

Developing Baltic cod recruitment models.

II. Incorporation of environmental variability and species interaction

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Abstract: We investigate whether a process-oriented approach based on the results of field, laboratory, and modelling studies can be used to develop a stock–environment–recruitment model for Central Baltic cod (*Gadus morhua*). Based on exploratory statistical analysis, significant variables influencing survival of early life stages and varying systematically among spawning sites were incorporated into stock–recruitment models, first for major cod spawning sites and then combined for the entire Central Baltic. Variables identified included potential egg production by the spawning stock, abiotic conditions affecting survival of eggs, predation by clupeids on eggs, larval transport, and cannibalism. Results showed that recruitment in the most important spawning area, the Bornholm Basin, during 1976–1995 was related to egg production; however, other factors affecting survival of the eggs (oxygen conditions, predation) were also significant and when incorporated explained 69% of the variation in 0-group recruitment. In other spawning areas, variable hydrographic conditions did not allow for regular successful egg development. Hence, relatively simple models proved sufficient to predict recruitment of 0-group cod in these areas, suggesting that key biotic and abiotic processes can be successfully incorporated into recruitment models.

Résumé : Nous cherchons à savoir si une approche axée sur les processus et basée sur des études de terrain, de laboratoire et de modélisation peut servir à développer un modèle stock–milieu–recrutement pour la morue franche (*Gadus morhua*) de la Baltique centrale. À la suite d'une analyse statistique exploratoire, des variables significatives qui influençaient la survie des premiers stades et qui variaient systématiquement d'un site de fraie à un autre ont été incorporées dans des modèles de stock–recrutement, d'abord pour les sites de fraie les plus importants et ensuite combinés pour toute la Baltique centrale. Les variables identifiées comprennent la production potentielle d'oeufs par le stock de géniteurs, les conditions abiotiques qui affectent la survie des oeufs, la prédation des oeufs par les clupéidés, le transport des larves et le cannibalisme. Les résultats indiquent que le recrutement durant la période 1976 à 1995 au site de fraie le plus important, le bassin de Bornholm, était en relation avec la production d'oeufs; cependant, d'autres facteurs significatifs affectaient la survie des oeufs (oxygénation, prédation) et, une fois incorporés, ils expliquaient 69% de la variation dans le recrutement du groupe 0. À d'autres sites de fraie, les conditions hydrographiques variables ne permettaient pas un développement normal et réussi des oeufs. Ainsi, des modèles relativement simples se sont avérés adéquats pour prédire le recrutement des morues du groupe 0 dans ces sites, ce qui laisse croire que des processus dominants abiotiques et biotiques peuvent être incorporés avec succès dans les modèles de recrutement.

[Traduit par la Rédaction]

Introduction

Resolving processes driving recruitment variability in fish populations is one of the major challenges facing fisheries scientists and oceanographers (Cushing 1995). For the vast majority of fish stocks, processes causing interannual variations in recruitment remain largely unexplained, resulting in

a major source of uncertainty in the management of fish stocks (e.g., defining biological reference points). A number of key processes have been identified as candidates for reducing uncertainty in the prediction of fish stock recruitment. For example, it is now evident that variations in stock structure and condition of the adults can affect the level of egg production (Marshall et al. 1998; Marteinsdottir and

Received August 18, 2000. Accepted April 25, 2001. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on July 18, 2001.
J15931

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Thorarinsson 1998; Marshall and Frank 1999) and impact on egg viability and buoyancy. Variations in egg viability and buoyancy influence the survival probability of eggs and larvae (e.g., Kjesbu et al. 1996; Nissling et al. 1998; Trippel 1998) and, combined with variations in stock reproductive effort, are targeted as being responsible for recruitment fluctuations (Marshall et al. 1998; Marteinsdottir and Thorarinsson 1998; Jarre-Teichmann et al. 2000). Furthermore, the effects of predation on fish eggs and larvae (e.g., Bailey and Houde 1989) have the potential to reduce the reproductive success of a stock. Similarly, the loss of eggs and larvae due to transport to suboptimal environments (e.g., Heath and Gallego 1998) can influence recruitment negatively.

In the last 10–15 years, it has been possible to examine many of the major processes currently believed to affect recruitment variability of the cod (*Gadus morhua*) in the Central Baltic (e.g., Bage and Thurow 1994; MacKenzie et al. 1996). As a result, several new time series are becoming available for variables relating to these processes. In particular, data series have been compiled for egg production (including sex-specific maturity ogives, Tomkiewicz et al. 1997; individual fecundity, Kraus et al. 2000), egg characteristics (buoyancy and viability; Nissling et al. 1998), abiotic factors affecting egg survival (Plikshs et al. 1993; Wieland et al. 1994; MacKenzie et al. 2000), estimates of egg and larval abundances in spawning areas (e.g., Plikshs et al. 1993; Wieland et al. 2000), hydrographic processes affecting larval and 0-group distribution (Voss et al. 1999; Hinrichsen et al. 2001), predation on early life history stages (Köster and Möllmann 2000a), and cannibalism (Sparholt 1996; Neuenfeldt and Köster 2000).

It is of interest, therefore, to use this material to investigate whether a process-oriented recruitment model can be developed and to identify what information might be lacking to make such a model reliable. Our approach attempts to follow the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage according to Paulik's (1973) framework for examining the entire life history process, a concept broadly accepted but not really implemented yet (Rothschild 2000).

Materials and methods

Stock–recruitment relationships are constructed for different subdivisions of the Central Baltic Sea (see code of International Council for the Exploration of the Sea (ICES)) containing spawning areas with distinct hydrographic regimes (MacKenzie et al. 2000), recruitment success, and stock development trends (Sparholt and Tomkiewicz 2000). The variability in stock–recruitment relationships has been established based on area-disaggregated multi-species virtual population analysis (MSVPA) (Köster et al. 2001). Here, we extend this exercise to investigate the potential environmental processes affecting reproductive success. Environmental variables included are listed in Table 1 and are described in detail below. Based on time series of these variables identified to have a significant impact on production or survival rates of the various life stages, stock–recruitment models are constructed for Subdivisions 25, 26, and 28 containing the major cod spawning areas of the Bornholm Basin, Gdansk Deep, and Gotland Basin. Stock–recruitment models having the highest predictive power were then utilised to establish a combined stock and recruitment model for

the entire Central Baltic by integrating predicted values over the different subdivisions.

Spawning stock size and distribution

Spawning stock abundance and biomass estimates for Subdivisions 25, 26, and 28 were obtained by performing area-disaggregated MSVPA runs for the period 1977–1996 (Köster et al. 2001). In order to extend the time series to include 1976, a year with well above average reproductive success, the MSVPA abundance estimates were extrapolated backwards. This was achieved by assuming the same age-specific natural mortalities in 1976 as in 1977, applying absolute fishing mortality rates derived for 1976 by the regular stock assessment (ICES 1997) and relative quarterly fishing mortalities as determined by the area-disaggregated MSVPA runs for 1977.

Recruitment

Recruitment estimates for ages 0 and 1 in the different subdivisions were derived by area-disaggregated MSVPA runs (Köster et al. 2001). It should be noted that estimates of recruitment in 1996 were omitted from the analysis, as they are heavily dependent on the tuning performed. Alternative area-specific recruitment indices of age-group 1 were utilised for validation of model output. These were derived by CORE (1998) from international bottom trawl surveys conducted since 1982 (Sparholt and Tomkiewicz 2000).

Potential egg production

To estimate the basin-specific seasonal egg production by the spawning stock, first, sex ratios and female maturity ogives were applied to basin-specific population abundances according to age derived by area-disaggregated MSVPA runs. Annual sex ratios and proportions of sexually mature individuals were utilised for Subdivision 25 in 1986–1996 and for Subdivision 26 in 1993–1996; otherwise, 5-year averages were used (Tomkiewicz et al. 1997). Revised estimates of basin- and sex-specific spawning stock biomass (SSB) were coupled to a time series of average relative fecundity values, i.e., individual fecundity per unit of total body weight (Shapiro 1988; Bleil and Oeberst 1996; Kraus et al. 2000), to estimate the annual potential egg production (Appendix Tables A1 and A2). Missing information (Table 1) was derived by linear interpolation. The applied procedure was enabled by the observation that relative fecundity in Baltic cod is independent of body size (Kraus et al. 2000). It should be noted that a significant variability in relative fecundity was detected between years but not between spawning areas within a specific year (Kraus et al. 2000); hence, relative fecundity was assumed to be similar among areas.

Observed egg and larval standing stocks and production

Mean annual egg and larval abundance values are available for the different subdivisions from ichthyoplankton surveys in 1976–1996 (Appendix Tables A1 and A2) based on data compiled by Karasiova (1995), E.M. Karasiova (Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia, personal communication), MacKenzie et al. (1996), Makarchouk (1997), A. Makarchouk (Latvian Fisheries Research Institute, Riga, Latvia, personal communication), R. Voss (Institute of Marine Sciences, Kiel, Germany, personal communication), and Wieland et al. (2000). Egg abundance estimates are based on a 3-month period encompassing the main spawning period, i.e., April–June up to 1989 and successively shifted to May–June (1990–1992) and June–August (1993–1996) to take into account a shift in the spawning period in recent years (Wieland et al. 2000). A more detailed estimate of daily egg production rates was utilised for the Bornholm Basin based on ichthyoplankton surveys performed from 1986 to 1996 (Appendix Table A1). Estimates of abundance were

Table 1. Variables incorporated into the statistical exploratory analysis and subsequent recruitment modelling, information on methodology, time periods and areas covered as well as data sources.

Variable	Basis	Time period	Subdivision(s)	Source of time series
Potential egg production	Stock numbers from MSVPA	1977–1996	25, 26, 28	Köster et al. 2001
	Sex ratios, maturity ogives	1980–1996	25, 26, 28	Tomkiewicz et al. 1997
	Average relative fecundity	1976–1978, 1983–1984	26, 28	Shapiro 1988
		1987–1992, 1995–1996	25, 26	Kraus et al. 2000
Egg and larval abundance	Ichthyoplankton surveys	1994	25	Bleil and Oeberst 1996
		1994–1996	26	Karasiova 1995; E.M. Karasiova, unpublished data
		1976–1985	25	MacKenzie et al. 1996
		1991–1996	26, 28	Makarchouk 1997; A. Makarchouk, unpublished data
		1976–1990	26, 28	Plikshs et al. 1993
Oxygen-related egg survival	Vertical distribution of eggs in relation to density	1986–1996	25	Wieland et al. 2000; R. Voss, unpublished data
			25	This study, based on Wieland and Jarre-Teichmann 1997
Egg consumption by clupeids	Experiments on viable hatch		25, 26	Wieland et al. 1994; Rohlf 1999
	Cod egg consumption rates	1988–1996	25	Köster and Möllmann 2000a
Recruitment age 1	Predator populations	1976–1996	25	Köster and Möllmann 2000b; Köster et al. 2001
	Vertical predator–prey overlap	1976–1996	25	This study, based on above information
Larval transport index	Cumulative wind energy	1976–1996	25	Jarre-Teichmann et al. 2000
	Direction of transport dependent on wind forcing	1976–1996	25	This study, based on model runs (Hinrichsen et al. 2001)
Cannibalism rates of juveniles	MSVPA	1977–1996	25, 26, 28	Köster et al. 2001
Recruitment age 1	Bottom trawl survey	1980–1996	25, 26, 28	CORE 1998

Note: See text for addresses of authors of unpublished data.

obtained based on egg stage (Thompson and Riley 1981) specific abundance data and egg development – temperature relationships (Wieland et al. 1994). Temperatures at the depth of the centre of mass of eggs were utilised for the estimation of developmental period. These were obtained from CTD (conductivity–temperature–depth) casts performed concurrently with the vertically resolving ichthyoplankton sampling (Wieland and Jarre-Teichmann 1997). Finally, daily egg production rates were calculated by dividing the stage-specific abundance of live eggs by the development time of each egg stage. Larval abundance data refer to a period similar to the 3-month period of egg abundance estimates but shifted to account for the 2- to 4-week period of development from egg to larvae (Wieland et al. 1994).

Impact of oxygen concentration on egg survival

Estimates of the “reproductive volume,” i.e., the volume of water suitable for successful egg development (Plikshs et al. 1993), in the different subdivisions were obtained from MacKenzie et al. (2000) for the peak spawning periods (Appendix Tables A1 and A2). However, for the Bornholm Basin, two modifications of this index were performed based on the suitability of the spawning volume for successful egg development.

The first modification was based on the oxygen conditions within the salinity range over which cod eggs are neutrally buoyant, giving a measure of the quality of the reproductive volume for successful development of cod eggs (Appendix Table A1). This modification is based on an integration of the mean oxygen concentrations per 1-m depth interval over the thickness of the spawn-

ing layer using stations similar to those employed in the original calculation of the spawning volume (MacKenzie et al. 2000).

