.

Recruitment of 0-group cod in the Western Baltic is more variable, with high values in 1979–1982, a decreasing trend until 1987, and an increase to relatively high levels in recent years (Fig. 3c, d). Numbers of age 0 consumed were about 24–31% at the beginning of the time series, a decrease to a minimum of 7% in 1991, and an increase to 23% in 1995. As in the Central Baltic, consumption of 1-group was considerably lower. Annual removal was estimated at 12–18% until the mid-1980s and well below 10% in the remaining years. Annual removals of age-group 2 cod were relatively low in both assessment areas, i.e. <10% and <5% in the Eastern and Western Baltic, respectively.

Periods of high cannibalism coincide in both areas with high predator stock sizes (Fig. 4) and only to a lesser extent with a high amount of cod in the stomach contents (Fig. 1). In the Central Baltic, the highest diet contributions of cod were recorded in 1977–1979 and 1987, while cannibalism in terms of numbers consumed as determined by MSVPA peaked in 1979–1983. Also in the Western Baltic, highest predation mortalities were estimated for years when the amount of cod in stomachs was fairly low to moderate (1978–1980). The estimated increase in predation pressure in recent years is not reflected in the diet.

Alternative estimates of cannibalism in the Central Baltic

When the standard suitability submodel is replaced by the original suitability submodel, the dynamics of

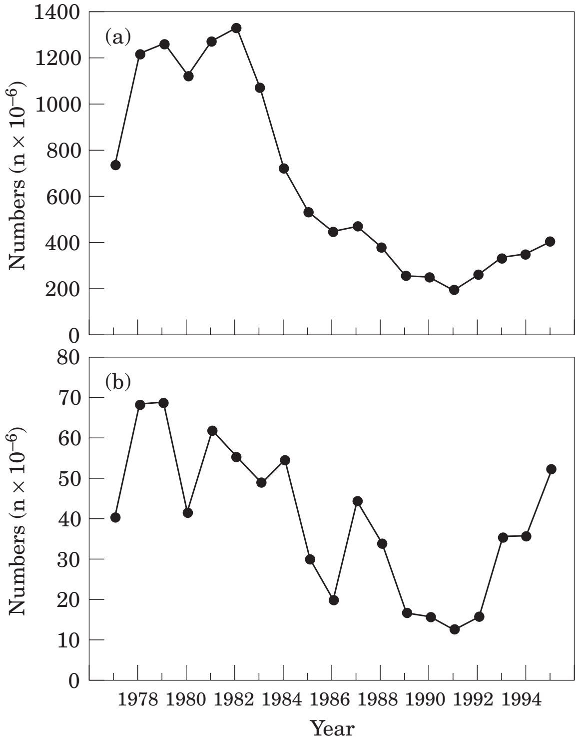

Figure 4. Predator stock sizes (age group 2+) in the Central Baltic (a) and the Western Baltic (b).

