Stock-recruitment relationships of Baltic cod incorporating environmental variability and spatial heterogeneity

F.W. Köster, H.-H. Hinrichsen, D. Schnack[1]

M.A. St. John, B. MacKenzie, J, Tomkiewicz [2]

M. Plikshs[3]

[1] Institute of Marine Sciences, Düsternbrooker Weg 20, D-24105 Kiel

[2] Danish Institute for Fisheries Research, Charlottenlund Castle, DK-2920 Charlottenlund

[3] Latvian Fisheries Research Institute, Daugavgrivas Street 6, LA-1007 Riga

Abstract

Stock-recruitment relationships of Central Baltic cod are constructed for different ICES Subdivisions containing spawning areas with distinct hydrographic regimes, recruitment success and stock development trends. Based on an exploratory statistical analysis, variables identified to have significant influence on the reproductive success are incorporated into modified stock-recruitment models for single subareas and utilized to establish a combined model for the entire Central Baltic.

The statistical model obtained for prediction of recruitment at age 0 in Subdivision 25 based on the potential egg production by the spawning stock explained 69% of the variance. Besides the egg production, corrected for egg predation by clupeids, the sum of oxygen in the reproductive volume was introduced as a significant variable, as well as the larval transport index as being nearly significant. In the more eastern spawning areas the hydrographic regime did in general not allow successful egg development in the period 1981-92. Thus, only relatively simple models based on the egg production by the spawning stock and the reproductive volume are required to achieve a reasonable explanation of recruitment variability.

To obtain an indication about the sensitivity of the parameter estimates and the predictive power of the established statistical models, re-fitting of the models over different shorter time periods utilizing sub-sets of the data series was conducted. The exercise demonstrates that the models derived for the different Subdivisions are able to capture the trend of decreasing recruitment success during the 1980s and the increase in the early 1990s, though they overestimated recruitment in most recent years and regularly underestimated recruitment in early years to a certain extent. If, however, all years with maximum observed recruitment were excluded from the model fitting, the deviations between observed and predicted recruitment were considerably higher.

1 Introduction

One prerequisite for prediction of future stock and fisheries development is a quantifiable relationship between spawning stock and recruitment. Such a relationship is in general very difficult to derive from given time series of stock and recruitment observations due to the large environmentally-induced variation in recruitment success.

In the case of cod in the Central Baltic, there is some evidence of a relationship between spawning stock biomass and recruitment (Plikshs et al. 1993, Sparholt 1996). However, this relationship is sensitive to environmental conditions and trophic interactions (Jarre-Teichmann et al. 1999). For example, low oxygen concentrations at cod spawning sites (Nissling 1994, Wieland et al. 1994), cannibalism on juvenile cod (Sparholt 1994) as well as clupeid predation on cod eggs (Köster and Schnack 1994) have both been shown to be important determinants of recruitment.

In the present study a new stock-recruitment modelling approach will be presented for the Central Baltic cod stock and its applicability, limitations and predictability will be demonstrated and discussed. In contrast to previous approaches (e.g. Sparholt 1996, Jarre-Teichmann et al. 1999) stock-recruitment relationships are constructed for different Subdivisions of the Central Baltic containing spawning areas with distinct hydrographic regimes, recruitment success and stock development trends. The variability in stock-recruitment relationships established on basis of spatially dis-aggregated Multispecies Virtual Population Analysis (ICES 1999/H:5) is investigated with respect to the effect of environmental processes. Variables identified within the Baltic CORE project (Schnack and Köster 1998) having the potential of explaining significant portions of the variability encountered are:

a) potential egg production by the basin specific spawning populations, incorporating information on age-specific sex ratios and female maturity ogives (Tomkiewicz et al. 1997) as well as individual fecundity (Kraus et al. 1999),

b) actual egg production as estimated by field estimates based on stage specific egg abundance estimates (for a time series sub-set in Subdivision 25, Wieland 1995),

c) egg and larval abundance from ichthyoplankton surveys (Makarchouk 1997, Grønkjær et al. 1995, Voss 1996),

d) reproductive volume adjusted to peak spawning time (MacKenzie et al. 1999), alternatively for Subdivision 25 the oxygen content in the reproductive volume and estimates of egg survival at different levels of oxygen considering explicitly the vertical distribution of eggs encountered in the field (CORE 1998),

e) egg consumption rates by the herring and sprat populations in Subdivision 25 (Köster and Möllmann 1999),

f) cumulative wind energy, expressing wind stress and direction in Subdivision 25 as a measure of transport of larvae to nursery areas or retention in spawning areas (Hinrichsen et al. 1999).

g) cannibalism rates on juvenile cod following a procedure introduced by ICES (1993/Assess:17) for herring and sprat.

Based on time series of variables identified to produce a significant impact on the stock-recruitment relationships, modified stock-recruitment models with biologically based combinations of these factors are constructed for Subdivision 25, 26 and 28. Stock-recruitment models having the highest predictive power, are utilized to establish a combined model for the entire Central Baltic.

The presented modelling approach is still preliminary, as input data series are presently in the process of being validated. Furthermore, processes potentially affecting the reproductive success, e.g. fertilization in relation to salinity (Westin and Nissling 1991), egg and larval viability in relation to parental condition (Nissling et al. 1998), contamination by toxic substances (Petersen et al. 1997) and a potential starvation of larvae due to shortage in suitable food supply (Grønkjær et al. 1997) or limited capture success in relation to turbulence conditions (MacKenzie and Kiørboe 1995) have not been included in the present analyses.

2 Material and methods

2.1 Input data

2.1.1 Spawning stock size and structure

Population estimates used for the different Subdivisions of the Central Baltic (both in numbers and weight units) are derived on basis of spatially dis-aggregated MSVPA runs covering the period 1977-1996 (ICES 1999/H:5). The results were extrapolated back to 1976 assuming the same age-specific natural mortalities as in 1977, and applying fishing mortalities derived for 1976 by ICES (1997/Assess:12) with a seasonal F-pattern as determined by the MSVPA for 1977. Basin specific spawning stocks were then calculated by applying area specific maturity ogives combined for both sexes (established for 5 years periods (ICES 1997/Assess:12). Area dis-aggregated catch rates from international bottom trawl surveys conducted in pre-spawning periods, which could potentially be used as a measure of population abundance are available since 1982 only, i.e. are not covering time periods of highest reproductive success. Thus they were utilized for tuning of the MSVPAs only.

2.1.2 Recruitment estimates

Recruitment estimates for the different Subdivisions were also derived by area dis-aggregated MSVPA. Estimates of age-group 0 in the most recent year were omitted, as they are heavily dependent on the tuning performed. Alternative recruitment estimates from trawl surveys are not available for age-group 0 and thus corresponding catch rates for age-group 1 were utilized for validation of model output.