For the second modification, the fraction of the egg production surviving in each year (Appendix Table A1) was estimated based on (i) the predicted vertical distribution of cod eggs in 5-m depth intervals relative to water density (see below), (ii) the oxygen concentration measured at each depth interval, and (iii) an oxygen concentration – cod egg survival relationship derived from laboratory experiments (Wieland et al. 1994) with percent survival up to the end of the yolk-sac phase (v) given by

$$v = -0.5689 + 0.3368 \times O_2 - 0.0173 \times O_2^2 \quad (n = 15, r^2 = 0.94)$$

where O_2 is the oxygen concentration at depth of incubation (Rohlf 1999). To model the vertical distribution of eggs, the observed distribution of the youngest egg stage (IA) obtained from vertically resolving ichthyoplankton sampling in 1986–1996 (Wieland and Jarre-Teichmann 1997) was examined in relation to water density profiles by fitting a parabolic function to the log relative distribution data (IA):

$$\ln(\text{IA}_z) = a + b \times \rho_z + c \times \rho_z^2$$

where ρ_z is the water density at depth interval z . However, cod eggs become less buoyant after inflows when higher salinity occurs in the bottom water (Wieland and Jarre-Teichmann 1997). Hence, these hydrographic situations were modelled separately. In order to adjust for this change in buoyancy, we defined inflow situations in

the Bornholm Basin by the depth at which the oxygen concentration reached $2 \text{ mL}\cdot\text{L}^{-1}$ (inflow >85 m) and by the average salinity within the reproductive volume (inflow salinity >13.5 psu). Furthermore, upon inspection of the data, a seasonal effect in the vertical distribution of cod eggs was detected. Hence, the following hydrographic and spawning situations were defined to group the data: (i) stagnation/early spawning, (ii) stagnation/late spawning, (iii) inflow/early spawning, and (iv) inflow/late spawning. The fitted parabolic functions explain between 69 and 80% of the variance in the relative vertical distribution of cod eggs.

Predation on cod eggs by clupeids

Consumption of cod eggs by sprat (*Sprattus sprattus*) has a significant impact on egg survival in the Bornholm Basin in spring and early summer, while later in the cod spawning season, herring (*Clupea harengus*) replaces sprat as the principal predator (Köster and Möllmann 2000a). Predation pressure by sprat decreased throughout the 1990s, while the impact of herring increased (Köster and Möllmann 2000a), due to a delay in spawning of cod (Wieland et al. 2000). Apart from intra- and interannual trends, spatial variation in the intensity of egg predation occurs, with consumption in the Gdansk Deep and Gotland Basin being considerably lower than in the Bornholm Basin. This difference has been attributed to (i) the lack of light for successful feeding on the transparent and motionless cod eggs at the increased depth of occurrence in these eastern spawning basins caused by lower salinity within and below the halocline (Geldmacher 1998) and (ii) a related limited vertical overlap between cod eggs and their clupeid predators (CORE 1998). Thus, predation on cod eggs by clupeids was included as a parameter in the model only in Subdivision 25.

Köster and Möllmann (2000a) found that low oxygen concentration in the bottom water limited the vertical distribution of clupeids during the daylight feeding period, while the density regime determined the vertical distribution of cod eggs. Based on these observations, the average capture depth of the clupeids (Köster and Möllmann 2000a) and the average depth in which highest concentrations of cod eggs occurred (Wieland and Jarre-Teichmann 1997) were combined into an index of vertical predator-prey overlap determined for sampling dates in 1990–1996. Assuming an average residence depth of clupeids to correspond to the depth of occurrence of an oxygen concentration of $2 \text{ mL}\cdot\text{L}^{-1}$, corrected by an offset of 3 m as observed in 1990–1996, allowed, in combination with observed (1986–1989) and modelled vertical distributions of cod eggs (1976–1985), the calculation of predator-prey overlap indices for the entire time series. In inflow situations, when oxygenated water occurred over the whole water column, the maximum average depth of capture encountered in 1994, a year when anoxic conditions did not exist in the basin, was utilised as dwelling depths of clupeids. Applying a linear relationship between the ratio of hourly consumption and egg abundance with the vertical predator-prey overlap index ($n = 8$; sprat: $r^2 = 0.77$, herring: $r^2 = 0.42$) enabled the prediction of consumption rates by predator populations (Köster and Möllmann 2000b) for the main spawning periods in May 1976–1992. For the period from 1993 on, characterised by late cod spawning activity (Wieland et al. 2000), the mean observed consumption relative to cod egg availability was utilised. Predation pressure was introduced into the analysis as a relative index expressed as consumption per standing stock of eggs (Appendix Table A1) scaled to the potential egg production, setting the maximum predation pressure to result in a 95% egg removal. This approach allowed inclusion of predation on eggs into the time series by subtracting the amount consumed from the amount produced.

Larval retention and transport

Jarre-Teichmann et al. (2000) demonstrated that the cumulative wind energy at peak spawning time impacts on cod recruitment

success, the suggested process being a transport of larvae and pelagic juveniles to coastal nursery habitats favourable for recruitment during periods of high wind energy and a retention in the central basins during periods of low wind stress of variable wind direction (Hinrichsen et al. 2001).

To incorporate these transport processes into our exploratory analysis, the cumulative wind energy as utilised by Jarre-Teichmann et al. (2000) was modified. The starting point for the integration of wind energy was set to the annual date of peak larval abundance assuming a larval drift period of 45 days. Studies by Voss et al. (1999) and Hinrichsen et al. (2001) demonstrated that larval drift towards the west and north is caused primarily by winds of westerly and southerly direction, whereas winds of opposite direction result in larval transport to the south and east. Periods of transport identified are those in which sufficient wind energy occurs during 45 days (or less) after hatch to transport more than 50% of the hatched larvae to the northern or southern coastal environments of the Bornholm Basin (<30 m water depths). Periods of lower wind energy are defined as periods of retention. Thus, differences in cumulative wind energy between winds coming from the southern to western direction (defined as positive cumulative wind energy differences) and northern to eastern direction (negative differences) were calculated and converted into a relative frequency of occurrence of larval transport from the spawning ground towards coastal environments (Appendix Table A1). Wind energy was derived from a wind data time series at Christiansø (CORE 1998). The relative frequencies of larval occurrence within different coastal environments are based on results of hydrodynamic scenario modelling analysing drift patterns associated with wind forcing of different direction (Hinrichsen et al. 2001).

Cannibalism within the 0-group stage

Cannibalism has been implicated as an important density-dependent mechanism influencing Baltic cod recruitment success (Sparholt 1996). Estimates of cannibalism on 0-group cod are available for the time series from area-disaggregated MSVPA runs (Köster et al. 2001). These mortality rates can be utilised to estimate age-group 1 recruitment from 0-group abundance predicted by established stock-recruitment models, applying a residual mortality of $0.2\cdot\text{year}^{-1}$. However, in order to construct predictive models of recruitment at age 1 beyond the time period covered by the MSVPA, we related mortality due to cannibalism linearly to the adult biomass. This procedure has been suggested by ICES (1993) for herring and sprat as prey for cod.

Model construction and validation

The basis for developing stock-recruitment relationships for Baltic cod based on environmental and spatial heterogeneity is the identification of causal relationships between survival rates of different early and juvenile life stages, environmental factors, and species interactions. In order to do so, simple and multiple linear regression techniques were applied to the complete data series from 1976 to 1996 and a more extensive subset of these data available for Subdivision 25 from 1986 to 1995. Based on the resulting significant variables, stock-recruitment models with combinations of different factors were constructed for Subdivisions 25, 26, and 28 and subsequently combined for the entire Central Baltic.

The parameters of the area-specific models are based on the entire time series of data available. However, in order to obtain an indication of the sensitivity of parameter estimates for model configurations having the best predictive capabilities and to evaluate the accuracy of model predictions for time periods not represented by the model, the first 4 and 5 years of data, i.e., years with high reproductive success, were excluded and the models refitted utilising only data sets 1979–1995 and 1980–1995 for parameter estimation. Predictions from the refitted models were then compared with

observations for 1976 to 1979–1980. A similar test was performed for the periods 1991–1992 to 1995 utilising data subsets covering the periods 1976–1990 and 1976–1991 in order to establish whether the models are able to reproduce the increase in recruitment, which followed increased inflow activity since 1991 and especially the last major Baltic inflow in early 1993 (Matthäus and Lass 1995). As a further validation of the model, predicted 0-group abundance and cannibalism rates acting on 0-group were utilised to predict recruitment at age 1 and compared with corresponding area-specific recruitment indices obtained from international bottom trawl surveys (Sparholt and Tomkiewicz 2000).

Results

Explaining variability in stock–recruitment relationships

Survival during the egg stage

The two primary mechanisms influencing cod egg survival in Subdivision 25 are predation by clupeids and the oxygen conditions at the depth of incubation. In order to examine the effects of these processes on egg survival, the daily production of egg stage III from ichthyoplankton surveys was related to the potential egg production. Egg production at stage III was utilised as a proxy for the production of the oldest egg stage IV, as the abundance of this stage is highly variable due to a relatively short stage duration and hatching, which in Baltic cod already commences at this stage (Wieland et al. 1994). Justification for the use of potential egg production as an estimate of the reproductive effort is based on a high correlation between the production estimates of stage IA cod eggs from ichthyoplankton surveys and potential egg production (statistical model 1, $r^2 = 0.74$). Coefficients and significance levels as well as Durbin Watson statistics are given in Table 2 for each regression analysis performed. A linear regression of the egg survival up to stage III versus the oxygen-related egg survival (model 2, $p = 0.04$) explains 39% of the variance encountered, with a high positive residual in 1994 and negative residuals observed in 1995 and 1996 (Fig. 1a). Utilising the egg consumption index, a negative linear relationship (model 3, $p = 0.09$) explained 29% of the variance in egg survival until stage III (Fig. 1b). Incorporating both processes into the potential egg production (i.e., subtracting the consumed eggs and multiplying by the oxygen-related relative survival) revealed a significant linear regression (model 5, $p = 0.003$) with egg production at stage III ($r^2 = 0.66$). However, the potential egg production explained 53% of the variance alone (model 4). Again, difficulties in explaining values in recent years occurred, especially in 1994 (Fig. 1c). Excluding 1994 from the regression analysis increased the explained variance to 83% (model 6).

For Subdivisions 26 and 28, linear regressions of observed egg abundance values versus the potential egg production revealed a significant relationship ($p = 0.012$) only for Subdivision 28 (models 26 and 27, Table 3). However, a time trend in the residuals was obvious, with high positive residuals in the beginning of the time series, i.e., up to 1980, and primarily negative residuals thereafter. Since the beginning of the 1980s, egg abundance was less than expected from the available SSB, an observation explained by the occurrence of unfavourable oxygen conditions resulting in extremely high egg mortality. This is confirmed when observed egg

abundance versus potential egg production is regressed on the reproductive volume, yielding significant relationships for both areas (model 28, $p < 0.001$; model 29, $p = 0.001$), explaining 55 and 44% of the variance encountered, respectively (Table 3).

Survival until the larval stage

Linear regressions of the ratio of larval abundance to potential egg production, as a measure of survival to the larval stage, versus the oxygen-related egg survival as well as the consumption index revealed no significant relationships for Subdivision 25 (models 7 and 8, Table 2). Replacing the oxygen-related egg survival with the oxygen content in the reproductive volume revealed an improved, but still only weak relationship (model 9, $r^2 = 0.15$), while a significant relationship was derived for the larval abundance versus the potential egg production (model 10, $p = 0.026$). However, the relationship still explains only 23% of the variance encountered (Fig. 2a). A significant linear relationship of larval abundance per unit of egg production at stage III versus the oxygen-related egg survival as well as the predation index was found (model 11 and 12), but with a negative relationship for the oxygen impact and a positive one for the predation. The statistical models indicate a reduction in larval survival with increasing reproductive volume and decreasing egg predation pressure, both relationships being biologically not reasonable. There is also no direct relationship between larval abundance and egg production at stage III (model 13). The only sensible statistical model derived by the exploratory analyses is a multiple linear regression including potential egg production corrected for egg consumption ($p = 0.085$) and the oxygen content in the reproductive volume ($p = 0.062$) as independent variables (model 14). The model explained 31% of the variance in the larval abundance. The time series of observed and predicted values (Fig. 2b) clearly demonstrate that the model was unable to explain high larval abundances in 1980 and 1981 and resulted in negative residuals from 1992 to 1996. It should be noted that a significant autocorrelation in the residuals occurred (Table 2).

For Subdivisions 26 and 28, the larval abundance per unit of potential egg production was significantly related to the reproductive volumes (model 30, $r^2 = 0.58$; model 31, $r^2 = 0.41$) (Table 3). Although these relationships show high variability in the survival to the larval stage, intermediate to high reproductive volumes obviously have an impact on survival until the larval stage. An anomalous situation was encountered in 1994, as no larvae were observed in either area, despite the existence of a fairly high reproductive volume.

Survival from the larval to the 0-group stage

Recruitment at age 0 in Subdivision 25 was higher when larvae were more abundant (model 15, $r^2 = 0.65$) (Fig. 3a). The significant intercept of the relationship is primarily caused by recruitment observations originating from very low larval abundance values in 1992–1993 and 1995. These low abundances resulted in extremely high ratios of recruitment at age 0 to larval abundance, pointing to a problem in the larval abundance data in the most recent years. Comparing the ratio of recruitment at age 0 to larval abundance, as a measure of larval survival, with the oxygen content in the reproductive volume or the larval transport index did not

Table 2. Results of exploratory analyses and stock–recruitment relationships for Subdivision 25: parameter estimates and their significance levels, r^2 values, and Durbin Watson (DW) statistics indicating serial correlation in residuals.