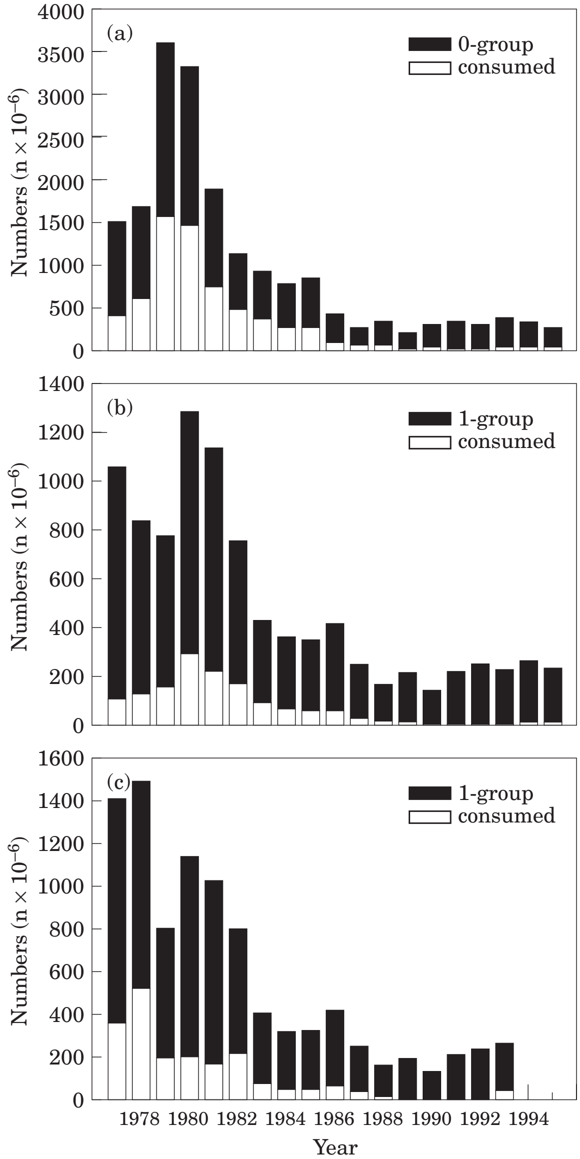

Figure 5. Abundance of recruits and numbers consumed by cod in the Central Baltic estimated by MSVPA with original suitability submodel for 0-group (a) and 1-group (b) as well as without suitability submodel for 1-group (c).

cannibalism and recruitment during the time series remain basically unaffected (cf. Fig. 5a, b and Fig. 3a, b). However, both the level of cannibalism and, as a consequence, the recruitment of 0- and 1-group cod have changed. The annual removals due to cannibalism were 25–43% (age 0) and 30–46% (age 1) lower than in standard MSVPA. Maximum deviations occurred in years of low cannibalism. Recruitment of 0-group cod determined on the basis of the original suitability submodel was 11–55% lower than in the standard MSVPA. The corresponding deviations for age 1 were only 4–24%.

The calculations for the model without a suitability submodel do not allow estimates of predation for years without stomach content data and therefore the time series is restricted to 1977–1993 (Fig. 6c). Cannibalism was particularly high in 1978, when 35% of the initial abundance was consumed. Estimated predation levels were also high in 1977, 1979, and 1982 (23–27 removal per year), a level reached in the standard MSVPA not before 1979. The high predation mortality at the beginning of the period along with considerably lower values derived for 1980/1981 resulted in highest recruitment of age 1 in 1977/1978 instead of 1980/1981. However, the decreasing trend in recruitment from 1981 to 1990 is common to both analyses, with the no-suitability procedure estimating in general lower abundances due to lower rates of cannibalism.

When comparing annual predation mortality rates derived from standard MSVPA and without a suitability submodel (Fig. 7a), the latter resulted in higher mortality rates in 3 years (1977, 1978, and 1993), all characterized by relatively high contributions of cod in the diet (Fig. 1). All other predation mortalities were either similar or below the estimate derived from standard MSVPA. When the no-suitability estimates are

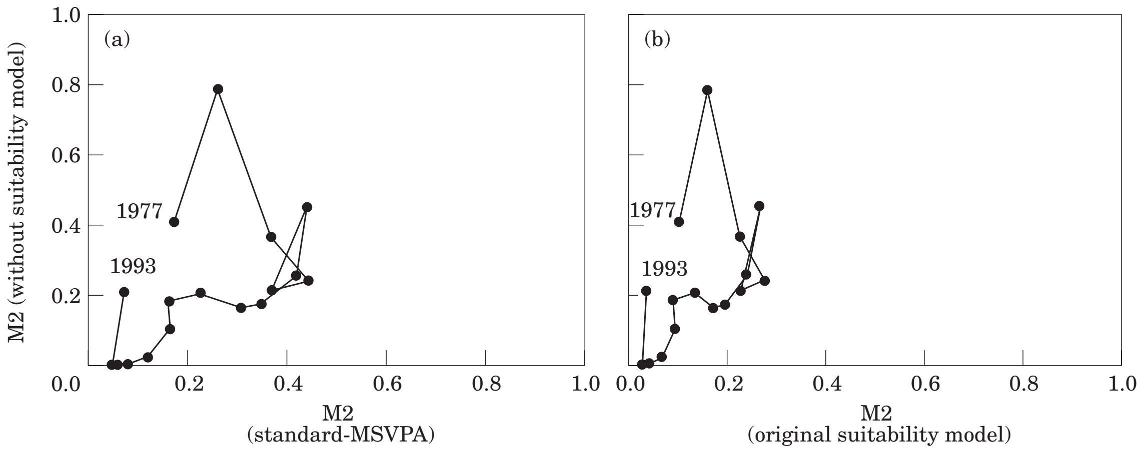

Figure 6. Predation mortality rates (M2) in Eastern Baltic 1-group cod estimated by MSVPA without suitability submodel versus corresponding estimates from standard MSVPA (a) and MSVPA using the original suitability submodel (b).