2.1.3 Potential egg production

To estimate the basin specific potential egg production of the spawning populations, annual sex ratios and female maturity ogives were applied for time periods with sampling coverage considered to be adequate (Tomkiewicz et al. 1997), i.e. for Subdivision 25: 1986-96 and for Subdivision 26: 1993-96. When data were insufficient, 5 year means of these variables were utilized. As a second step, a time series of relative individual fecundity values (Bleil and Oeberst 1996, Kraus et al. 1997, Shapiro 1988 and unpublished data summarized in CORE 1998) was applied to the female spawning stock biomass to estimate the total annual egg production. As significant variability in relative fecundity was detected only between years (CORE 1998), but not between spawning areas within a specific year (Kraus et al. 1999), similar relative fecundity values were used for all subareas.

2.1.4 Egg and larval standing stocks and production

Mean annual egg and larval abundance values for the different Subdivisions were employed during this study as compiled by CORE (1998) based on data presented by Karasiova (1997), Plikshs et al. (1993), Makarchouk (1997), Voss (1996), Wieland (1995). The egg abundance data refer to a three month period resembling the main annual spawning time (Wieland et al. 1999), while the larval abundance refers to a

similar period but shifted to one month after peak spawning. Larval abundance values in the Bornholm Basin were corrected for differences in area coverage and drift out of the surveyed area for years 1987-1996 (CORE 1998).

Daily production rates of different egg stages at peak spawning time were determined for the Bornholm Basin on basis of above abundance data coupled to development rates (Wieland et al. 1994). These are based on ambient temperatures in water depths in which the centre of mass of eggs occurred (see below). In years prior to 1986, no egg production values could be estimated due to lack of information on developmental stages or insufficient spatial/temporal coverage of the surveys. Before calculating daily egg production rates, the mean abundance per survey was corrected for different area coverage as done for the larval stage.

2.1.5 Impact of low oxygen concentration on egg survival

Estimates of the size of the reproductive volume (Plikshs et al. 1993) at peak spawning time in the different Subdivisions were obtained by Jarre-Teichmann et al. (1999) and refined by MacKenzie et al. (1999). However, for the Bornholm Basin, two additional methods of characterising the suitability of the environmental conditions for successful egg development were utilised as they were believed to more accurately represent the conditions for egg development:

1) Sum of oxygen in the reproductive volume:

    Oxygen content of the salinity range over which cod eggs are neutrally buoyant was used as a measure of the inherent environmental quality condition for successful development of cod eggs. This estimate was obtained by calculating the sum of oxygen over the thickness of the spawning layer (same specification as the reproductive volume) at specific deep water locations in the Bornholm Basin. A comparison of the original reproductive volume estimate and the sum of oxygen in the reproductive volume generates a statistically significant linear relationship ($r^2 = 0.70$), however with rather high deviations in 1976/77, 1979/80, 1986 as well as 1992 and 1994 (Fig. 2a).

2) Egg survival factor considering the vertical distribution and oxygen concentrations in-situ:

    The fraction of the egg production surviving in each specific spawning season was estimated on basis of the predicted vertical distribution of cod eggs in relation to measured oxygen concentrations in combination with an oxygen concentration/cod egg survival relationship derived from laboratory experiments (CORE 1998). To model the vertical distribution of eggs, the observed distribution of the youngest egg stage (IA) obtained from vertically resolving ichthyoplankton sampling in 1986-96 (Wieland and Jarre-Teichmann 1997) was examined in relation to water density profiles utilising the following parabolic function:

    LOG (relative distr. stage IA) = a + b * density + c * density ^{2}

    Cod eggs become less buoyant after inflows when higher salinity occurs in the bottom water (Wieland and Jarre-Teichmann 1997), probably due to water uptake during hydratisation (i.e. the final gonadal maturation process) and shortly after fertilization. During inflow periods, cod eggs were floating at an average density of 1011.3 kg/m^3 relative to periods of stagnation with 1010.4 kg/m^3. Hence, these hydrographic situations were handled separately. Inflow situations into the Bornholm Basin (Tab. 1) were identified by the depths in which the oxygen concentration is reduced to 2ml/l (inflow if > 85 m) as well as by the average salinity within the reproductive volume (inflow if > 13.5 psu). As furthermore a

seasonal effect in the vertical distribution of cod eggs is apparent, following situations were defined to group the data:

a)   stagnation/early peak spawning
b)   stagnation/late peak spawning
c)   inflow periods/early peak spawning
d)   inflow periods/late peak spawning

As the current model does not take into account temperature, also known to effect the vertical distribution (Wieland and Jarre-Teichmann 1997), a correction was made for low temperatures (< 1.7°C) by transferring the predicted relative abundance of eggs to the next deeper water layer (5 m intervals). The fitted parabolic functions for the four different scenarios are shown in Fig. 1. The explained variance ranged between 72 and 82% with the least explained variability for the inflow/spring spawning scenario.

The relationship between the egg survival factor and the reproductive volume appears to be rather scattered (r^2 = 0.34) indicating that the reproductive volume is a rough measure of egg survival only (Fig. 2b). Two distinct groups of data exist, one having low survival indices (< 35%) at mostly low reproductive volumes (1981/82 and 1986-90 as well as 1992) with the remaining years having relatively high indices (>50%), virtually independent from the magnitude of the reproductive volume. In contrast, a comparison of the egg survival factor and the sum of oxygen in the reproductive volume generates a significant relationship (r^2 = 0.46) suggesting this measure of habitat suitable for egg development is more appropriate for resolving the effects of oxygen content on egg survival. However, considerable deviations in the relationship exist, especially at low oxygen content in the reproductive volume (Fig. 2c).

2.1.6 Predation on cod eggs by herring and sprat

Consumption of cod eggs by herring and sprat populations is significant in the Bornholm Basin (Köster and Schnack 1994), but not in the Gdansk Deep and the Gotland Basin (Fetter and Davidjuka 1996, Patokina 1996, CORE 1998). This difference might be explained by a combination of different food availability and light intensity in dwelling depths of clupeids during their daily feeding period resulting in deviating prey selection patterns (Geldmacher 1998). Consequently, predation of eggs was included in the analysis only for Subdivision 25. Available diet composition data show that the ratio of cod eggs in the stomachs and in the plankton linearly depends on the vertical overlap of predator and prey (CORE 1998), which to a large extend is driven by ambient hydrographic conditions:

–   the oxygen concentration in the bottom water limiting the depths in which herring and sprat are able to dwell during their daily feeding period, but also the depths in which egg development is possible,

–   the density regime encountered, determining where cod eggs are floating in the water column.

To establish a predator/prey overlap index for the time series 1986-96, the average depth in which highest concentrations of cod eggs occurred (see above) and the corresponding depths in which herring and sprat concentrate during their daily feeding period were related. Based on information derived from trawl and hydroacoustic surveys conducted in 1990-96, the depths in which herring and sprat dwell during day-time, was set to 3 m above the water depths at which the 2ml/l oxygen concentration was reached. In case of oxygenated water extending to the bottom, the maximum average catching depths encountered during inflow periods was chosen. Utilizing the relationship between the ratio of individual cod egg consumption rate and

cod egg abundance in the plankton (determined for sampling dates in April-June 1990-96) and the overlap index, enabled in combination with predator stock sizes (for methodology see Köster and Möllmann 1997) the prediction of consumption rates for the main spawning periods in May 1976-92. For the period since 1993 (peak spawning in July), observed average ratios of cod eggs in stomachs and in the food supply were derived directly from sampling covering July/August 1993/94 (inflow) and 1995/96 (stagnation). The predation pressure was introduced in the analysis in terms of a relative index expressing the predation as consumption per standing stock of eggs scaled to the potential egg production by the spawning stock by setting the maximum predation to cause a 95% mortality. This scaling allowed inclusion of predation on cod eggs into the time series of surviving egg production, by subtracting the amount eaten from the magnitude produced.