Model	Dependent variable	Time series	Independent variable	Parameter estimate	p	r^2	DW
1	Egg production stage IA	1986–1996	Intercept	-2.42×10^{10}	0.089		
			Potential egg production	2.80×10^{-3}	0.001	0.74	1.30
2	Ratio egg production stage III to potential egg production	1986–1996	Intercept	5.53×10^{-5}	0.156		
			Oxygen-related survival	2.08×10^{-4}	0.040	0.39	2.30
3		1986–1996	Intercept	1.88×10^{-4}	0.001		
			Egg consumption index	-4.77×10^{-4}	0.088	0.29	2.70
4	Egg production stage III	1986–1996	Intercept	-1.08×10^9	0.453		
			Potential egg production	1.89×10^{-4}	0.011	0.53	1.98
5		1986–1996	Intercept	9.67×10^8	0.206		
			Potential egg production corrected for egg survival	3.15×10^{-4}	0.003	0.66	2.38
6		1986–1996	Intercept	1.34×10^9	<0.001		
		Without 1994	Potential egg production corrected for egg survival	1.54×10^{-4}	<0.001	0.83	1.98
7	Ratio larval abundance to potential egg production	1976–1996	Intercept	1.13×10^{-3}	0.031		
			Oxygen-related survival	2.00×10^{-4}	0.833	<0.01	1.45
8		1976–1996	Intercept	1.21×10^{-3}	0.002		
			Egg consumption index	1.92×10^{-4}	0.958	<0.01	1.49
9		1976–1996	Intercept	6.86×10^{-4}	0.071		
			Oxygen content in reproductive volume	7.10×10^{-6}	0.084	0.15	1.21
10	Larval abundance	1976–1996	Intercept	1.39×10^9	0.935		
			Potential egg production	1.15×10^{-3}	0.026	0.23	1.06*
11	Ratio larval abundance to egg production stage III	1986–1996	Intercept	20.20	0.007		
			Oxygen survival factor	-29.10	0.068	0.32	2.12
12		1986–1996	Intercept	0.26	0.963		
			Egg consumption index	76.30	0.071	0.32	2.62
13	Larval abundance	1986–1996	Intercept	1.77×10^{10}	0.051		
			Egg production stage III	-0.073	0.972	<0.01	1.43
14		1976–1996	Intercept	-2.23×10^9	0.873		
			Potential egg production – egg predation	2.39×10^8	0.085	0.38	
			Oxygen content in reproductive volume	9.12×10^{-4}	0.062	Adj. 0.31	0.74*
15	Recruitment at age 0	1976–1995	Intercept	1.43×10^8	0.004		
			Larval abundance	4.70×10^{-3}	<0.001	0.65	0.99*
16	Ratio recruitment at age 0 to larval abundance	1976–1991	Intercept	0.010	0.001		
			Oxygen content in reproductive volume	-1.16×10^{-5}	0.625	0.02	1.73
17		1976–1991	Intercept	9.78×10^{-3}	<0.001		
			Larval transport index	-6.41×10^{-5}	0.586	0.02	1.75
18	Recruitment at age 0	1976–1995	Intercept	9.51×10^7	0.074		
			Larval abundance	3.97×10^{-3}	<0.001	0.70	
			Oxygen content in reproductive volume	9.96×10^5	0.106	Adj. 0.66	1.39
19		1976–1995	Intercept	1.07×10^8	0.067		
			Larval abundance	3.83×10^{-3}	<0.001		
			Oxygen content in reproductive volume	1.09×10^6	0.095	0.70	
			Larval transport index	-9.55×10^5	0.549	Adj. 0.65	1.45
20	Predation mortality at age 0	1977–1996	Intercept	7.74×10^{-3}	0.874		
			SSB	3.08×10^{-9}	<0.001	0.68	1.55
21	Recruitment at age 0	1976–1995	Intercept	1.89×10^7	0.747		
			Potential egg production – egg predation	8.39×10^{-6}	<0.001	0.69	
			Oxygen content in reproductive volume	1.39×10^6	0.022	Adj. 0.66	0.96*
22		1976–1995	Intercept	4.40×10^7	0.452		
			Potential egg production – egg predation	8.34×10^{-6}	<0.001		

Table 2 (concluded).

Model	Dependent variable	Time series	Independent variable	Parameter estimate	<i>p</i>	<i>r</i> ²	DW
23		1976–1995 Without 1979	Oxygen content in reproductive volume	1.51×10^6	0.012	0.74	
			Larval transport index	-2.36×10^6	0.118	Adj. 0.69	1.38
			Intercept	3.77×10^7	0.370		
			Potential egg production – egg predation	7.52×10^{-6}	<0.001		
24	ln(recruitment at age 0)	1976–1995	Oxygen content in reproductive volume	1.56×10^6	0.001	0.84	
			Larval transport index	-1.80×10^6	0.105	Adj. 0.80	1.28
			Intercept	6.56	0.016	0.70	0.74*
			ln(potential egg production – egg predation)	0.398	<0.001	Adj. 0.66	
25		1976–1995	ln(oxygen in reproductive volume)	0.188	0.155		
			Intercept	6.97	0.010	0.74	0.94*
			ln(potential egg production – egg predation)	0.384	<0.001	Adj. 0.69	
			ln(oxygen in reproductive volume)	0.223	0.091		
			ln(larval transport index)	-0.084	0.151		

Note: *Significant at 5% level.

reveal significant relationships, even when removing years after 1991 from the analysis (models 16 and 17). Nevertheless, including the oxygen content in the reproductive volume in a multiple linear regression, assuming that oxygen concentration impacts on survival of early larvae found within and below the halocline (GrønkJær and Wieland 1997), resulted only in a slightly better fit of the recruitment to larval abundance relationship (model 18), with the significance level of the regression coefficient being $p = 0.106$. Including the larval transport index as a variable did not increase the explained variance or remove the significant positive intercept (model 19). However, the intercept becomes insignificant if the last 4 years of data are omitted from the model fitting.

A linear regression of the recruitment at age 0 on larval abundance (Fig. 3b) for Subdivision 26 explains less variability than in Subdivision 25 (model 32, $r^2 = 0.40$) but is, however, still significant ($p = 0.003$). In contrast, the corresponding relationship for Subdivision 28 is not significant (model 33), with a rather high number of zero observations and a large scatter observed in the remaining data points (Fig. 3c). As in Subdivision 25, significant positive intercepts were encountered in both areas, i.e., even with no larvae obtained in the ichthyoplankton surveys, recruitment regularly occurred.

Cannibalism within the 0-group stage

Predation mortality rates of 0-group cod are linearly related to the SSB of cod as determined by the MSVPA runs (Fig. 4). The relationships are highly significant in all areas under consideration (models 20, 34, and 35, $p < 0.001$ in all cases, $r^2 = 0.68$ – 0.82).

Stock–recruitment relationships including environmental factors and species interaction

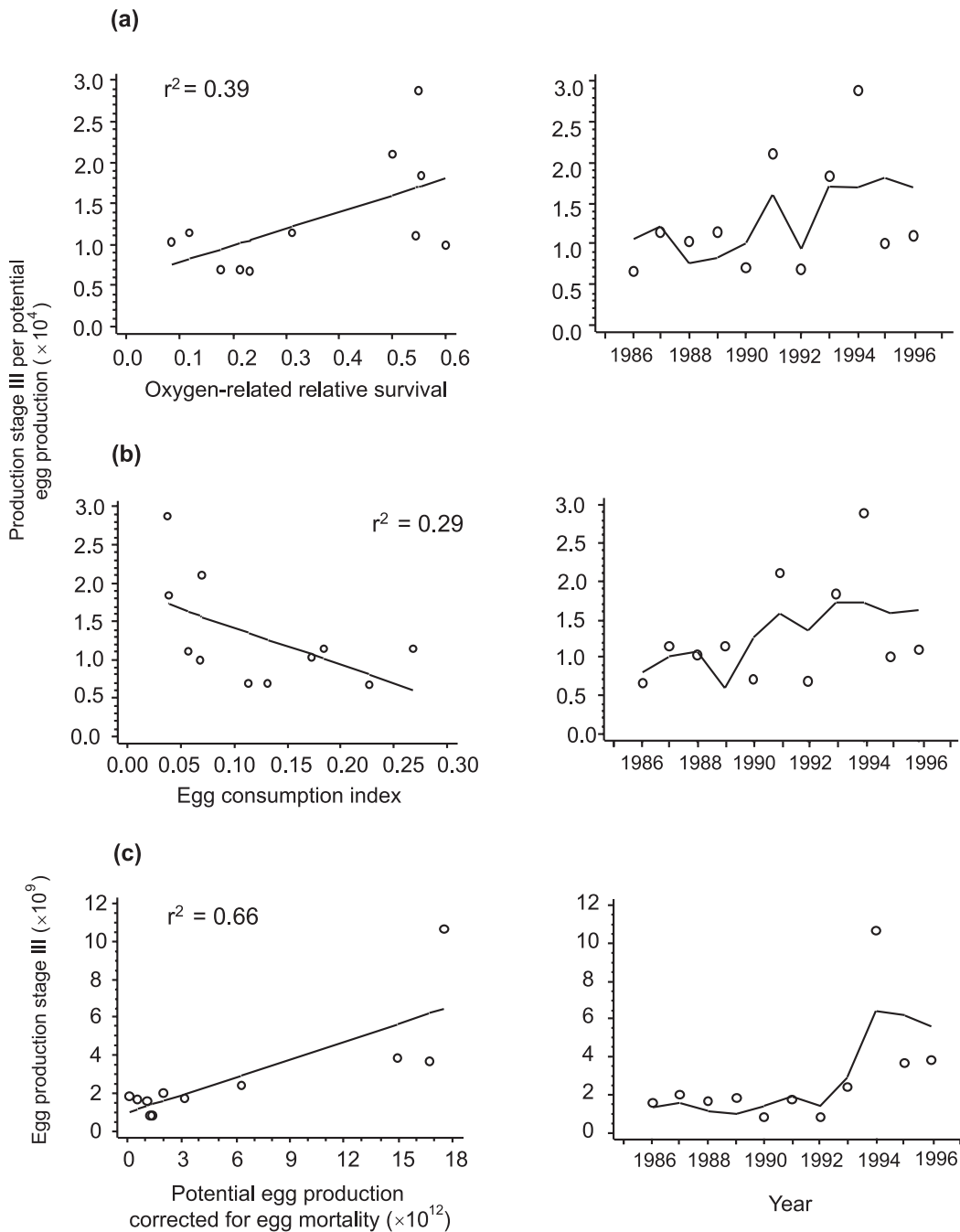
Based on significant variables identified in the exploratory analysis (potential egg production corrected for the removal

by egg predation and the oxygen content in the reproductive volume), a multiple regression based stock–recruitment relationship was developed for Subdivision 25 (model 21, Fig. 5a). The statistical model explained 66% of the variance encountered, with both regression coefficients being significant ($p < 0.001$ and $p = 0.022$). However, a significant autocorrelation was observed in the residuals (Fig. 5c). The statistical model developed showed high deviations from observed values in 1979 (positive residuals) as well as in 1984, 1993, and 1994 (negative residuals). Incorporating the larval transport index as an additional variable improved model 23 ($r^2 = 0.69$) (Fig. 5b), with the regression coefficient being nearly significant and the autocorrelation of the residuals being no longer significant (Fig. 5c).

As recruitment at age 0 is lognormally rather than normally distributed (Shapiro–Wilks test), a multiplicative model was established by natural logarithm (ln) transforming the dependent and independent variables. The simpler model 24, without the larval transport index as a variable, also explained 66% of the variance (Fig. 6a); however, the regression coefficient for the logarithmic sum of oxygen concentration in the reproductive volume was not significant, contrary to the other coefficient (Table 2). Deviations between observations and predicted values were especially obvious for the beginning of the time series until 1981, where the model underestimated recruitment, while in the most recent years (1993–1995), the model overestimated recruitment. Residuals were significantly autocorrelated (Fig. 6c). Including the larval transport index as an additional variable (Fig. 6b) increased the explained variance (model 25, $r^2 = 0.69$). However, the regression coefficient for the transformed transport index was not significant ($p = 0.151$) either, and again, the relationship was negative. The behaviour of the model with respect to time trends and autocorrelation in residuals was similar to that described for the simpler model 24.

In Subdivision 26, potential egg production and the repro-

Fig. 1. Linear regressions of daily cod egg production at stage III in Subdivision 25 per unit of egg potential production (as a measure of egg survival) on (a) oxygen-related relative egg survival (see model 2) and (b) an index of egg consumption (see model 3) and (c) linear regression of daily egg production at stage III on potential egg production corrected for oxygen-related mortality and consumption (model 5). Circles, observed values; lines, predicted values.



ductive volume were utilised in a multiple linear regression (model 36) that explained 55% of the variance in recruitment at age 0 (Fig. 7a). Both regression coefficients were significant ($p = 0.005$ and $p = 0.032$), and no autocorrelation was indicated. A large positive deviation between observed and predicted recruitment occurred in 1979, with relatively small negative residuals encountered throughout the period 1982–1988. The corresponding logarithmic model 40 fitted the data better (Fig. 7b), with an explained variance of 61%,

but again, an underestimation of recruitment at the beginning of the time series as well as autocorrelation of residuals was apparent (Fig. 7c).