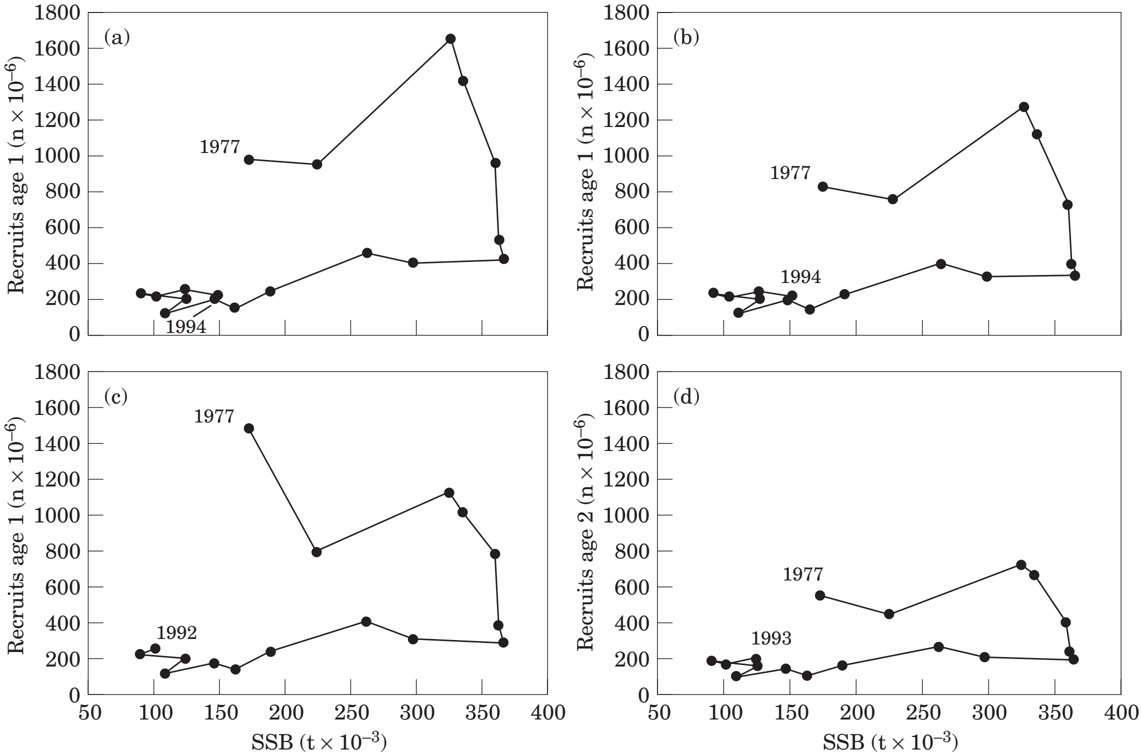

Figure 7. Stock-recruitment relationships of Eastern Baltic cod based on 1-group from standard MSVPA (a), MSVPA with original suitability submodel (b), MSVPA without suitability submodel (c) and based on 2-group cod from standard MSVPA.

compared with those derived from MSVPA with the original suitability submodel (Fig. 7b), coefficients were estimated by the latter model to be lower or at the same level in most years. In summary, the highest predation mortality rates were obtained with standard MSVPA (on average 0.33 year^{-1} in years of high cannibalism, 1977–1986, and 0.10 year^{-1} in the remaining years). Similar (during the first period) or intermediate values (0.07 year^{-1} during the latter) were obtained without a suitability submodel, and the lowest values with the original suitability submodel (0.20 and 0.05 year^{-1}, respectively).

Recruitment and spawning stock biomass

Stock-recruitment plots derived for Eastern Baltic cod based on the different approaches (Fig. 8) reveal largely the same pattern in more or less compressed form. Temporal development is characterized by two distinct recruitment levels during 1977–1980 and 1982–1995, respectively. Recruitment was highest in 1979 and 1980 at high SSB values. In 1981, recruitment started to drop and continued at a reduced level, even though SSB remained high initially.