2.1.7 Larval retention and transport

The cumulative wind energy at peak egg abundance described in Jarre-Teichmann et al. (1999) was modified as follows: The starting point for the calculations was set to the dates of peak larval abundance and the drift period was shortened to 45 days, considering exclusively the duration of the larval stage. A study by Hinrichsen et al. (1999) suggests that larval drift towards the west and north is primarily due to winds of westerly and southerly direction, whereas winds of opposite direction result in larval transport to the south and east. Differences in cumulative wind energy between winds coming from southern to western direction and northern to eastern direction were calculated (CORE 1998). Secondly, differences in cumulative wind energy were converted into the relative frequency of occurrence of larval transport from the spawning ground towards potential nursery areas. A parabolic fit was applied in order to take into account that wind forcing of different origins result in larval transport into different coastal environments.

2.2 Model construction and validation

The complete data series 1976-95 have been utilized to identify causal relationships between survival rates of different early and juvenile life stages, environmental factors and species interactions by means of simple and multiple linear regression techniques. Based on factors identified to have a significant impact on early and juvenile life stage survival, modified stock-recruitment models with combinations of different factors were constructed for Subdivision 25, 26 and 28. The parameters of the final models were determined by utilizing the entire time series available. In order to get an indication of the sensitivity of the parameter estimates and the predictive power, validation was performed by re-fitting of the models, excluding the first 4 and 5 years of data, respectively. This resulted in two different scenarios: the first includes the extraordinary high recruitment in 1980, but not 1979 and the second excludes these outstanding values. After re-fitting of the model, predictions were conducted for these excluded years for comparison with observed values. A similar test has been performed for the most recent 5 years in the 1990s in order to establish if the models are able to reproduce the expected increase in recruitment during this period. By excluding the last 5 years of data, the last major Baltic inflow (Matthäus and Lass 1995) as well as preceding and subsequent smaller inflow events (MacKenzie et al. 1999) were excluded from the model fitting. Utilisation of data from the period prior to 1991 (i.e. excluding only 4 years) allowed for the inclusion of the first smaller inflow event after the stagnation period. In both cases, a considerable reduction in egg predation by sprat, partly compensated by an increase in consumption by herring (caused by the shift in the main spawning time of cod to summer month) has been excluded from the analysis. Thus, this test will evaluate whether the model is robust enough to handle these types of shifts in hydrographic environment and related species behaviour.

To describe the spawning stock and recruitment development in the Central Baltic, predicted recruitment was summed over the different Subdivisions comprising the three major cod spawning grounds. Occasionally an estimated negative recruitment (occurs especially in recent years in Subdivision 28) was set to zero.

3 Results

3.1 Standard stock-recruitment relationships

Stock-recruitment plots for combinations of recruiting age-groups 0 and 1 and areas are presented in Fig. 3. For Subdivision 25 an increasing recruitment with increasing spawning stock size is indicated for age-group 0. However, high outlying recruitment values occurred in this basin in 1976-80. The general pattern is similar in the recruitment estimate for age group 1, but the tendency of increasing recruitment success with increasing spawning stock is reduced.

In Subdivision 26 there appears to be a tendency of decreasing recruitment with decreasing spawning stock sizes (Fig. 3b, correlation $p < 0.05$, however with significant auto-correlation of residuals). Again, a relatively high recruitment occurred in 1976-78 at intermediate SSB-values. The highest recruitment, at high spawning stocks was encountered in 1979-80 with a decrease in reproductive success in the following years, even though the spawning stock remained at a high level.

In Subdivision 28, recruitment at age 0 was virtually independent of the spawning stock in the period from 1976-83 (Fig. 3c). This can also be stated for recruitment at age 1 until 1981. In 1984/85 reproductive success was obviously rather low despite high spawning stocks, followed by a steady decline in recruitment and with a time lag by the stock.

In summary recruitment failures occurred in all Subdivisions during the 1st half of the 1980s. The negative trend started earliest in Subdivision 26 in 1980 and was also most pronounced, followed by Subdivision 25, however, being less severe. In Subdivision 28, the decrease in recruitment success (age-group 0) started latest, i.e. in 1984, but continued nearly to extinction of this stock component.

3.2 Explaining variability in stock-recruitment relationships

3.2.1 Subdivision 25

Two different data series are utilized to explain the variability and the time trends in the stock-recruitment relationships presented for Subdivision 25. For the period since 1986, detailed information on the daily production of different egg developmental stages and their vertical distribution in relation to hydrographic variables are available. In preceding years the information is more scattered. However, variability in recruitment success and size of the cod spawning population is much more pronounced. Due to the lack of data, processes potentially having influence on cod egg survival were investigated first for the shorter time series and then for the complete data set.

Potential egg production and production of late egg stages

As a first test, the variability of the cod egg stage III production per day obtained by ichthyoplankton surveys divided by the total potential egg production determined via the female spawning stock biomass was investigated. Egg production at stage III was utilized as a proxy of the abundance of the oldest egg stage IV as the abundance of stage IV is rather variable in the ichthyoplankton surveys. This is due to that hatching of Baltic cod eggs commences during this stage and the duration of this stage is relatively short (Wieland et al. 1994). Potential egg production by the spawning stock is available for the entire 21 year time series, while

the egg production of stage IA derived from ichthyoplankton surveys are only available since 1986. There is, however, a significant correlation between both variables ($r^2=0.74$) justifying the utilization of potential egg production as an estimate of reproductive effort (Tab. 2, containing all coefficients and significance levels of the performed statistical analyses). A linear regression of the egg production at stage III divided by the potential total egg production (as a measure of egg survival) on the oxygen related egg survival factor explains 39% of the variability encountered (Fig. 4a). Especially at high egg survival some scatter occurred with a high positive residual in 1994 and relatively high negative residuals in 1995/96.

Utilizing the egg consumption index, a regression vs. egg production at stage III per potential egg production by SSB revealed a negative correlation explaining 29% of the variance (Fig. 4b). Again, a high positive residual in 1994 and negative residuals in 1995/96 are obvious.

Incorporating both processes into the potential egg production (i.e. subtracting the consumed egg consumption and multiplying by the oxygen related survival factor) revealed a significant linear regression with egg production at stage III ($r^2 = 0.66$). Again difficulties in explaining the values in most recent years, especially 1994, occurred (Fig. 4c). Additionally it has to be stated, that the potential egg production alone explains 53% of the variance (Tab. 2). Auto-correlation introduced by the decline in egg production through declining SSB from 1986-92 was not detectable.