Models 38 and 41 for Subdivision 28 explained 66% and 78% of the variance in recruitment and $\ln(\text{recruitment})$, respectively (Figs. 8a and 8b). In the multiplicative model, the regression coefficient of the reproductive volume was not significant, and residuals again showed a time trend and were also significantly autocorrelated at a time lag of 1 year

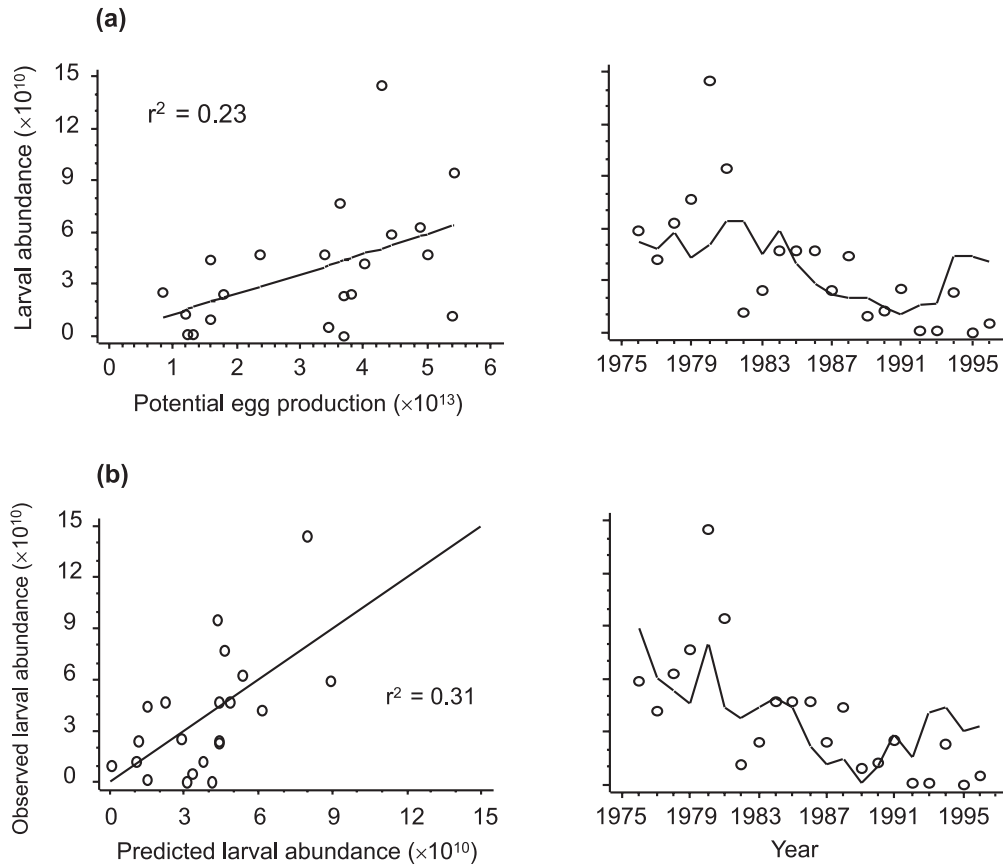
Table 3. Results of exploratory analyses and stock–recruitment relationships for Subdivisions 26 and 28: parameter estimates and their significance levels, r^2 values, and Durbin Watson (DW) statistics indicating serial correlation in residuals.

Model	Dependent variable	Subdivision	Time series	Independent variable	Parameter estimate	p	r^2	DW
26	Egg abundance	26	1976–1996	Intercept	1.64×10^{10}	0.903		
				Potential egg production	6.19×10^{-3}	0.106	0.13	0.59*
27		28	1976–1996	Intercept	2.82×10^{10}	0.813		
				Potential egg production	1.18×10^{-2}	0.012	0.29	2.07
28	Ratio of egg abundance to potential egg production	26	1976–1996	Intercept	3.18×10^{-3}	0.853		
				Reproductive volume	1.10×10^{-3}	<0.001	0.55	1.34
29		28	1976–1996	Intercept	7.65×10^{-3}	0.005		
				Reproductive volume	1.50×10^{-4}	0.001	0.44	2.11
30	Ratio of larval abundance to potential egg production	26	1976–1996	Intercept	5.56×10^{-6}	0.950		
				Reproductive volume	1.30×10^{-5}	<0.001	0.58	1.26
31		28	1976–1996	Intercept	4.87×10^{-4}	0.400		
				Reproductive volume	3.26×10^{-5}	0.002	0.41	1.69
32	Recruitment at age 0	26	1976–1995	Intercept	1.95×10^8	0.044		
				Larval abundance	7.80×10^{-3}	0.003	0.40	1.25
33		28	1976–1995	Intercept	1.32×10^8	0.009		
				Larval abundance	7.67×10^{-4}	0.150	0.11	0.55*
34	Predation mortality at age 0	26	1977–1996	Intercept	-0.115	0.095		
				SSB	5.64×10^{-9}	<0.001	0.82	2.56
35		28	1977–1996	Intercept	-0.049	0.381		
				SSB	1.09×10^{-8}	<0.001	0.82	1.65
36	Recruitment at age 0	26	1976–1995	Intercept	-7.40×10^7	0.523		
				Potential egg production	1.08×10^{-5}	0.005	0.60	
37		26	1976–1995 Without 1979	Reproductive volume	2.78×10^6	0.032	Adj. 0.55	1.40
				Intercept	-6.68×10^7	0.159		
38		28	1976–1995	Potential egg production	8.31×10^{-6}	<0.001	0.89	
				Reproductive volume	3.05×10^6	<0.001	Adj. 0.87	1.19
39		28	1976–1995 Without 1979	Intercept	-3.59×10^7	0.383		
				Potential egg production	8.18×10^{-6}	<0.001	0.70	
40	ln(recruitment at age 0)	26	1976–1995	Reproductive volume	7.45×10^5	0.088	Adj. 0.66	1.47
				Intercept	-2.68×10^7	0.486		
41		28	1976–1995	Potential egg production	7.24×10^{-6}	<0.001	0.67	
				Reproductive volume	7.83×10^5	0.058	Adj. 0.63	1.42
40		26	1976–1995	Intercept	-5.44	0.467		
				ln(potential egg production)	0.792	0.004	0.65	
				ln(reproductive volume ^d)	0.142	0.044	Adj. 0.61	0.80*
				Intercept	-18.00	0.001		
41		28	1976–1995	ln(potential egg production)	1.190	<0.001	0.81	
				ln(reproductive volume ^d)	0.115	0.137	Adj. 0.78	0.79*

Note: *Significant at 5% level.

^dA constant unity of 0.1 was added before ln transformation.

Fig. 2. Linear regressions of cod (a) larval abundance on potential egg production in Subdivision 25 (see model 10) and (b) observed larval abundance from ichthyoplankton surveys and predicted by a multiple linear regression (model 14) utilising potential egg production and oxygen content in the reproductive volume as independent variables. Circles, observed values; lines, predicted values.



(Fig. 8c). Although the time trend in residuals is less pronounced in the additive model, considerable positive residuals occurred in 1976 and 1979 and negative residuals in 1984–1985.

The sum of the area-specific predicted recruitment at age 0 from the additive models 22, 36, and 38, with occasionally predicted negative recruitment by the latter set to zero, compares favourable with the observed recruitment of the cod stock as derived from area-disaggregated MSVPAs ($r^2 = 0.72$) (Fig. 9a). Recruitment in 1979 was underestimated by the model and overestimated in 1984. Some smaller deviations occurred during the later part of the time series when the model predicted higher recruitment than observed. The corresponding multiplicative model showed considerably larger deviations in the beginning of the time series, consistently underestimating recruitment ($r^2 = 0.65$) (Fig. 9b). In the most recent years, deviations between observed and predicted recruitment were less than in the additive model.

Validation of stock–recruitment models

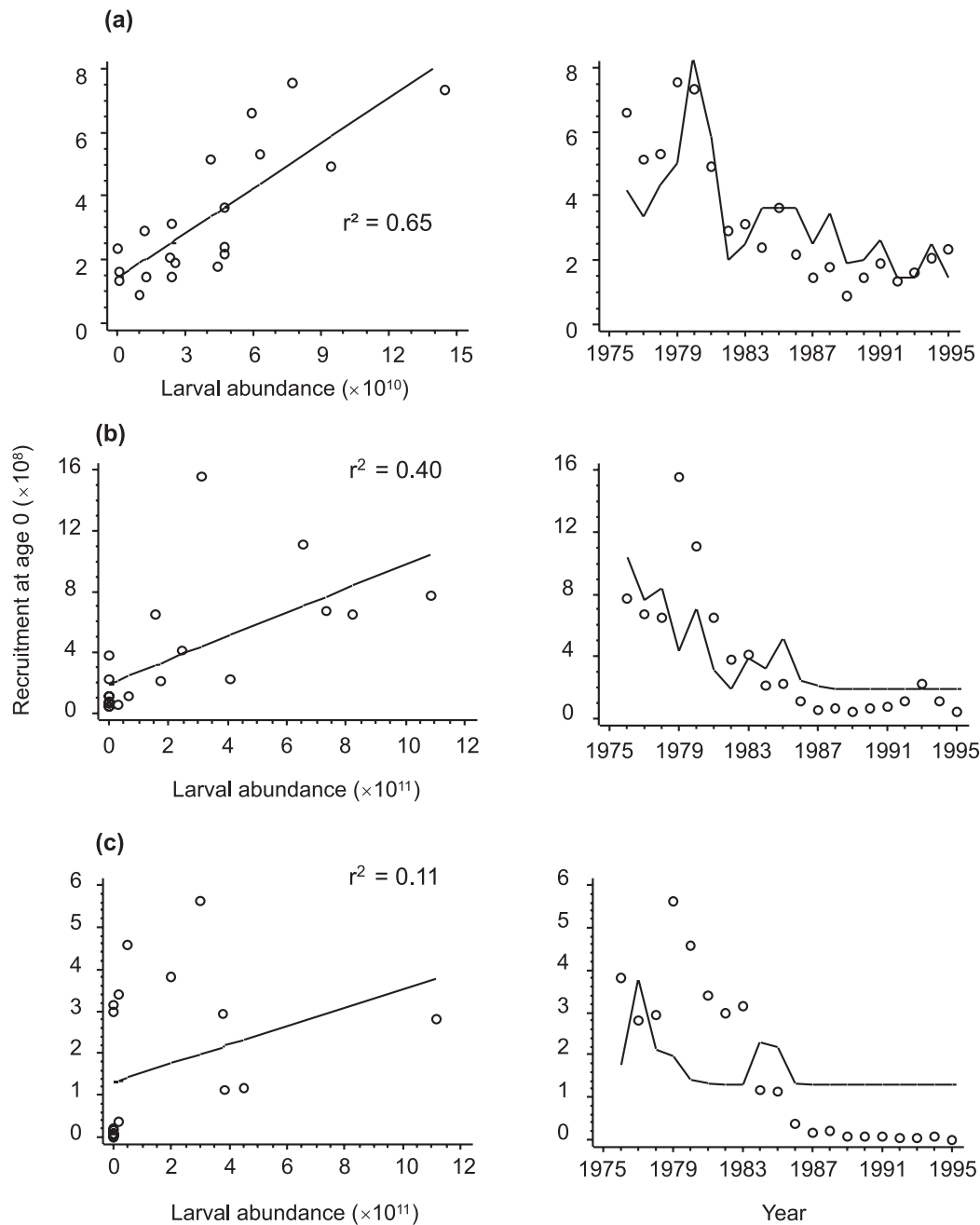
To test the sensitivity of the parameter estimates and the predictive power of the stock–recruitment relationships utilised to estimate recruitment in combined areas, model parameters were refitted excluding the first and last 4–5 years of data, respectively. For Subdivision 25, all data series revealed highly significant multiple linear regressions (Table 4). The explained variance was lowest when excluding

the data for 1976–1980, i.e., time periods with high recruitment. Furthermore, the variable oxygen content in the reproductive volume was not significant in this model, while it was in all other scenarios. For Subdivision 26, the overall fit of the model was better than in the original version when excluding data from 1976 to 1979 and from 1976 to 1980, explaining 69 and 85% of the variance, respectively (Table 4). In contrast, runs excluding the most recent years resulted in a reduction of the explained variance (47–49%). In Subdivision 28, the explained variance was lowest when fitting the model to the period 1981–1995, while omitting the most recent data from the parameter estimation had a limited impact only.

Comparing the observed and predicted recruitment at age 0 summed over Subdivisions 25, 26, and 28 revealed a similar fit, independent of whether the last 4 or 5 years of data were used in the parameter estimation or not (Figs. 10a and 10b). Thus, the models were able to predict the increase in recruitment observed in 1993–1995. The models overestimated the recruitment in these years by 53–89%, while recruitment in 1992 was underestimated by 61–63%. However, this corresponds to the behaviour of the original model.

Excluding data from 1976–1979 revealed, in general, a good fit to the observed recruitment in the combined stock (Fig. 10c), with the recruitment in 1976 and 1980 being slightly more underestimated than by the original model version. Deviations in 1979, however, were rather pronounced,

Fig. 3. Linear regressions of cod recruitment at age 0 on larval abundance in (a) Subdivision 25 (see model 15), (b) Subdivision 26 (see model 32), and (c) Subdivision 28 (see model 33). Circles, observed values; lines, predicted values.