The stock-recruitment relationship for age 2 derived from standard MSVPA shows similar dynamics. This plot is only marginally different from the one obtained from single-species assessment (ICES, 1997a), suggesting that the incorporation of predation does not markedly change our perception of the relationship between stock and recruitment at an older age.

Discussion

The stomach sampling procedure and stomach content analysis as well as the data compilation procedure (Sparholt, 1993; Sparholt *et al.*, 1992) applied in the two areas have been reviewed recently with respect to the reliability of data on cod in cod stomachs (ICES, 1997a). The most critical point in the stomach sampling scheme is that sampling has not always been evenly distributed over the areas inhabited by the older age groups, but has been concentrated in areas where juvenile cod are generally abundant. This is because data collections were associated with trawl surveys directed to estimation of cod year-class strength. ICES (1997a) has identified a time and area effect in the amount of cod found in cod stomachs based on stomach content data from the Western Baltic. However, neither a detailed analysis nor the application of appropriate spatial weighting of stomach contents is presently possible, because no spatial resolution within Subdivisions is incorporated in the stomach content database. For the Central Baltic, Uzars and Pliksh (this volume) present a first analysis of the inter dependence of juvenile cod distribution and intensity of cannibalism.

Feeding in trawls may also bias stomach content data, if not dealt with appropriately during sampling and analysis. However, ICES (1997a) considers that the impact on cod as prey is probably not higher than for other prey species and may well be below 10% in terms of stomach content in weight. Other potential sources of errors (feeding on discards, misidentification, data compilation methods) also appear to be of minor importance.

Reliability of MSVPA is subject to many problems related to reliability of input catch at age, weight-at-age data, consumption rates, etc. (ICES, 1997a, b, 1999). However, this should not affect the intercomparisons of different submodels because the same data set was used in all calculations.

The biomass of other food available in the systems was assumed to be constant. Although the actual value has no impact on MSVPA results (Sparholt, 1994), keeping the amount of other food constant might be misleading. A prolonged stagnation period (Matthäus and Lass, 1995) reduces the suitable habitat for macrozoobenthos in deeper areas of the Central Baltic and improves environmental conditions for benthos in intermediate depths due to the concurrent lowering of the halocline (HELCOM, 1997).

The original suitability submodel of MSVPA described by Gislason and Sparre (1987) was created for application in the North Sea, for which extensive stomach content data were only available for one particular year. This submodel has also been used in the Baltic MSVPA until a modification was introduced (ICES, 1992b). Although the limitations and advantages of both models have been intensively discussed (ICES, 1994a), no consensus about the method to be preferred has been reached.

There are two reasons for trying to circumvent any suitability submodel by using only available stomach content data in estimating predation rates. Firstly, it seems inconsistent to assume that suitability coefficients remain constant, when weight at age varies between years and even shows a time trend. Secondly, considerable changes have occurred in the relative distribution of adult and juvenile cod in relation to the decline of the Eastern Baltic stock. This would violate the assumption that an average suitability coefficient for the entire period reflects the mean relative spatial distribution of predator and prey as well as the probability that the predator will catch the prey once encountered (Larsen and Gislason, 1992). In avoiding any suitability submodel, missing quarterly stomach content values were replaced by an average of remaining quarters in a given year. Other substitutions would have been possible, e.g. between quarters in preceding and succeeding years. However, as the coverage with stomach samples in the Central Baltic is quite good (ICES, 1997a), the few substitutions required are expected to have had a minor impact on the estimated consumption. Up to 1990, there are only three cases of missing data in the third quarter. For recent years, the coverage is less satisfactory because for instance no stomachs have been sampled in the second quarter at all. Thus, the estimated predation on cod in 1991–1993 has to be considered as uncertain.