Egg production and larval abundance

Correlating larval abundance per egg production by SSB (as a measure of survival to the larval stage) vs. the oxygen related egg survival factor as well as the consumption index revealed no significant relationships (Tab. 2), regardless of whether the 21 year or the 11 year time period (latter with a better ichthyoplankton survey coverage) has been used. This result, however, is not unexpected for a number of reasons:

a) even if egg mortality is significantly influenced by low oxygen conditions and predation, larval survival may be related to other factors not considered here, e.g. transport to suitable nursery areas, feeding conditions and prey utilization,

b) the oxygen related egg survival factor may not be a good measure for larval survival, even when hatching occurs at the same depths. The sum of oxygen in the reproductive volume is probably a better measure for the overall oxygen conditions in and below the halocline (see Figure 5a),

c) the larval abundance data is expected to be noisy, as these integrate all larval developmental stages.

The larval abundance plotted vs. the egg production by the SSB yielded a significant relationship over the 21 year time series (explaining 23% of the variance encountered, Fig. 5b). However, for the most recent 11 year period, no relationship is obvious (Tab. 2). Replacing the egg production by the SSB with observed egg production values at stage III from ichthyoplankton surveys and repeating the exercise resulted in a significant linear relationship of larvae per egg production vs. the oxygen related survival factor as well as the predation index (Tab. 2). However, a negative relationship was observed for the oxygen impact and a positive 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. Not surprisingly, there is also no direct relationship between larval abundance and egg production at stage III (Tab. 2).

The only sensible statistical model derived by the exploratory analyses is a multiple linear regression including: the egg production by the SSB corrected for egg consumption and the sum of oxygen in the reproductive volume as independent variables. This multiple regression resulted in significant regression

coefficients for both variables on the 90% level (egg production: $p = 0.065$ and sum of oxygen: $p = 0.089$) and a non significant constant, explaining 31% (adjusted for degrees of freedom) of the variance in the larval abundance. The time series of observed and predicted values (Fig. 5c) clearly demonstrates, that the model was unable to explain high larval abundances in 1980/81 and resulted in relatively high negative residuals in 1982/83 and 1988 as well as from 1992-96. This might indicate problems with the timing of the ichthyoplankton surveys after the shift of peak spawning activity into summer months. Furthermore it should be noted, that a significant auto-correlation in the residuals has been detected (Tab. 2).

Larval abundance and recruitment at age 0

Plotting the recruitment at age 0 vs. larval abundance from 1976-95 revealed a highly significant linear relationship ($r^2 = 0.65$) with both a significant regression coefficient and intercept (Fig. 6a). The intercept is primarily caused by recruitment observations originating from very low larval abundance values derived by ichthyoplankton surveys conducted in 1992/93 and 1995. These resulted in extremely high ratios of recruitment at age 0 to larval abundance, again pointing to a problem in the larval abundance data. In order to detect factors explaining variability in survival success from the larval to the 0-group stage, years after 1992 were removed from the analysis, due to the indicated lack in temporal overlap of larval occurrence and surveys. Correlating the ratio of recruitment at age 0 to larval abundance (as a measure of larval survival) against the sum of oxygen in the reproductive volume as well as the cumulative wind energy index, based on the drift modelling experience in the Bornholm Basin, did not reveal any significant relationships (Tab. 2). Nevertheless, including the sum of oxygen in the reproductive volume in a multiple linear regression (assuming that the above presented significant impact on the larval abundance - egg production relationship is not only restricted to the egg stage, but also acting on early larvae) resulted in a slightly increased fit of the recruitment vs. larval abundance relationship, with a nearly significant regression coefficient for the sum of oxygen content in the reproductive volume (Fig. 6b), but only if the entire time series is used. Similarly including the wind energy index as a variable did not increase the r^2-value (Tab. 2).

Recruitment at age 0 and at age 1

The predation mortality of 0-group cod resulting from cannibalism as determined by MSVPA, is linearly related to the spawning stock biomass (Fig. 7a). This significant relationship can be used to predict the recruitment at age 1 from the number of recruits surviving until age 0. A relatively high positive residual occurred in 1983 and a considerable negative residual in 1984.

3.2.2 Subdivision 26 and 28

For Subdivision 26 and 28 encompassing the Gdansk Deep/southern Gotland Basin and the central Gotland Basin respectively, no egg production values are available. Furthermore information on the vertical distribution of cod eggs did not allow a prediction of the relative vertical distribution at different density layers and hence the application of the egg survival function in relation to the oxygen condition in a given depths. Furthermore, drift modelling was performed primarily in Subdivision 25 as it has been the only important spawning area in the last 10 years. Thus, the exploratory analyses conducted in these Subdivisions are restricted to ichthyoplankton abundance data in relation to the reproductive volume. However, as the hydrographic changes were much more pronounced in the more eastern spawning areas of cod, strong signals in the reproductive success might nevertheless be explained using the reproductive volume as environmental variable.

Potential egg production and egg abundance

Linear regressions of egg abundance values from ichthyoplankton surveys on the estimated egg productions by the spawning populations revealed a significant relationship for Subdivision 28 only (Tab. 2). However, even in this case a time trend in the residuals is obvious, with high positive residuals in the beginning of the time series, i.e. up to 1980, and mostly negative residuals afterwards. Obviously, since the beginning of the 1980s egg abundance was less than to be expected from the available spawning stock computed. This observation can be explained by the unfavourable hydrographic conditions causing extremely high egg mortalities even for younger egg stages. This is confirmed when observed egg abundance per egg production by the spawning stock is regressed on the reproductive volume. This exercise yields highly significant relationships for both areas, explaining 55% and 44% of the variance encountered (Tab. 2).

Egg production and larval abundance

Correlating the observed larval abundance per unit of egg production by the spawning stock vs. the reproductive volume resulted in both areas in significant linear relationships (Fig. 8) Subdivision 26: r^2 = 0.58 and 28: r^2 = 0.41). Although the relationships, especially in Subdivision 28, show high variability in the survival to the larval stage, occurrence of intermediate to high reproductive volumes have obviously an impact on egg and probably also early larval survival. An exception is 1994, when no larvae were encountered in both areas, although a fairly high reproductive volume was available.

Larval abundance and recruitment at age 0

A linear regression of the recruitment at age 0 against the larval abundance (Fig. 9a) for Subdivision 26 showed, compared to Subdivision 25, a less correlated but still significant relationship (r^2=0.40). In contrast, the corresponding relationship for Subdivision 28 is not significant, displaying a rather high number of zero observations and a huge scatter of the remaining data points (Fig. 9b).

Recruitment at age 0 and at age 1

Predation mortality of 0-group cod caused by cannibalism are, similar to Subdivision 25, linearly related to the spawning stock biomass (Fig. 7b). For Subdivision 26, substantial deviations between observed and predicted values were determined for 1983 (high positive residual) and in 1984 (negative residual). A corresponding pattern can be observed for Subdivision 28 (Fig. 7c), with a high observation in 1983 and negative but small residuals for 1984-88.