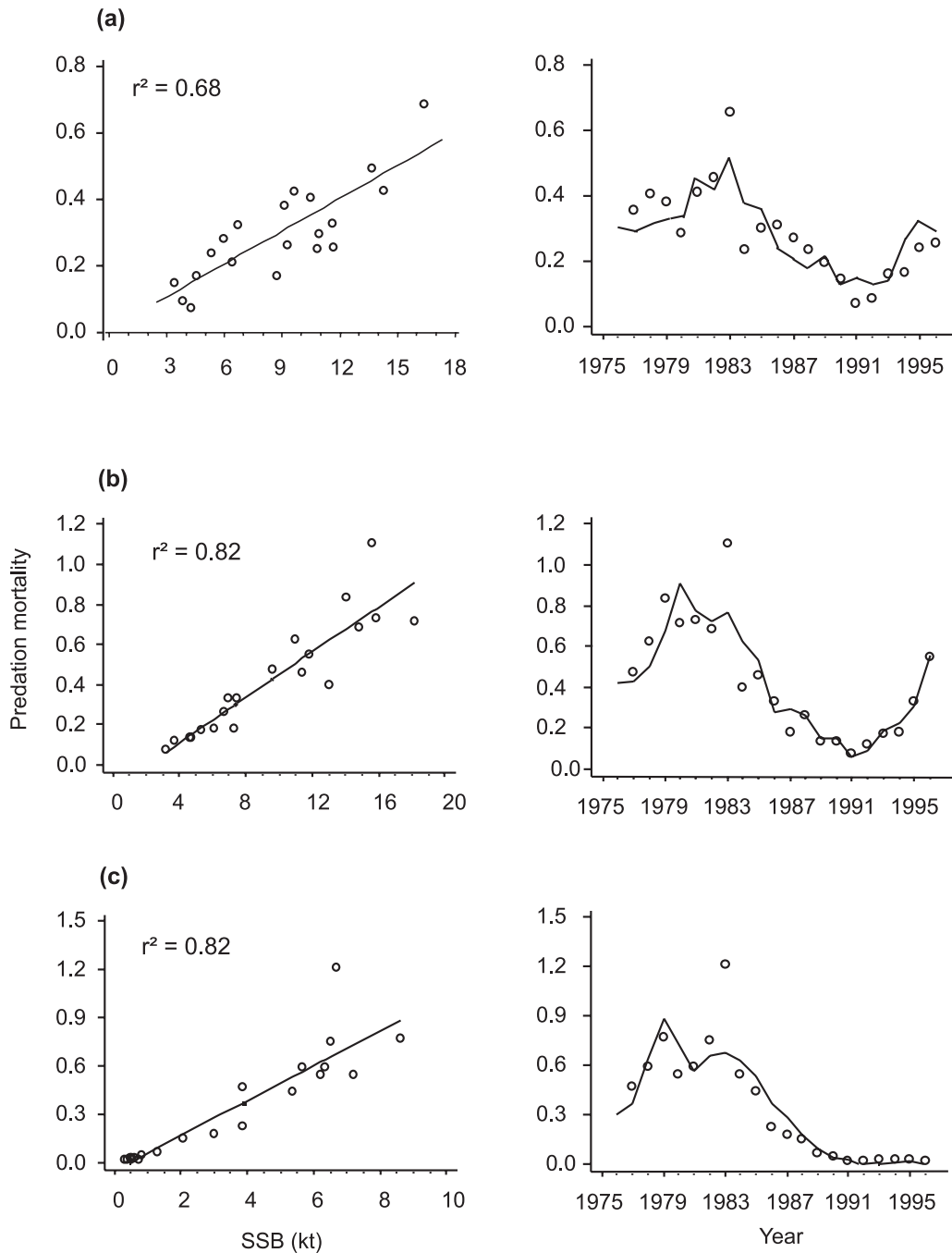


with the observed value well outside the 95% prediction limit of the mean. This deviation is not caused by a single outlying event in a specific subdivision but is a general trend for all areas, being most pronounced in Subdivisions 25 and 26. Contrary to the reasonable behaviour of the models in the first three cases, starting the parameter estimation procedure in 1981 produced large deviations between observed and predicted recruitment in 1976–1980 (Fig. 10d). The model always substantially underestimated recruitment for these years and had considerably broader 95% prediction limits of the mean, with observed values being outside these limits in 1976, 1979, and 1980.

The predicted and observed recruitment at age 1 in the

Central Baltic (Fig. 11a) showed somewhat higher deviations than recruitment at age 0, but still, an overall rather good agreement is evident ($r^2 = 0.65$). As a test, predicted recruitment at age 1 was compared with observed recruitment indices obtained by bottom trawl surveys. In general, the comparison revealed similar trends with declining recruitment throughout the first half of the 1980s and increasing recruitment in the 1990s (Fig. 11b). However, considerable deviations are apparent for some years, indicated also by the relatively low r^2 of 0.40. Predicted recruitment declined earlier, i.e., from 1981 onwards, compared with 1983 in the trawl survey but reached lowest levels not before 1989, while the trawl survey indicated low recruit-

Fig. 4. Linear regressions of predation mortality coefficients of cod age-group 0 (second half of the year) on cod SSB in (a) Subdivision 25 (see model 20), (b) Subdivision 26 (see model 34), and (c) Subdivision 28 (see model 35). Circles, observed values; lines, predicted values.



ment already in 1985. In contrast, the increase in recruitment was already apparent in the trawl survey in 1991, while the predicted recruitment did not increase before 1993.

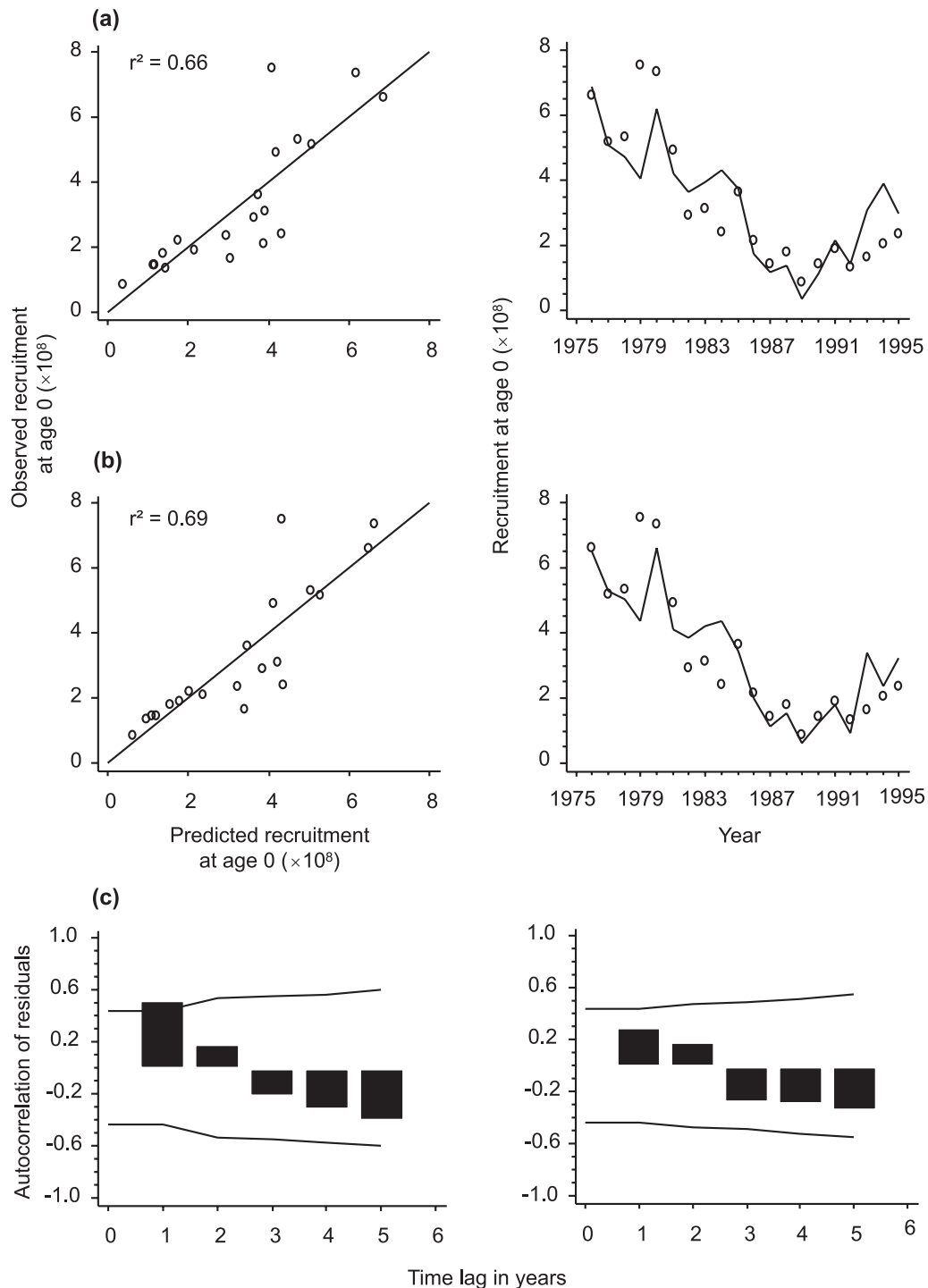
Discussion

Application of process-oriented recruitment modelling approaches including the results of detailed investigations of egg production, egg, larval, and juvenile survival, as well as oceanographic conditions has seldom been employed to examine variations in recruitment success of marine fish

populations. Notable exceptions in the marine environment include plaice in the North Sea and the Irish Sea (e.g., Beverton and Iles 1992), walleye pollock in the North Pacific (e.g., Megrey et al. 1996), and anchovy in the Benguela Current (e.g., Painting et al. 1998). In these aforementioned cases, attempts are still ongoing, as indeed they are in the Baltic, with the major problem in all systems being the lack of availability of time series of key processes and the variety and complexity of processes involved.

Investigation of the link between environmental factors, spawning stock features, and reproductive success of Baltic

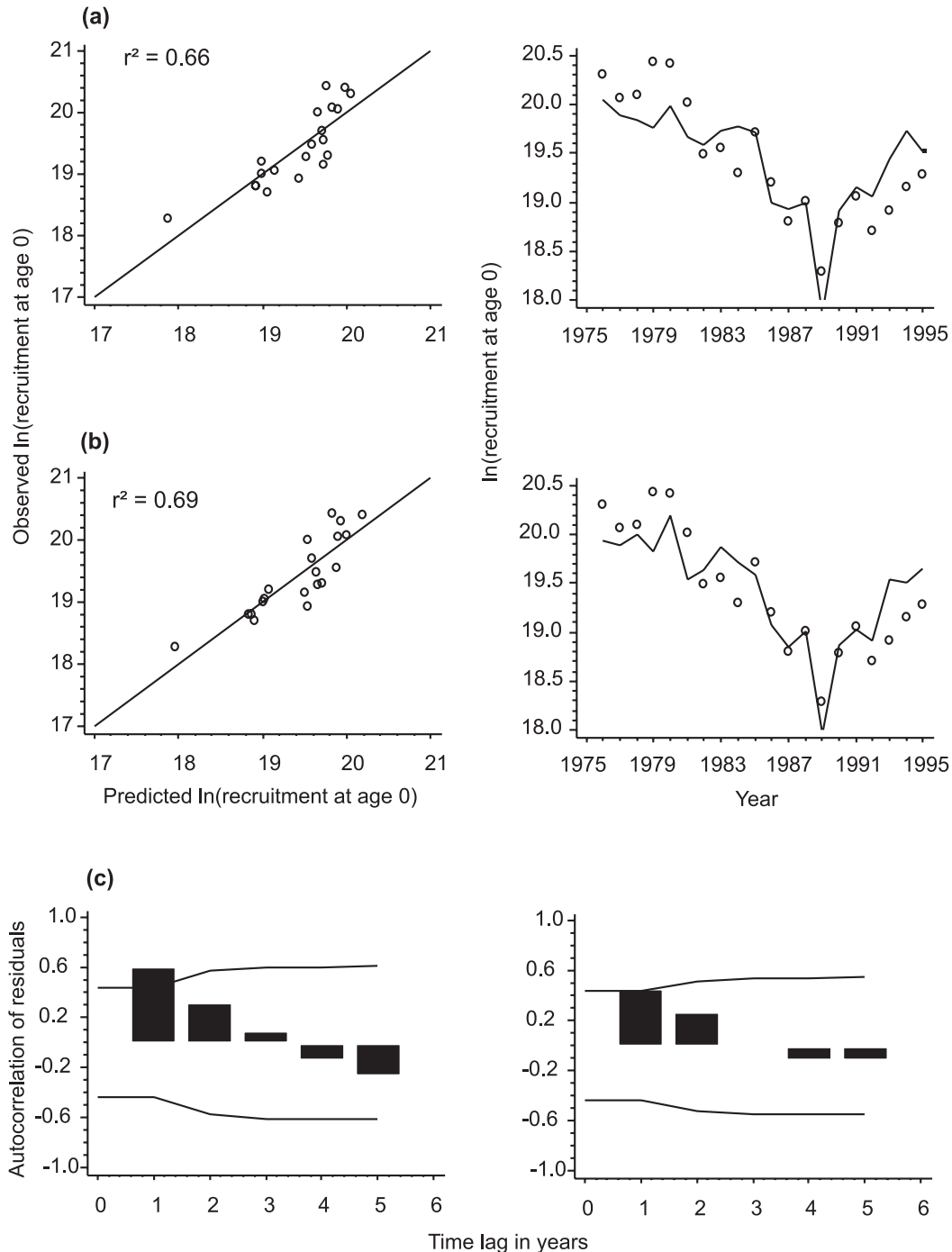
Fig. 5. Multiple linear regressions of cod recruitment at age 0 in Subdivision 25 on potential egg production corrected for egg consumption and oxygen content in the reproductive volume (see model 21). (a) Observed versus predicted recruitment; (b) same statistical model including the larval transport index as a further independent variable (see model 22); (c) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; lines, predicted values.



cod has previously been performed by several investigators (e.g., Plikshs et al. 1993; Sparholt 1996; Jarre-Teichmann et al. 2000). A number of differences between these approaches and the present analysis exist. First, variables and processes considered in our exploratory analysis were based on extensive field, laboratory, and modelling activities, with their

impact on specific early life stages well justified and not only detected via statistical analysis. Based on these activities, the key variables and approaches utilised included (i) disaggregation of recruitment success and spawning stock sizes into major spawning areas having distinct hydrographic regimes (MacKenzie et al. 2000) and exhibiting dif-