The food composition of cod in the Baltic has been studied intensively since the 1960s (e.g. Arntz, 1977/1978; Zalachowski, 1986; Schulz, 1988; Uzars, 1993). The international database contains the majority of the data collected during the period 1977–1993 and thus the results are not particularly new. Although cannibalism has been regularly encountered, the incidence and also the relative contribution to the total diet in terms of weight was low, which led to the exclusion of cod as prey from the first MSVPA modelling approaches (ICES, 1987). However, as demonstrated by Jensen and Sparholt (1992), even the comparatively small contribution to the diet resulted in a considerable predation mortality at high predator stock levels. Inspired by this result, Uzars (1995) analysed the Latvian diet composition data, consisting of 69 000 stomachs sampled in the period 1963–1990, with respect to cannibalism. High weight percentages of cod as prey of adult cod (over 10%) were encountered in Subdivision 28 in 1975–1979 and intermediate values (5–10%) in 1963/64 and 1985. In Subdivision 26, similar high contributions to the diet were only found in 1968 and intermediate values in 1964, 1975, and 1977. In general, these data fit the time trend presented for the whole Eastern Baltic cod stock very well, which could be expected because the Latvian data are included in the database. However, the contribution to the diet in terms of weight is on average lower in the Latvian analysis, as Polish data (Zalachowski, 1986) integrated into the international database showed higher incidences of cannibalism.

An analysis conducted by Uzars and Plikshs (2000) has revealed that cannibalism in Subdivision 28 was most intense in coastal waters at 40–80 m depth during late autumn and early winter, which can be explained by the spatial overlap of settling 0-group and adult cod on their feeding grounds. In Subdivision 26, cannibalism was highest in the Gdańsk Deep at water depths below 80 m during March/April, indicating predation by pre-spawning cod concentrations. From a comparison of juvenile cod abundance, indices obtained by trawl surveys and concurrently sampled cod stomach contents, they concluded that cannibalism is positively related to the size of the recruiting year class, suggesting a density-dependent process. The declining intensity of cannibalism, especially since the late 1980s, may thus be related to a reduced reproductive success and consequently decreased abundance of recruits. However, other explanations are possible: (1) the decrease in the cod stock and concurrent increase in the sprat stock, one of the major prey species, support the hypothesis that cannibalism occurs especially in times of limited availability of preferred prey; (2) the shift in the horizontal distribution of cod from the Gotland Basin to the Bornholm Basin may have reduced cannibalism due to limited predator/prey overlap (ICES, 1999); (3) the unfavourable oxygen conditions during the stagnation period may have caused a shift in the vertical distribution of older cod to a more pelagic life style in and around the main basins (Plikshs *et al.*, 1990; Tomkiewicz *et al.*, 1998), while juvenile cod were probably avoiding these areas because of the limited food supply. The first explanation is related to prey switching (Murdoch, 1969), which is not accounted for in the MSVPA suitability submodel. The other two hypotheses could only be modelled taking a spatially disaggregated approach.

The temporal and spatial sampling coverage in the Western Baltic is considerably lower than in the Central Baltic. The third quarter, in particular, is often not well represented, while stomach sampling in Subdivision 22 ceased completely in 1989. Thus, the calculation of predation mortalities independently of a suitability submodel appears to be unreliable, unless missing stomach content data can be estimated statistically. The change in sampling scheme might explain why cannibalism was not encountered in the Western Baltic since 1989, because a comparison of stomach contents from different areas revealed a considerably lower incidence of cannibalism in Subdivision 24 (ICES, 1997a).

Using the original stomach data together with MSVPA-generated predator stock sizes led to a peak in Eastern Baltic cod cannibalism on age 1 in 1977/1978. This is a direct consequence of the stomach data, which displayed the highest weight contributions of cod to the diet during the same period, and of the relatively high predator abundance. In contrast, the application of the standard suitability submodel shows the highest rates of cannibalism in 1980/1981. This may be explained by partly averaging out the effect of annual variations in stomach content as well as diet composition by applying constant suitability coefficients. Thus, predation mortalities are driven mainly by high predator abundance and by the age structure of the cod stock. Cod as prey has a higher suitability for older predator ages. Age 4 cod reached a maximum abundance in 1980 and thus evoked a peak in cannibalism on 1-group fish, while the even higher predator stock sizes in 1981/1982 consist to a large extent of 2-group. The trends in predator stock size and structure are, of course, the same for the calculations without a suitability submodel, but in that case the effect of predator stock on predation is apparently overridden by the stomach content data.