3.3 Stock-recruitment relationships including environmental factors and predator/prey interaction

3.3.1 Subdivision 25

Incorporating significant processes identified in the exploratory analysis in a stock recruitment relationship covering the entire early life stage from egg production to recruitment at age 0 resulted in a multiple regression with the egg production by the spawning stock (corrected for the removal by egg predation) and the sum of oxygen in the reproductive volume as independent variables (Fig. 10a). The statistical model explained 66% of the variance (adjusted for degrees of freedom) encountered with both regression coefficients being significant (corrected egg production: p = <0.001, sum of oxygen in the reproductive volume p=0.025), but with a significant autocorrelation in the residuals (Fig. 10c). The statistical model developed showed highest deviations from observed values in 1979/80 (positive residuals), and in 1984 as well as in 1993/94 (negative residuals). Incorporating the cumulative index of wind energy as an additional

10

variable improves the model (r^2=0.69, Fig. 10b), with the regression coefficient being nearly significant (p=0.113), and removes the significance of the auto-correlation in the residuals (Fig. 10c). However, the regression coefficient of the larval transport index is negative, which suggests, that an increase in wind energy would result in a decline in recruitment success indicating that: retention of larvae in the central basins is conducive to survival or in another interpretation that larvae are transported to other basins thus reducing survival success in Subdivision 25.

As recruitment at age 0 is log-normal rather than normal distributed (Shapiro-Wilks test) a multiplicative model was established by log transforming the dependent and independent variables. The model explained also 66% of the variance (Fig. 11a), however, the regression coefficient for the logarithmic sum of oxygen concentration in the reproductive volume was not significant, contrary to the other coefficient (Tab. 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 most recent years (1993-95) the model overestimated recruitment. Including the larval transport index as an additional variable increased the r^2 to 0.69 (Fig. 11b). However, the regression coefficient was not significant (p=0.151) either and again the relationship was negative. For both models, the Durbin Watson statistics indicated auto-correlation in the residuals (Fig. 11c).

3.3.2 Subdivision 26

Incorporating the reproductive volume into a stock recruitment relationship containing the egg production by the spawning population as a second independent variable revealed a significant linear relationship explaining 55% of the variance in recruitment at age 0 (Fig. 12a). Both regression coefficients were significant, but not the model intercept (Tab. 2). No auto-correlation was indicated by the Durban Watson statistics. A large positive deviation between observed and predicted recruitment occurred in 1979, with negative residuals encountered throughout the period 1982-88, i.e. the model always overestimated recruitment, however, the absolute deviations were relatively small. The corresponding logarithmic model fit the data better (Fig. 12b), with an explained variance of 61%, but again significant auto-correlation of the residuals (Fig. 12c).

3.3.3 Subdivision 28

The corresponding models for Subdivision 28 showed the best fit of the different sub-areas explaining 66% and 78% of the variance with the normal and the log-version respectively (Fig. 13a,b). However, in the latter the regression coefficient of the reproductive volume was not significant and again auto-correlation of the residuals was indicated (Fig. 13c). When comparing observed and predicted values obtained from the normal model it becomes obvious that at high to intermediate recruitment levels, i.e. up to 1985, quite some deviations occurred, while in the later years consistently low recruitment was predicted and observed.

3.3.4 Comparison of non- and log-transformed models

Observed vs. predicted recruitment at age 0 in Subdivision 25, 26 and 28 obtained by the multiple regression models (normal and log-transformed versions) for the time series 1976-96 are presented in Fig. 14. The non-transformed models showed, in general, lower deviation between observed and predicted recruitment. The log-transformed models always underestimated high recruitment values with considerable deviations from observed values especially in Subdivision 26 and 28. The non-transformed models showed a similar, but much less pronounced behaviour in Subdivision 25 and 26. In the latter area, the model had one outstanding value in 1979, when the predicted abundance was less than half of the observed. In Subdivision 25, the

11

deviations were smaller, however, similarly 1979 showed highest deviations. In Subdivision 28, the non-transformed model behaved differently. High over-estimations of recruitment occurred at intermediate recruitment levels, especially in 1984-86.

3.3.5 Stock-recruitment relationships for the entire Central Baltic

Combining the area specific recruitment estimates at age 0 and plotting observed against predicted recruitment as well as the corresponding time series (Fig. 15a) revealed an overall rather good agreement, with the exception of especially 1979 (underestimated by the model) and 1984 (being overestimated). Some smaller deviations occurred in the most recent years, when the model predicted higher recruitment than observed. The total predicted and observed recruitment at age 1 for the Subdivisions 25, 26 and 28, based on the estimates of recruitment at age 0 and applied predation mortalities, are presented in Fig. 15b. Somewhat higher deviations between predicted and observed recruitment are obvious when compared to the corresponding age-group 0 recruitment predictions (especially in 1980 and 1983).

3.4 Predicting recruitment from larval abundance

3.4.1 Subdivision 25

Recruitment at age 0 may also be predicted on basis of larval abundance data. Fig. 16a contains observed vs. predicted recruitment values for Subdivision 25 obtained by: a) a simple linear regression of recruitment on larval abundance and b) a multiple linear regression incorporating the sum of oxygen in the reproductive volume as well as the larval transport index. In general, the model fits were quite reasonable with only a slight improvement at higher recruitment levels when utilizing the more complicated statistical model.

3.4.2 Subdivision 26 and 28

The corresponding plots of observed vs. predicted recruitment derived by the simple model version for Subdivisions 26, however, indicated higher deviations and a poor fit was also observed for Subdivision 28 (Fig. 16b). In both cases the intercept resulted in relatively large recruitment, even when no larvae were encountered in the ichthyoplankton surveys. The existence of an intercept is noteworthy, as in fact recruitment is regularly observed (not only by MSVPA but also by trawl surveys) although no larvae were encountered on the ichthyoplankton stations. The largest deviation between observed and predicted recruitment was computed in Subdivision 26 for 1979, with a substantial underestimation generated by the statistical model. In Subdivision 28, observed recruitment appears to be virtually independent of the larval abundance, which is caused mainly by the fact that at very low to zero larval abundance values considerable recruitment occurred.

3.4.3 Entire Central Baltic

Combining all area related estimates is not affected by the lack of fit in Subdivision 28, i.e. the observed vs. predicted plot reveals a reasonable agreement (Fig. 17). There is, however, a clear tendency of overestimating recruitment at low observed recruitment levels, caused by the relatively large intercepts in the models. Additionally a tendency of underestimation at high recruitment is encountered.

3.5 Validation of stock-recruitment models

In order to get an indication of the sensitivity of the parameter estimates and the predictive power of the established stock-recruitment relationships a re-fitting of model parameters was conducted excluding:

   a) the first 4 years,

b) the first 5 years,

c) the last 4 years,

d) and finally the last 5 years data.