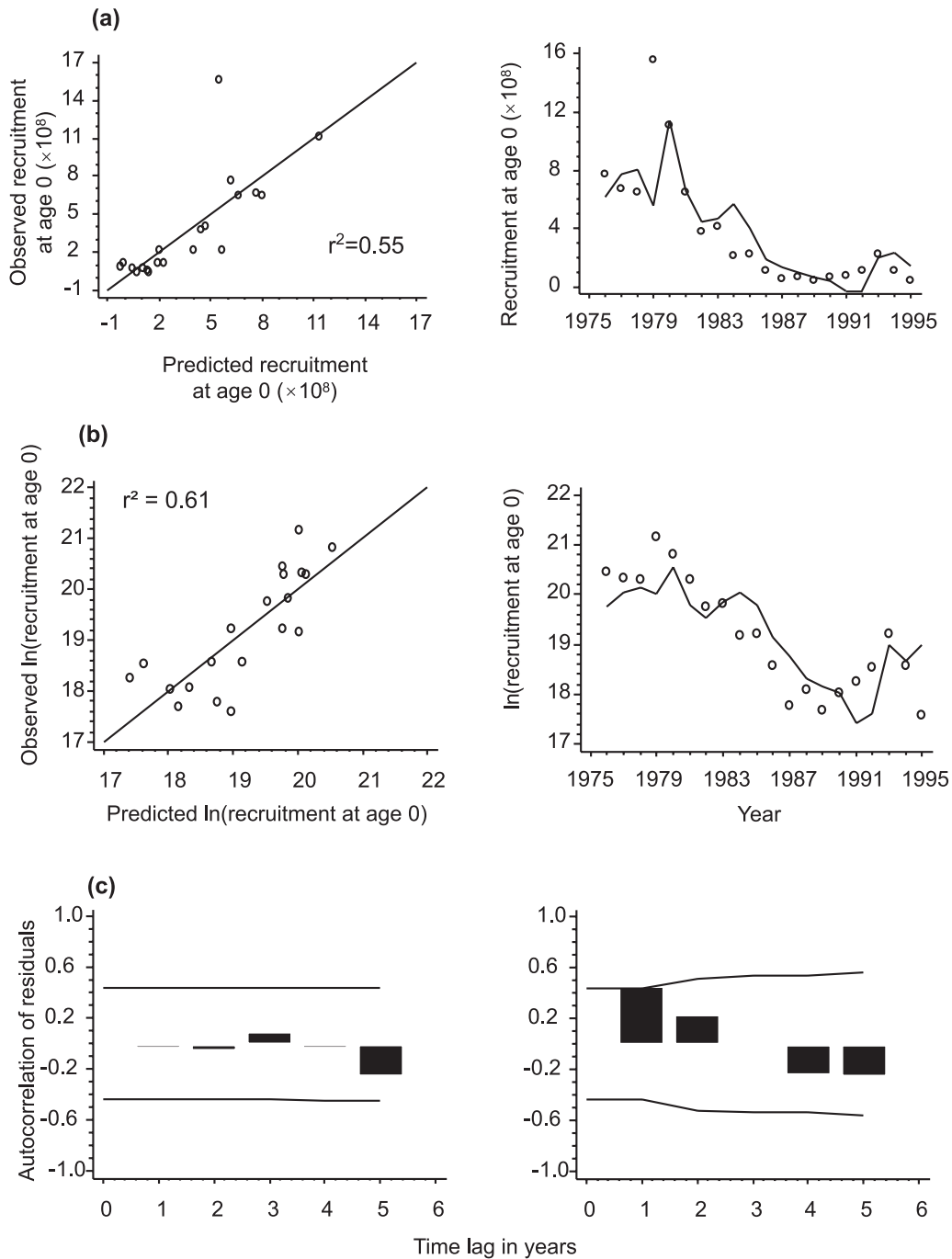
Fig. 6. Multiple linear regressions of ln-transformed cod recruitment at age 0 in Subdivision 25 on ln-transformed potential egg production corrected for egg consumption and oxygen content in the reproductive volume (see model 24) (a) Observed versus predicted recruitment; (b) same statistical model including the ln-transformed larval transport index as a further independent variable (see model 25); (c) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; lines, predicted values.



ferences in the individual maturation process (Tomkiewicz et al. 1997), recruitment success, and stock development trends (Sparholt and Tomkiewicz 2000; Köster et al. 2001), (ii) utilisation of the potential egg production as a measure of reproductive effort by applying time series of sex-specific maturity ogives (Tomkiewicz et al. 1997) and relative fecundity values exhibiting significant interannual variability (Kraus

et al. 2000), (iii) quantifying the impact of suboptimal but not lethal oxygen concentrations (Rohlf 1999) in the reproductive volume of the Bornholm Basin, the only spawning area typically characterised by conditions suitable for cod egg development (MacKenzie et al. 2000), (iv) incorporation of cod egg predation by clupeids (Köster and Möllmann 2000a), and (v) testing the effect of a cumulative wind energy

Fig. 7. Multiple linear regressions of cod (*a*) observed versus predicted recruitment at age 0 in Subdivision 26 on potential egg production and reproductive volume (see model 36); (*b*) same variables with ln-transformed data (see model 40); (*c*) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; line, predicted values.



index as a measure of larval retention in spawning basins or transport to nursery areas (Voss et al. 1999; Hinrichsen et al. 2001).

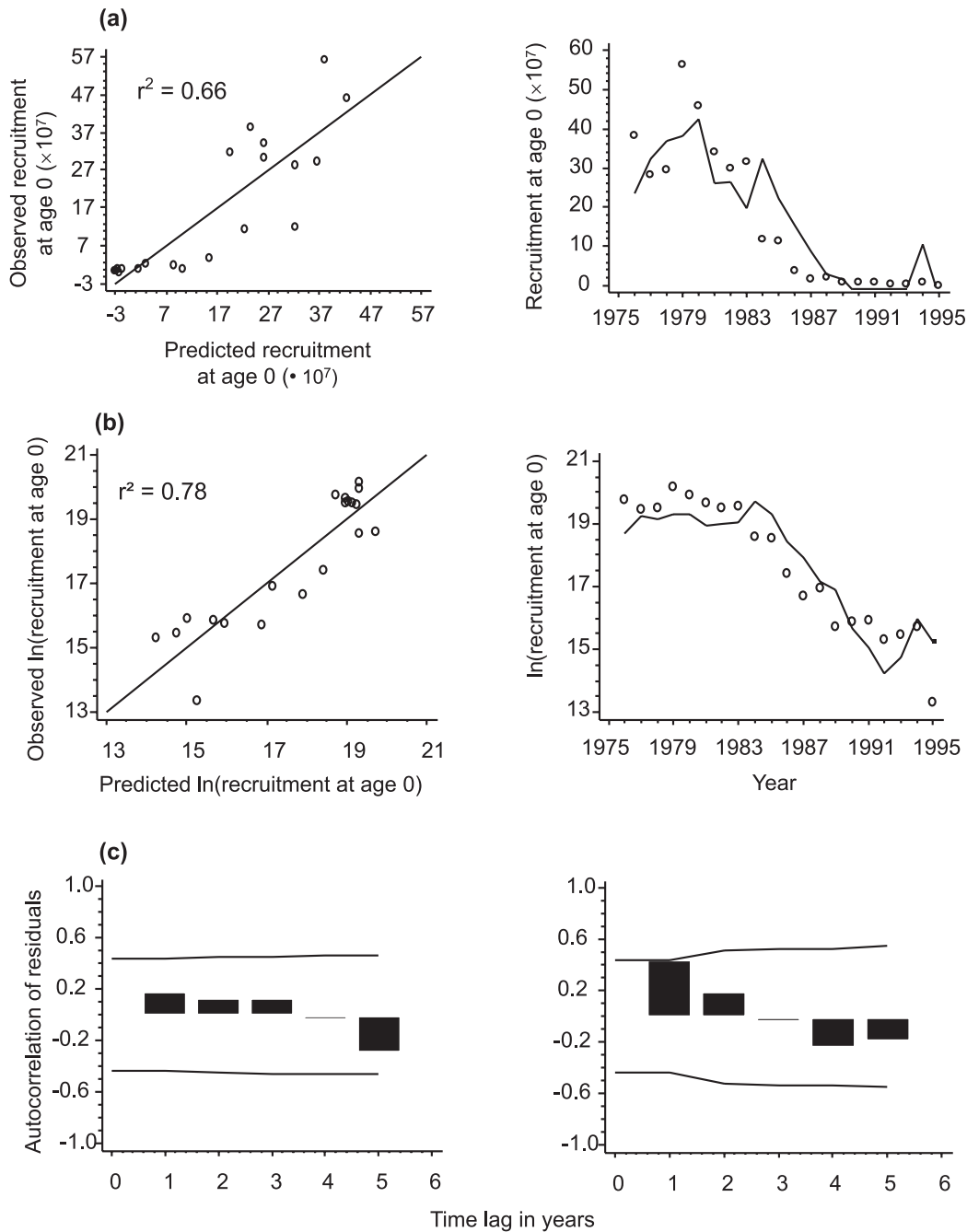
Explanation of variability in stock–recruitment relationships

Survival during the egg stage

The present analysis assumes that potential egg produc-

tion based on the spawning stock characteristics is an unbiased measure of the actual egg production in the field, an assumption justified by a significant relationship between daily production of egg stage IA during main spawning time obtained from ichthyoplankton surveys in Subdivision 25 and the estimated potential production by the SSB in 1986–1996. Thus, it appears to be unlikely that encountered deviations between observed and predicted egg survival rates can be explained by grossly erroneous egg production estimates.

Fig. 8. Multiple linear regressions of cod (a) observed versus predicted recruitment at age 0 in Subdivision 28 on potential egg production and reproductive volume (see model 38); (b) same variables with ln-transformed data (see model 41); (c) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; line, predicted values.



However, a remarkable deviation between potential and realised egg production was encountered in 1996, with the former estimate being considerably higher than the latter.

The performed exploratory analysis revealed a significant impact of oxygen and predation on egg survival until developmental stage III in Subdivision 25. It should be noted that an “observed” high egg survival in 1994 and relatively low survival in 1995 and 1996 were not consistent with the statistical model developed. The hydrographic regime in 1994 was characterised by higher than average salinities and, in the beginning of the spawning season, high oxygen concen-

trations in and below the halocline. However, as the spawning peak was late in the year, eggs were nevertheless exposed to relatively low oxygen levels (MacKenzie et al. 1996), thereby resulting in oxygen-related survival rates similar to those in 1995 and 1996 (54–60%). Egg predation by sprat was lower from 1993 on than in preceding years and was caused by (i) a continuous shift in spawning time of cod to a later month (Wieland et al. 2000), resulting in a limited temporal overlap between sprat as predators and cod eggs as prey (Köster and Möllmann 2000a) and (ii) a limited vertical overlap between predator and prey due to the

Fig. 9. Observed and predicted cod recruitment at age 0 in combined Subdivisions 25, 26, and 28 based on potential egg production including environmental factors incorporated into (a) additive models 22, 36, and 38 and (b) multiplicative models 25, 40, and 41. Open circles, observed values; solid circles, predicted values.

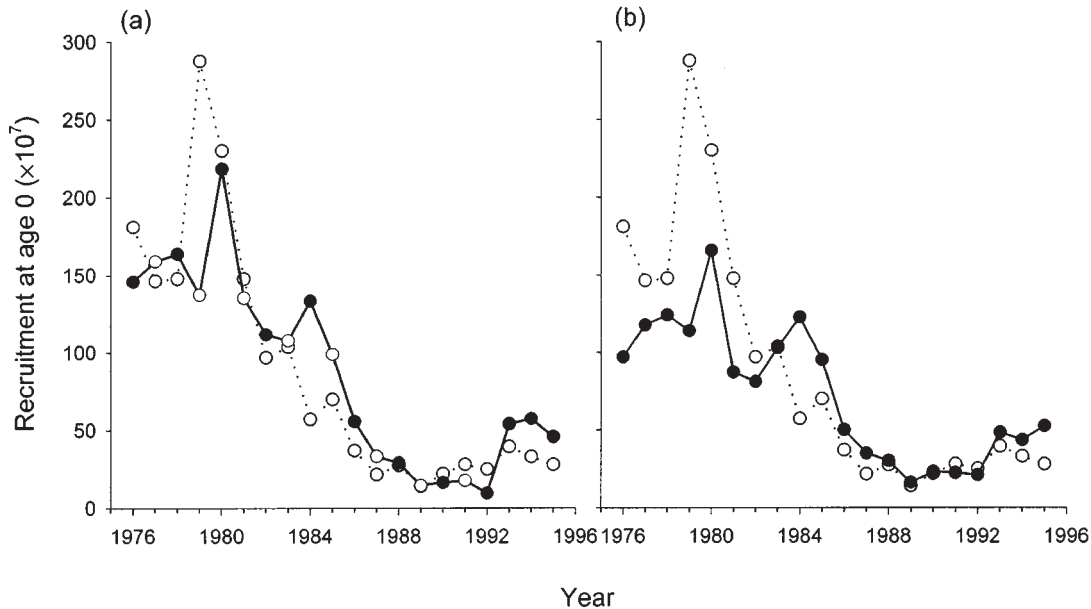


Table 4. Coefficients of determination and significance levels of parameters of multiple linear regressions relating recruitment at age 0 in different subdivisions with potential egg production and environmental variables (model configurations 22, 36, and 38) utilising different data subsets of the time series for estimation of the parameter values.

Subdivision		1976–1995	1980–1995	1981–1995	1976–1990	1976–1991
25	r^2 value (adjusted)	0.69	0.69	0.57	0.69	0.71
	Intercept	0.452	0.400	0.023	0.337	0.271
	Potential egg production – egg predation	<0.001	<0.001	<0.001	0.008	0.003
	Oxygen content in reproductive volume	0.012	0.012	0.655	0.020	0.015
	Larval transport index	0.118	0.189	0.450	0.330	0.237
26	r^2 value (adjusted)	0.55	0.85	0.69	0.47	0.49
	Intercept	0.523	0.115	0.608	0.657	0.722
	Potential egg production	0.005	<0.001	<0.001	0.048	0.037
	Reproductive volume	0.032	0.002	0.234	0.064	0.055
28	r^2 value (adjusted)	0.66	0.69	0.56	0.61	0.58
	Intercept	0.383	0.518	0.710	0.431	0.393
	Potential egg production	<0.001	<0.001	<0.001	<0.001	<0.001
	Reproductive volume	0.088	0.961	0.952	0.058	0.063

changed hydrographic regime (Köster and Möllmann 2000a). This decrease in predation pressure was partly offset by an increase in consumption by herring in summer. Thus, observed differences in egg survival rates between 1993–1994 and subsequent years are not explainable by the considered environmental processes. A validation of the MSVPA results based on independent population estimates revealed an overestimation of the cod spawning population in Subdivision 25 in 1996 (Köster et al. 2001). Consequently, the potential egg production is an overestimation as well, which in turn leads to an underestimation of the observed egg survival rates, hence, partly explaining the discrepancy.