In other words, application of the standard suitability submodel instead of the original stomach content data creates temporal dynamics of cannibalism which are largely dependent on predator abundance and age structure, while the signal in the original data is suppressed. The original suitability submodel behaves similarly, but the estimated predation mortality was consistently lower than from the standard procedure.

Cannibalism has also been described for various other cod stocks (Pálsson, 1994; Bogstad *et al.*, 1994). Comparing the average weight percentage contribution of cod with the diet of cod indicates considerable variability between ecosystems. Cod constituted on average 1.1% of the diet in Newfoundland waters (1979), 3.9% in the Barents Sea (1949–1992), 6% in Icelandic waters (1979–1992), and in the North Sea 4% in 1981 and 1.6% in 1991 (Pálsson, 1994). In comparison, the average contributions in the Central and Western Baltic were 6.9 and 8.2%, respectively, indicating a more pronounced effect of cannibalism.

The size frequency of cod ingested by cod in the North Sea (Daan, 1973) is similar to that in the Baltic, the bulk being <15 cm. The occurrence of 20–30 cm cod is slightly higher in the Baltic, and cod >30 cm were absent in the North Sea samples. Compared with Icelandic waters (50 cm) and the Barents Sea (60 cm), the maximum size of cod as prey is small in the Baltic (38 and 42 cm in the Central and Western Baltic, respectively), but is in the range found in Newfoundland waters (Pálsson, 1994).

The average predation mortality for the Central Baltic is comparable to the estimate derived from MSVPA for the North Sea (ICES, 1994b), while predation mortality in the Western Baltic was on average lower, even when predator and prey abundance were relatively high. Nevertheless, the contribution to the diet in terms of weight was in general higher.

Regardless of whether cannibalism and recruitment are estimated from MSVPA utilizing different suitability submodels or directly on the basis of stomach contents, the stock-recruitment relationships derived for Eastern Baltic cod are similar with respect to shape and temporal dynamics.

The phase change from high recruitment in 1977–1980 to relatively low recruitment after 1982, independently of SSB, indicates substantial environmental influence on recruitment (Sparholt, 1996). Specifically, the volume of water suitable for successful egg development (Plikshs *et al.*, 1993) and the wind energy driving the transport of larvae to suitable nursery areas (Hinrichsen *et al.*, 2000) may be important factors in explaining part of the recruitment variability. Other potentially important factors are viability of the eggs produced in relation to stock structure (Vallin and Nissling, 1999), contamination with toxic substances (Pedersen *et al.*, 1997), and predation on early life stages (Köster and Möllmann, 2000). Thus, high recruitment is unlikely to occur unless environmental conditions allow a high survival of eggs and larvae, independently of parental stock size (at least within historical limits) or cannibalism. However, if the environmental conditions are suitable for reproduction, cannibalism may have a considerable impact on the survival of juvenile cod. Depending on the choice of the suitability submodel, on average 25–38% and 11–17% of 0- and 1-group cod, respectively, are removed by cannibalism from the Central Baltic. The independent estimate for 1-group cod was intermediate (14%). In the Western Baltic, on average only 19% and 9% of the 0- and 1-group cod were consumed according to standard MSVPA.

The explanation as to why inclusion or exclusion of cannibalism in stock assessment does not affect the stock-recruitment relationship to any large extent is simple: recruitment is mainly governed by the prevailing environmental conditions in the Baltic. However, this does not imply that cannibalism can be ignored in exploratory approaches to model reproductive success or in predictive recruitment models. Recruitment estimates derived by a VPA-type of analysis without cannibalism will have the tendency to mask high survival of early life stages by the compensatory nature of cannibalism and therefore reduce the chance for identifying the appropriate factors affecting reproductive success. Also, cannibalism has of course to be considered in models predicting recruitment, as this process might remove up to half of the surviving offspring within the first 2 years of life. To keep a balance between sufficient quantity and quality of egg production by the parental stock and the cannibalism exerted later by the same stock is an important issue for management of the Baltic cod fisheries. However, other factors that are presently not accounted for in stock assessment may influence cannibalism, such as the degree of predator/prey overlap driven by specific hydrographic features (Uzars and Plikshs, 2000) and the availability of other prey. Clearly, more information is needed for a reliable forecast of the impact of cannibalism on recruitment.

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