For Subdivision 25, all data series revealed highly significant multiple linear regressions (Tab. 3). The explained variance was lowest when excluding the first 5 years of data, i.e. time periods with high recruitment events. Furthermore, the regression coefficient of the sum of oxygen in the reproductive volume was not significant in this model, while it was in all other scenarios. A similar observation with respect to the exclusion of 1980 was obvious for Subdivision 26, although the overall fit of the model was better than in the original version, explaining 73% of the variance. This was caused by the exclusion of 1979, the year producing the highest residual in this Subdivision. Correspondingly, the best fit was reached with the time period 1980-96 ($r^2 = 0.85$). Excluding the most recent 4 and 5 years (contrary to Subdivision 25) resulted in a reduction of explained variance (down to 54% in the latter series). As well, in Subdivision 28, a drastic decline in the r^2-values was encountered, when excluding 1980. However, the regression coefficient of the reproductive volume was already not significant when excluding only the first 4 years of the time series. Excluding most recent years from the analysis resulted in slightly reduced r^2-values only.

Tab. 4 demonstrates the effect of shortening the time period sequentially by one year increments. The table gives the r^2-values for model fits obtained after excluding successively 1977 to 1981 as well as 1990 to 1995 together with the significance levels of the regression coefficients. In general for Subdivision 25 and 26 a decrease in explained variance was observed with reduced temporal periods. However, there are some exceptions, i.e. starting the fitting procedure for Subdivision 25 with 1980 gave a similar fit as the original model and excluding the most recent inflow years 1993 by stopping at 1992 increased the explained variance. In Subdivision 26, starting with 1980/81 resulted in a better fit than the original model. For Subdivision 28, relatively high r^2-values were derived independent of the starting year between 1977-80, excluding more years reduced the explained variance drastically. Apart from that the r^2-values were relatively high, the regression coefficients of the reproductive volume were far from being significant. Omitting the last three years of the time series did not change the fit of the model, however, reducing the time span further does.

Comparing the observed and predicted recruitment at age 0 for the entire Central Baltic revealed a similar fit to the original model when dropping the last 4 or 5 years of data in the parameter estimation procedure (Fig. 18). Thus the model was able to predict the increase in recruitment occurring in 1993-95, however, it over-estimated the recruitment in these years by 53-89%. On the contrary, for 1992 the model underestimated the recruitment by 61-63%, which to a lesser extent is also true for 1991 (31%). When comparing observed vs. predicted recruitment in single Subdivisions, larger deviations between the original model estimates and those derived by the test versions were encountered. Rather high overestimations occurred in Subdivision 25 in 1993 and especially in Subdivision 28 in 1994. The relatively high deviation between observed and predicted recruitment for the combined stock in 1993 is caused by a high oxygen concentration in the reproductive volume in the Bornholm Basin coupled to a low predation pressure at a relatively low egg production. The high outlier in Subdivision 28 in 1994 is caused by the extremely high reproductive volume (since 1977 the highest on record). However, the inflow replaced especially deeper parts of the bottom water, resulting in an intermediate layer with very low oxygen concentration having densities sufficient to keep at least a part of the cod eggs floating and thus not sustaining their development. This indicates, that

also for the more eastern spawning areas the vertical distribution of the cod eggs has to be considered, when describing the environmental conditions.

Excluding the first 4 years of data actually gave an in general good fit to the observed recruitment in the combined stock (Fig. 19). However, this approach underestimated the recruitment in 1976 and 1979/80 slightly more than the original model version (Fig. 10) (30, 58 and 15% compared to 19, 52 and 5%). Deviations in 1979 were rather pronounced 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 appears to be a general trend for all areas. 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 1976-80 (Fig. 19). The model always substantially underestimated recruitment (32-69%) for 1976-80 and had considerably broader 95% prediction limits of the mean, with observed values being outside of these limits in 1976 and 1979/80.

On basis of the combined stock, a further test of the recruitment model was conducted by comparing predicted recruitment at age 1 with observed independent recruitment indices obtained by the international bottom trawl survey. The comparison between the arithmetic mean of the catch rates and predicted recruitment showed poor coherence, with large deviations especially in 1981/82 and 1984 (Fig. 20). Since 1990, the time trend in both data series appears to be in line with increasing recruitment until 1994 where after a substantial decline was observed in 1995. In general, observed recruitment as output of an applied GLM-model (according to Sparholt and Tomkiewicz 1998) was significantly better correlated to the predicted recruitment than the arithmetic means and showed a similar trend over the covered time period 1981-95. However, low catch rates were encountered in 1985/86, while the predicted recruitment lagged, not reaching the lowest levels until 1989.

4   Discussion

Analysis of environmental factors and spawning stock features with respect to their impact on reproductive success of Baltic cod have previously been conducted by several investigators (e.g. Bagge 1993; Berner et al., 1989, Kosior and Netzel 1989; Lablaika et al. 1989; Plikshs et al. 1993; Sparholt 1996, Jarre-Teichmann 1999). Obvious differences between these approaches and the presented analysis are:

a) dis-aggregation of recruitment success and spawning stock sizes into major spawning areas, having distinct hydrographic regimes (e.g. Plikshs et al. 1993, MacKenzie et al. 1999), showing differences in the individual maturation process (Tomkiewicz et al. 1997) and deviate in recruitment success and stock development trends (Sparholt and Tomkiewicz 1998),

b) utilization of egg production instead of the spawning stock biomass as a measure of reproductive effort applying a time series of relative fecundity values showing significant interannual variability (Kraus et al. 1999),

c) quantifying the impact of sub-optimal but not lethal oxygen concentrations in the reproductive volume and introduction of the sum of oxygen as a corresponding measure,

d) incorporation of egg predation by clupeids in Subdivision 25 (Köster and Möllmann 1999),

e) application of a cumulative wind energy index as a measure of larval retention in spawning basins or transport to nursery areas (Hinrichsen et al. 1999).

4.1 Explanation of variability in stock recruitment relationships

Exploratory analysis of a sub-set of the time series (1986-96) available for Subdivision 25 revealed a significant impact of: a) the oxygen related egg survival factor and b) the predation index on the egg survival until developmental stage III.

Incorporation of egg production instead of using the spawning stock biomass increased the explained variance from 44 to 53% and inclusion of both survival/mortality indices resulted in a further increase to 66%. High egg survival in 1994 compared to low survival in 1995/96 could nevertheless not entirely be explained by the statistical model.

The present analysis assumes, that the potential egg production computed via the spawning stock is an unbiased measure of the actual egg production in the field. This was indicated by a significant relationship between production of egg stage IA obtained from ichthyoplankton surveys and the estimated potential production by the SSB in 1986-96 as well as during specific sampling dates in 1994-96 (CORE 1998). Thus, it appears to be rather unlikely that encountered deviations between observed and predicted egg survival rates can be explained by grossly erroneous egg production estimates.

The hydrographic regime in 1994 was characterized by high salinities and in the beginning of the spawning season high oxygen concentrations in and below the halocline. However, cod eggs at peak spawning time were exposed to nearly the same oxygen levels as in later years. This resulted in rather similar oxygen related survival indices from 1994-96 (54-60%). Also in 1993, a year characterised by a major inflow event (e.g. Matthäus and Lass 1995) the corresponding oxygen related survival factor was only slightly higher than in subsequent years (61%).