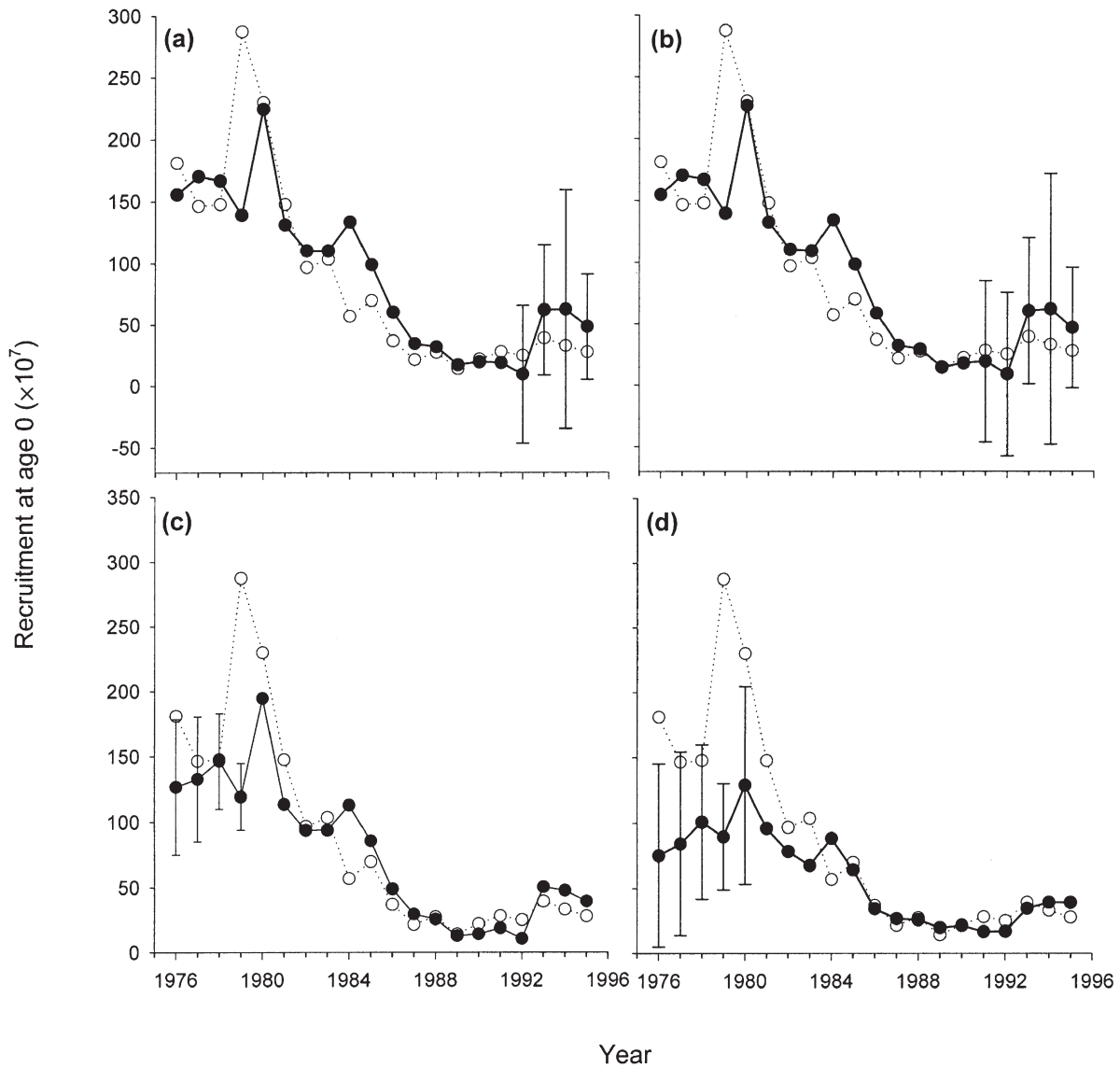
Survival until the larval stage

The exploratory analysis was unable to explain a considerable part of the variability encountered between different egg production measures and larval abundance in Subdivision 25. This indicates either that (i) factors other than oxygen- and

predation-related mortality influence the survival until the larval stage, (ii) the variability in larval abundance (integrated over all developmental stages) is too high to detect a major impact of both mentioned factors, or (iii) the abundance estimates of larvae may be too variable due to inadequate spatial and temporal sampling strategies.

Behaviour studies conducted with larvae demonstrated that low oxygen concentration has an impact on larval mortality (Nissling 1994) and that egg incubation at low oxygen concentration impacts on larval activity as well (Rohlf 1999). Furthermore, the experiments revealed that vertical migration into upper water layers is not started before day 4 after hatch. Hence, a significant impact of the environment within and below the halocline on larval survival can be expected. Due to differences in buoyancy and minimum lethal oxygen concentrations in the egg and larval stage (Rohlf 1999), it appears to be unlikely that the oxygen-related egg survival is a suitable measure of oxygen-related survival

Fig. 10. Observed and predicted cod recruitment at age 0 in combined Subdivisions 25, 26, and 38 based on potential egg production including environmental factors (models 22, 36, and 28) utilising different subsets of data for parameter estimation: (a) 1976–1991, (b) 1976–1990, (c) 1980–1995, and (d) 1981–1995. Shown are the 95% confidence limits of the predicted means for recruitment in years excluded from fitting the model. Open circles, observed values; solid circles, predicted values.



probability of larvae. In fact, the oxygen content in the reproduction volume performed better in the exploratory analysis and hence was also included in the more complex model configurations for Subdivision 25.

A multiple linear regression of larval abundance and potential egg production corrected for egg predation and the oxygen content in the reproductive volume exhibited large negative residuals in recent years. This suggests a mismatch in the timing of the plankton surveys and time periods of high larval abundance caused by a delayed spawning (Wieland et al. 2000) in these years. This of course has implications for the use of the larval abundance estimates as a potential predictor of recruitment.

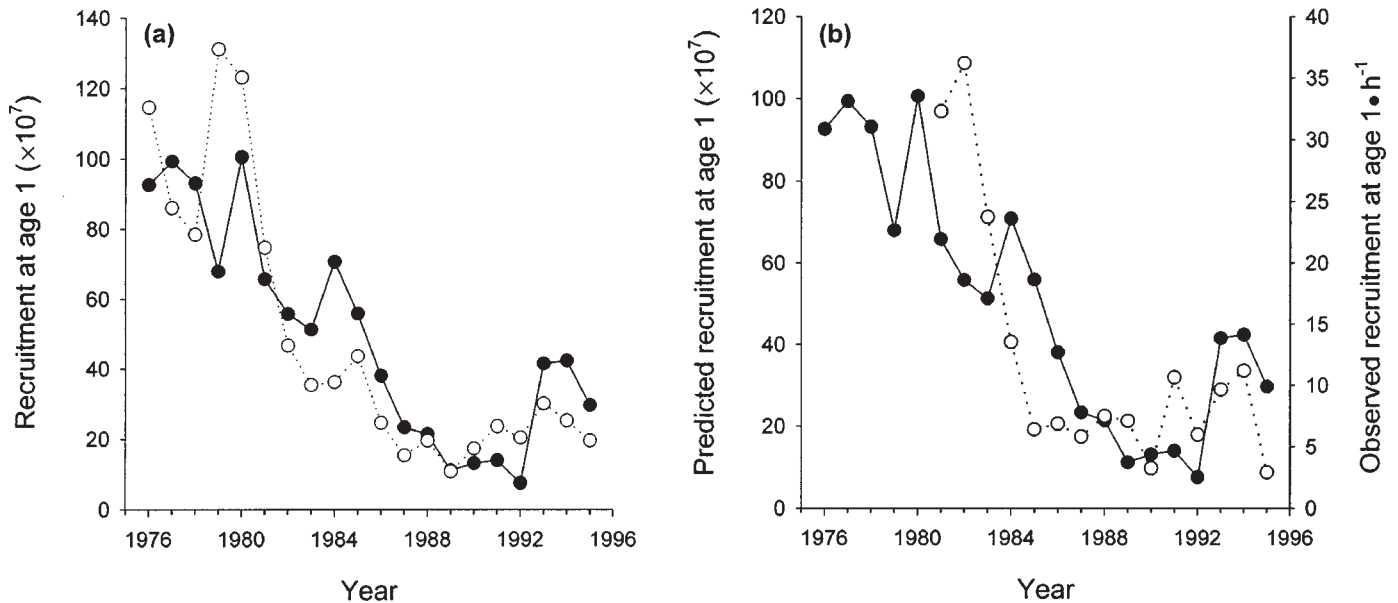
In the more eastern spawning areas, variability in larval abundance was more easily explained, as a highly significant impact of the hydrography is obvious. This result is not surprising, as the environmental conditions are less favourable for successful egg survival in these areas compared with the

Bornholm Basin (MacKenzie et al. 2000). However, a high reproductive volume does not necessarily result in high survival of early life stages. In 1994, an extremely high reproductive volume was encountered in the Gotland Basin due to an inflow into this basin. This inflow displaced the anoxic bottom water upwards (CORE 1998), resulting in an intermediate layer with insufficient oxygen concentration but densities sufficient to keep cod eggs floating, hence creating conditions detrimental to the development of cod eggs. Situations like these clearly demonstrate the potential for index improvement through the development of models for predicting the vertical distribution of cod eggs in all spawning areas relative to oxygen conditions.

Survival from the larval to the 0-group stage

The significant linear relationship between larval abundance and recruitment at age 0 in Subdivision 25 was not enhanced by inclusion of any additional variable, e.g., the

Fig. 11. Observed and predicted cod recruitment at age 1 in combined Subdivisions 25, 26, and 28 based on predicted 0-group recruitment from additive models 22, 36, and 38 and applied predicted 0-group predation mortalities (solid circles). Observed recruitment (open circles) as derived by (a) area-disaggregated MSVPA and (b) catch rates obtained from the international bottom trawl survey.



oxygen content in the reproductive volume or the larval transport index. This identifies the applicability of the simple model for predicting recruitment. In Subdivision 26, a significant relationship between larval abundance and recruitment was also obtained, but the fit of the model was less satisfactory, while for Subdivision 28, no significant relationship could be established. This can be explained by the fact that recruitment success occurred in this area despite the lack of larvae in the ichthyoplankton. As recruitment was not only determined by the MSVPA but also observed in the bottom trawl surveys as age-group 1, this indicates either (i) a problem in sampling efficiency of larvae at low larval abundance or (ii) a transport of larvae and the pelagic 0-group out of the Bornholm area into the more eastern Baltic basins. The latter hypothesis is supported by hydrodynamic modelling (Hinrichsen et al. 2001) and comparison of trawl survey results and MSVPA output (Köster et al. 2001) and is also indicated by the fact that the parameter estimate for the larval transport index is negative in Subdivision 25.

Survival during the 0-group stage

The linear relationship between MSVPA-derived cannibalism rates and cod SSB may to a certain extent be artificially created by the estimation procedure implemented in the MSVPA. Here, the predation mortalities depend to a considerable degree on the predator stock size, if consumption rates and suitability coefficients are kept constant over time (Neuenfeldt and Köster 2000). In MSVPA runs used for the present analysis, suitability coefficients averaged over years are still in use. This impacts on not only predation mortalities but also recruitment values utilised in our analysis. Neuenfeldt and Köster (2000) compared recruitment estimates derived by MSVPA with and without a suitability submodel, i.e., utilising available yearly stomach content data for estimation of the predation mortalities. According to this test, the impact on the derived Central Baltic cod recruitment is, in general, limited, i.e., the estimates are highly

correlated ($r^2 = 0.84$). However, the estimated strengths of the 1979 and 1980 year-classes are considerably overestimated by the MSVPA with a suitability submodel compared with the direct estimates (Neuenfeldt and Köster 2000), while the 1977 year-class strength is underestimated. As application of the MSVPA without a suitability submodel is restricted to years with sufficient stomach content data, this procedure is at present no alternative to the standard MSVPA. However, it indicates that a revision of the suitability submodel implemented in the MSVPA is needed to determine recruitment as reliably as possible.

Validation of stock–recruitment models

The models established for the eastern spawning areas are simpler than those established for the Bornholm Basin. In the latter area, a water volume suitable for successful development of eggs, the so-called reproductive volume, was always available (Plikshs et al. 1993; MacKenzie et al. 2000). Other factors such as egg predation (Köster and Möllmann 2000a) have a regular and also more pronounced influence on the reproductive success of cod in this basin. In the Gdansk Deep and especially in the Gotland Basin, the hydrographic regime did not, in general, allow successful egg development (MacKenzie et al. 2000). Hence, relatively simple models, incorporating the potential egg production and the reproductive volume as variables, were required for these areas to achieve a reasonable explanation of recruitment variability.

The statistical models 22 and 25 established for Subdivision 25 contain a larval transport index with a negative regression coefficient, i.e., recruitment success appears to be negatively related to high wind stress, suggesting that retention in the basin and low turbulent mixing lead to increased recruitment success, contradicting the hypothesis that a rapid transport into nursery areas is a process enhancing recruitment success (Jarre-Teichmann et al. 2000; Hinrichsen et al.

2001). However, this result is biologically sensible when interpreted as a transport into neighbouring Subdivisions 26 and 28, for which evidence exists (Köster et al. 2001). Jarre-Teichmann et al. (2000) demonstrated that wind energy is positively related to recruitment success at age 2 in Baltic cod, assuming the wind forcing in the Bornholm Basin to be representative of the entire Central Baltic. Thus, wind-induced advective gains and losses between different subdivisions are not resolved in their analysis. For detection of the impact of transport to coastal nursery areas on recruitment, this approach is of advantage, compared with ours in which rapid transport will result also in loss of specimens to neighbouring subdivisions. Inclusion of the larval transport index developed for Subdivision 25 in recruitment model 36 revealed a positive impact of the transport index on recruitment in Subdivision 26, but not being significant. Resolving advective processes between different areas more adequately is in principal possible, but requires further hydrodynamic modelling under various area-specific environmental forcing scenarios for development of enhanced larval transport indices.