In summary, the enhanced oxygen conditions in the Bornholm Basin in 1993/94 resulted in an increased oxygen related survival factor compared to preceding years (18-50% in 1990-92), however, a corresponding decrease in 1995/96 was not observed and does not explain lower egg survival rates in these years. Egg predation, especially by sprat was on a rather low level in 1993/94 caused by a: 1) continuous shift in spawning time of cod to later month resulting in a limited temporal overlap between sprat and cod eggs and 2) limited vertical overlap between predator and prey (Köster and Möllmann 1999). This decrease in predation pressure was compensated for to a considerable extent by an increase in consumption rates by herring in summer, thus partly explaining the observed differences in egg survival rates. A validation of the MSVPA results (ICES 1999/H:5) on basis of independent population estimates revealed an overestimation of the cod abundance in Subdivision 25 at least in 1996. Consequently the potential egg production for this year will be overestimated as well, a fact obvious also from comparison to egg production estimates derived by ichthyoplankton surveys. Thus in the present study the determined egg survival rate for 1996 is most likely underestimated, explaining partly the deviation.

The exploratory analysis conducted was unable to explain a considerable part of the variability encountered between egg production measures (potential production by SSB as well as egg stage III production from surveys) and larval abundance in Subdivision 25, which indicates either that:

a) other factors than oxygen related mortality of eggs and egg predation are substantially influencing the hatching and larval survival success,

b) the variability in larval abundance (integrated over all developmental stages) is too high to detect a major impact of both mentioned factors,

c) the abundance may be biased by non-representative sampling time and area coverage in specific years.

In fact, there is a significant linear relation between the ratio of larval abundance to egg production and the sum of oxygen in the reproductive volume. This indicates that this variable is a better measure of the environmental conditions faced by larvae than the oxygen related egg survival factor, as the vertical distribution is and the minimum lethal oxygen concentration may be different for both life stages. Behaviour studies conducted with larvae demonstrated that low oxygen concentration has an impact on larval mortality and that egg incubation at low oxygen concentration also impacts on larval activity (CORE 1998). Furthermore, the experiments revealed that vertical migration into upper water layers is not started before day 4 after hatch (Rohlf 1997). Hence, a significant impact of the environment within and below the halocline can be expected. Due to the better performance of the sum of oxygen in the reproduction volume compared to the oxygen related egg survival factor, the former factor was included in the subsequent exploratory analysis and also in the final model set-up for Subdivision 25. A multiple linear regression of larval abundance to the egg production by SSB corrected for egg predation and the sum of oxygen in the reproductive volume had considerable negative residuals in most recent years. This suggested a mis-match in the timing of ichthyoplankton surveys caused by a delayed spawning in later years. This of course has implications on the use of the larval abundance estimates as a predictor of recruitment (see below). In the more eastern spawning areas, variability in larval abundance was more easily explained, as a highly significant impact of the hydrography is obvious from a regression of larval abundance to egg production by the SSB on the reproductive volume. This result is not surprising as the environmental conditions are less favourable for successful egg survival in these areas compared to the Bornholm Basin.

Larval growth and survival as well as egg buoyancy in Baltic cod is related to egg size which in turn is correlated to female size (Nissling et al. 1998). Thus it can be expected that significant changes in the stock size/age structure have an additional impact on survival rates of early life stages. However, as egg size varies with female size, between females of similar size (probably due to condition) and with batch number (Vallin and Nissling 1999), further research is initiated in this area making the application of this approach for stock recruitment models premature.

The multiple regression of recruitment at age 0 in Subdivision 25 on larval abundance, considering the sum of oxygen in the reproductive volume and the larval transport index revealed a highly significant fit explaining 66% of the variance. The regression coefficient for the sum of oxygen was significant on the 90% level, whereas the one of the larval transport index was not. Additionally, the larval abundance explains 65% of the variance alone suggesting to utilize the simpler model for predicting recruitment. In Subdivision 26 a significant linear 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 despite the lack of larvae in the ichthyoplankton. As recruitment in this area was not only determined by the MSVPA but also observed in the bottom trawl surveys as age-group 1, this indicates either:

a) a problem in sampling efficiency of the gear in use at low larval abundance, i.e. not filtering sufficient water volume or

b) a transport of larvae and pelagic 0-group out of the Bornholm area into the more eastern Baltic basins.

The latter hypothesis is confirmed by the comparison of trawl survey results and MSVPA output (ICES 1999/H:5) and also indicated by the fact that the larval transport index is negatively related to recruitment in Subdivision 25.

The procedure of estimating cannibalism rates of age-group 0 by regressing predation mortalities obtained by MSVPA runs on the spawning stock biomass yielded highly significant relationships. A more sophisticated approach utilizing prey/predator age specific suitability coefficients might be applicable thereby reducing the noise introduced by the present procedure. In any case the assumption of constant suitability coefficients at varying prey abundance, distribution and growth may be questionable (e.g. Sparre 1993, ICES 1996/Assess:2, Neuenfeldt and Köster 1999) and should be solved before application in recruitment estimation procedures (see also section 4.3).

4.2 Stock-recruitment relationships including environmental factors and predator/prey interaction

The final statistical model established for recruitment at age 0 in the Bornholm Basin explained 69% of the variance in recruitment success. This approach included:

a) the egg production by the spawning stock (corrected for egg predation by clupeids),

b) the sum of oxygen in the reproductive volume,

c) as well as the larval transport index being nearly significant.

The regression coefficient of the latter variable was negative, i.e. recruitment success appears to be negatively related to high wind stress, suggesting that retention in the basin and low turbulent mixing leads to increased recruitment success, contradicting the hypothesis that a rapid transport into nursery areas is a process enhancing recruitment success (Hinrichsen et al. 1999). However, this result is biologically sensible, when interpreted as a transport into neighbouring Subdivisions, for which evidence exists (see above).

Although recruitment was log-normal rather than normally distributed and multiplicative instead of additive processes may in some cases be more appropriate (Sparholt 1996), the log-transformed model did not predict recruitment better. It consistently underestimated high recruitment in the beginning of the time series, a fact which was also obvious for both other spawning areas. Additionally 1st order correlations of recruitment were encountered regularly in all log-transformed models, whereas this was not observed in the non-transformed models.

Independent of the model choice, an underestimation of the recruitment at age 0 was encountered for 1979 in Subdivision 25 and 26. This is mainly caused by below average reproductive volume in both areas. As unfavourable hydrographic conditions were measured throughout the year in both basins on several occasions (MacKenzie at al. 1999), it appears to be likely that the observed recruitment derived by the MSVPA runs are causing the deviations. Substantial tuning problems referring to the oldest age-group of the year-class 1979 were not apparent and corresponding stock at age in older age-groups appeared well structured. However, rather high predation mortalities were estimated by the MSVPA resulting in the highest recruitment at age 0 within the time series in both areas. Bottom trawl surveys conducted in 1980 in Subdivision 25 revealed a low abundance of 1-group cod, but one year later the occurrence of 2 year old fish was rather high (considerably higher than the 1978 year-class but still below the 1980 year-class). The corresponding trawl survey in Subdivision 26 (starting in 1981) revealed also a relatively high abundance of the 1979 year-class but well below of the following cohort. In summary, evidence exists, that the 1979 recruitment estimate for age-group 0 derived by the MSVPA is too high and hence the deviation in observed and predicted recruitment is not caused by a model mis-specification, i.e. the predicted recruitment may be more reliable than the "observed" value.