To obtain an indication of the sensitivity of the parameter estimates and the predictive power, models 22, 36, and 38 were refitted over different shorter time periods and model predictions then compared with the excluded year's observations. The exercise clearly demonstrated that the models derived for the different subdivisions are not sensitive to the exclusion of periods from the parameter estimation procedure. The models were able to capture the trend of high recruitment during the late 1970s and early 1980s relatively well and the low recruitment in the early 1990s very well. However, if all observed high recruitment values were excluded from the time series utilised for parameter estimation, a substantial underestimation of recruitment in early years was obvious.

Recruitment was lognormally rather than normally distributed. Thus, multiplicative instead of additive processes may be more appropriate in some of the models (Sparholt 1996). Additionally, established multiplicative models explained more of the variance in recruitment in Subdivisions 26 and 28. However, the ln-transformed model did not exhibit better predictive power and consistently underestimated recruitment at high reproductive success in the beginning of the time series in all areas. Additionally first-order correlations in residuals were encountered regularly in all multiplicative models, whereas this was less pronounced in the additive models. Other measures about which model type to prefer were more inconclusive, e.g., normality of residuals, heteroscedasticity, and correlation of variables, with no model behaving considerably better. A possible correction of the multiplicative model for time series bias (Hilborn and Walters 1992) may, however, enhance its predictive performance.

Independent of the model choice, an underestimation of the recruitment was encountered for 1979 in all subdivisions. Although the potential egg production was lower than in preceding and subsequent years and the reproductive volume was well below average in all basins, recruitment at age 0 as determined by the MSVPA was highest. Sparholt (1996) described similar deviations between observed and predicted recruitment of the 1979 year-class when applying a multiplicative model for the Central Baltic incorporating cod SSB, the reproductive volume, and the SSB of sprat as independ-

ent variables and recruitment estimated by MSVPA as the dependent variable. As unfavourable hydrographic conditions were measured throughout 1979 in all basins (MacKenzie et al. 2000), egg and larval abundances, especially in the eastern areas, were intermediate (Plikshs et al. 1993), and 1-group abundance indices from trawl surveys were above average but not extraordinary high (ICES Baltic trawl survey database), it appears to be likely that the "observed" recruitment derived by the MSVPA caused the deviations. This is confirmed by a significantly lower recruitment of the 1979 year-class at age 1 derived by a MSVPA run without a suitability submodel (Neuenfeldt and Köster 2000) compared with the standard MSVPA. Excluding the 1979 data from the model fitting increased the explained variance in 0-group recruitment in Subdivisions 25 and 26 substantially to 80 and 87%, respectively.

Another bias affecting the estimation of cod recruitment by the MSVPA is misreporting, identified to have occurred especially in 1992–1994 (Köster et al. 2001). Underestimated catch at age most likely resulted in underestimated strengths of the 1990–1992 year-classes, partly explaining deviations between predicted and observed recruitment from the international bottom trawl survey.

Applicability of stock–recruitment models

The stock–recruitment models established here explain a considerable part of the variability encountered in cod recruitment in the Baltic Sea. The remaining variability may be due to a number of processes not included in the present exercise such as egg fertilisation (Vallin et al. 1999) and the influence of parental characteristics (age and size structure, condition) on egg and larval characteristics (buoyancy, survival probability, e.g., Marshall et al. 1998; Trippel 1998) and a potential starvation of larvae due to a shortage of suitable food supply (Grønkjær and Wieland 1997) but also uncertainties in the way that variables are assumed to represent processes of interest (e.g., reproductive volume effect on egg survival, predation relative to predator–prey overlap). Results from recent studies on these topics are becoming available for Baltic cod (e.g., Nissling et al. 1998) and potentially could also be incorporated into new generations of recruitment models (Vallin et al. 1999). Apart from these potential improvements, major difficulties in establishing environmentally sensitive stock–recruitment models are to (i) incorporate various factors affecting different early life stages (Paulik 1973) in one model relating egg production by the spawning stock to subsequent recruitment, (ii) resolve the potential nonlinearity and additive effects of different factors on subsequent early life stages, and (iii) determine the historical recruitment at age 0 or 1 originated by specific spawning components. The first problem has been described in detail previously (Rothschild 1986; Ulltang 1996). Bailey et al. (1996) and Campana et al. (1989) considered it explicitly when constructing survival curves of walleye pollock as well as Nova Scotia cod and haddock cohorts relative to their physical and biological environment. For the Baltic, however, this type of approach has not been conducted (for a discussion of previous stock–recruitment models, see Jarre-Teichmann et al. 2000). The third difficulty involves estimating recruitment before juveniles recruit to the fishery and is as well described theoretically (Hilborn and Walters 1992)

but is often neglected in recruitment modelling approaches (Ulltang 1996). In our analysis, problems in the estimation of recruitment are apparent when inspecting model residuals but also from discussions on the validity of the MSVPA approach to estimate recruitment, specifically for distinct areas (Köster et al. 2001).

Despite these shortcomings and uncertainties, the presented stock–recruitment models may be utilised for enhancing short-term recruitment predictions. The predictions could be based on (i) the most recent female SSB coupled to relative fecundity estimates, (ii) hydrographic conditions during spawning periods and at spawning sites, which would enable prediction of the egg and larval survival in relation to ambient oxygen concentrations, and (iii) cod egg predator population sizes as well as spatial overlap between predator and prey, both forced by hydrographic processes.

A number of potential improvements to the stock–recruitment models are possible through the better resolution of the influences of a number of key variables. Here, the most promising potential candidates are (i) including variations in buoyancy of eggs spawned by first-time and repeat spawners (Vallin et al. 1999), (ii) resolving the vertical distribution of cod eggs in relation to oxygen concentration in eastern spawning areas, and (iii) including the effects of hydrodynamic processes on the horizontal and vertical overlap of predator and prey including cannibalism also.

The spatially disaggregated approach presented here allows an investigation of the impact of different stock components on the reproductive success of cod in the Central Baltic. This is a necessary prerequisite for area-based fisheries management, i.e., an area closure within the Bornholm Basin during cod spawning time recommended by the International Baltic Sea Fisheries Commission (IBSFC 1999).

The stock–recruitment models developed here have the potential to be employed in medium- to long-term stock projections through the incorporation of simulated environmental variability and alternative exploitation scenarios. However, advances need to be made in a number of areas in order to improve these predictions. First, we would like to emphasise that processes coupling individual growth, sexual and gonadal maturation, as well as quantity and quality of produced spawning products to environmental conditions (e.g., Marshall and Frank 1999; Trippel 1998) are a promising field of research in this respect. Furthermore, anthropogenic impacts, such as contamination by toxic substances, potentially affecting the viability of spawning products and eutrophication and impacting the oxygen consumption rates in deep Baltic basins and thus the ambient oxygen conditions for cod egg development (e.g., MacKenzie et al. 1996) have to be verified and incorporated when projecting over longer time periods. Finally, the importance of structural uncertainty in medium- to long-term projection models, i.e., which variables to incorporate and how to incorporate them into the model (e.g., linear, exponential, additive), remains an area for further development; a key issue in the development of quantitative relationships between environmental variables and fish populations as interactions may be counterintuitive (Rose 2000).

Acknowledgements

All participants of the Baltic CORE (AIR 94 1226) and the

Baltic STORE (FAIR 98 3959) projects have contributed their experience, knowledge, and results to the present study, which was a prerequisite for performing the analysis, and are thus gratefully acknowledged here. The authors are grateful to Odd Nakken and one anonymous referee for their careful, thorough, and helpful comments. The present study has been carried out with financial support from the Commission of the European Communities, Agriculture and Fisheries (AIR and FAIR), specific RTD programmes CT94-1226 CORE and CT98-3959 STORE as a contribution to CT97-3805 SAP. This paper does not necessarily reflect the views of the Commission and in no way anticipates the Commission's future policy in this area.

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Appendix

Table A1. Potential seasonal cod egg production by the spawning stock, egg abundance, realised daily egg production at stages I and III during main spawning season, larval abundance from ichthyoplankton surveys, recruitment at age 0 from area-disaggregated MSVPA, reproductive volume, oxygen content within the reproductive volume (summed over 1-m depth intervals), oxygen-related proportions of egg survival, egg predation index, and larval transport index in Subdivision 25.

Year	Potential egg production (no. $\times 10^{12}$)	Egg abundance (no. $\times 10^9$)	Realised production egg stage I (no. $\times 10^9$)	Realised production egg stage III (no. $\times 10^9$)	Larval abundance (no. $\times 10^9$)	Recruits 0-group (no. $\times 10^6$)	Reproductive volume (km ³)	Oxygen content in reproductive volume (m-mL-L ⁻¹)	Oxygen-related egg survival	Egg predation index	Larval transport index (W-m ⁻²)
1976	44.25	936			59.25	661.6	251.2	215.3	0.90	0.004	138 076
1977	40.25	553			41.48	517.4	249.1	118.7	0.52	0.013	64 352
1978	48.94	691			62.81	532.9	128.7	73.9	0.74	0.040	12 821
1979	36.28	640			77.03	753.7	74.0	74.9	0.65	0.019	41 333
1980	42.80	1304			144.57	734.6	232.4	193.9	0.73	0.023	12 334
1981	54.41	249			94.80	493.6	62.5	27.6	0.20	0.058	92 364
1982	54.02	332			11.85	291.2	85.7	25.8	0.15	0.089	-8 203
1983	38.13	527			23.70	311.4	169.6	67.6	0.66	0.035	22 794
1984	50.02	486			47.39	240.3	120.2	69.0	0.64	0.068	84 371
1985	33.82	593			47.43	363.2	132.4	84.8	0.58	0.046	120 216
1986	23.75	658	11.39	1.60	46.99	218.4	98.5	84.3	0.23	0.226	45 903
1987	18.02	326	17.10	2.05	23.70	145.6	94.9	33.1	0.30	0.184	92 628
1988	15.99	172	14.66	1.66	43.93	180.0	99.9	48.9	0.08	0.173	-29 700
1989	16.03	178	13.42	1.83	9.66	87.5	70.7	9.4	0.12	0.267	31 016
1990	11.94	154	12.30	0.84	12.56	145.3	80.3	29.7	0.21	0.131	72 811
1991	8.30	201	18.80	1.74	25.24	189.3	184.7	105.5	0.50	0.069	132 791
1992	12.30	107	17.37	0.85	0.71	134.0	161.3	45.7	0.18	0.113	133 864
1993	13.24	395	16.54	2.43	0.59	164.5	207.7	137.8	0.61	0.039	-14 550
1994	36.96	1970	91.95	10.66	23.26	208.3	194.7	71.9	0.59	0.037	196 622
1995	36.86	1749	108.08	3.70	0.09	235.1	92.0	31.8	0.60	0.068	13 040
1996	34.53	602	50.18	3.83	5.24	661.6	126.0	43.2	0.54	0.057	

Table A2. Potential seasonal cod egg production by the spawning stock, egg abundance during main spawning season, larval abundance from ichthyoplankton surveys, recruitment at age 0 from area-disaggregated MSVPA, and reproductive volume in Subdivisions 26 and 28.

Year	Subdivision 26					Subdivision 28				
	Potential egg production (no. $\times 10^{12}$)	Egg abundance (no. $\times 10^9$)	Larval abundance (no. $\times 10^9$)	Recruits 0-group (no. $\times 10^6$)	Reproductive volume (km ³)	Potential egg production (no. $\times 10^{12}$)	Egg abundance (no. $\times 10^9$)	Larval abundance (no. $\times 10^9$)	Recruits 0-group (no. $\times 10^6$)	Reproductive volume (km ³)
1976	27.57	1163	108.59	768.0	142.3	15.89	240	57.60	382.3	141.0
1977	39.52	804	72.99	667.3	151.9	24.33	1334	320.64	280.6	174.9
1978	43.74	804	82.00	652.0	145.3	45.90	998	108.48	293.8	0
1979	46.01	27	31.09	1560.6	48.1	52.34	504	86.40	562.0	0
1980	72.68	518	65.33	1109.0	153.6	52.27	154	14.40	457.3	0
1981	68.09	355	15.77	645.0	1.1	39.52	1176	4.80	338.9	0
1982	48.20	9	0	378.1	1.1	39.81	119	0.00	298.8	0
1983	36.38	176	24.78	410.7	54.7	27.17	536	0.00	314.4	8.17
1984	53.25	121	17.12	210.8	23.8	43.81	230	129.60	119.3	23.00
1985	38.03	27	40.55	220.9	26.0	32.53	310	110.40	114.5	15.07
1986	23.51	20	6.76	114.8	4.7	24.89	61	4.80	36.6	0
1987	18.87	88	2.70	53.1	0.9	16.18	10	0	17.4	0
1988	16.62	0	0	71.2	0	8.63	0	0	22.6	0
1989	13.42	10	0	47.9	0	6.91	10	0	6.7	0
1990	11.51	34	0	67.6	0	2.54	26	0	7.8	0
1991	5.22	0	0	83.4	0	1.46	0	0	8.1	0
1992	6.77	29	0	111.8	0	0.74	11	0	4.4	0
1993	11.05	9	0	223.8	53.0	1.16	0	0	5.1	0
1994	13.18	116	0	115.4	81.0	1.55	38	0	6.8	175.0
1995	22.92	39	0	43.4	21.1	2.00	9	0	0.6	0
1996	34.44	22	0	768.0	20.5	1.51	17	0	382.3	0