When combining the recruitment estimates for the three spawning areas, it should be kept in mind that the models established for the eastern spawning areas are more simple than the one established for the Bornholm Basin. In the latter area, a suitable volume of water was always available for cod egg reproduction (of course in varying quantities). Other factors such as egg predation and larval drift 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 in general not allow successful egg development since 1981. Thus, only relatively simple models were required for these areas to achieve a reasonable explanation of recruitment variability (60-70% explained variance) as survival at later stages has only limited influence on recruitment success.

4.3 Validation of stock-recruitment models

The statistical stock-recruitment models established in the present study explain a considerable part of the variability encountered in recruitment at age 0 and 1. However, this does not mean that the models are able to predict the recruitment in a given year very precisely. To obtain an indication of the sensitivity of the parameter estimates and the predictive power, re-fitting of the models over different shorter time periods utilizing a sub-set of the data series was conducted. The exercise clearly demonstrated that the models derived for the different Subdivisions are able to capture the trend of decreasing recruitment success during the 1980s and an increase in recruitment success in the early 1990s. However, they overestimated recruitment in most recent years and regularly underestimated recruitment in early years of the time period (i.e. 1976 and 1979). When excluding both years with outstanding high recruitment from the parameter estimation procedure, e.g. 1979/80, the model showed high deviations in predicted and observed recruitment in all Subdivisions. For the combined stock, the observed values for 1976 and 1979/80 were actually outside the 95% prediction limits of the mean. However, starting the fitting procedure with 1980 revealed even a slightly better fit than the original model, due to the exclusion of the 1979 data which produced the highest residual (see above). In conclusion, it may be stated that the established models are not very sensitive to exclusion of periods from the parameter estimation procedure. However, if all observed high recruitment values were excluded from the time series, a substantial underestimation of recruitment was encountered.

Acknowledgement

References

Bagge, O. 1993: Possible effects on fish reproduction due to changed oceanographic conditions in the Baltic proper. ICES CM 1993/J: 31.

Berner, M., Müller, H. & D. Nehring 1989: The influence of environmental and stock parameters on the recruitment of cod stocks to the east and west of Bornholm described by regression equations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 190: 142-146.

Bleil, M. & R. Oeberst 1996: The fecundity of cod in ICES Subdivisions 22, 24 and 25 in the years 1992 to 1995 (preliminary results). ICES C.M. 1996/J:8.

CORE 1998: Mechanisms influencing long term trend in reproductive success and recruitment of Baltic cod: Implications for fisheries management. Final Report AIR 94 1226, part I, 504 pp.

Fetter, M. & A. Davidjuk 1996: Herring daily feeding activity in the eastern Baltic Sea. ICES C.M. 1996/J:26.

Geldmacher, A. 1998: Die Bedeutung von Heringen und Sprotten als Bruträuber in der östlichen zentralen Ostsee (Gdansk Tief and Gotland Tief). Dipl. thesis, Institute of Marine Sciences, Kiel, 99pp.

Grønkjær, P., Möllmann, C., & R. Voss 1995: Abundance,and distribution of larval cod (Gadus morhua) in the Bornholm Basin. ICES C.M. 1995/J:24.

Hinrichsen, H.-H., St. John, M.A., Aro, E., Grønkjær, P. & R. Voss 1999: Testing the larval drift hypothesis in the Baltic Sea: Retention vs. dispersion due to the influence of the wind driven circulation. ICES J. mar Sci. (submitted).

ICES 1993: Report of the Working Group on Assessment of pelagic Stocks in the Baltic. ICES C.M. 1993/Assess:17.

ICES 1996: Report of the Working Group on Multispecies Assessment of Baltic Fish. ICES C.M. 1996/Assess:2.

ICES 1997: Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1997/Assess:12.

ICES 1997: Report of the Study Group on Multispecies Model Implementation in the Baltic. ICES C.M. 1997/J:2.

ICES 1998: Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1998/ACFM:16.

ICES 1999: Report of the Study Group on Multispecies Model Implementation in the Baltic. ICES C.M. 1999/H:5.

Jarre-Teichmann, A., Wieland, K., MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M. & E. Aro 1999: Stock-recruitment relationships for cod (Gadus morhua callarias L.) in the central Baltic Sea incorporating environmental variability. ICES J. mar Sci., 56 (in press).

Karasiova, E.M. 1997: Pecurialities of cod eggs distribution in 1992-1995 in relation to hydrographic conditions in the South-Eastern Baltic Sea. ICES C.M. 1997/EE:10.

Köster, F.W. & D. Schnack 1994: The role of predation on early life stages of cod in the Baltic. Dana, vol. 10: 179-201.

Köster, F.W. & C. Möllmann 1997: Predation by sprat and herring on early life stages of cod and sprat in the central Baltic. Proceedings Symp. on Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program No 97-01: 41-70.

Köster, F.W. & C. Möllmann 1999: Trophodynamic control on recruitment success in Baltic cod: prey controls predator - clupeids vs. cod. ICES J. mar Sci., 56 (in press).

Kosior, M. & J. Netzel 1989: Eastern Baltic cod stocks and environmental conditions. Rapp. P.-v. Réun. Cons. int. Explor. Mer 190: 159-162.

Kraus, G., Müller, A & F.W. Köster 1997: Intra- and interannual variabilty in fecundity of Baltic cod. ICES, C.M. 1997/CC: 13.

Kraus, G., Müller, A, Trella, K. & F.W. Köster 1997: Temporal and spatial variability in fecundity of Baltic cod. Submitted to J. of Fish Biol.

Lablaika, I., Hoziosky, S.A. & M. Kalejs 1989: Abundance dynamics of eastern Baltic cod stocks and related factors. Rapp. P.-v. Réun. Cons. int. Explor. Mer 190: 163-165.

MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., Wieland, K. & A.S. Zezera 1999: Quantifying environmental heterogeneity: estimating the size of habitat for successful cod egg development in the Baltic Sea. Mar. Ecol. Progr. Ser. (accepted).

Makarchouk, A. 1997: Abundance and composition of ichthyoplankton in Eastern Baltic in early nineties. Proceedings of the 14th Baltic Marine Biologists Symposium: 149-155.

Matthäus, W. & H.U. Lass 1995: The recent salt inflow into the Baltic sea. J. Phys. Oceanogr. 25: 280-286.

Neuenfeldt, S. & F. W. Köster 1999: Trophodynamic control on recruitment success in Baltic cod: The influence of cannibalism. ICES J. mar Sci., 56 (accepted).

Nissling, A. 1994: Survival of eggs and yolk-sac larvae of Baltic cod (Gadus morhua L.) at low oxygen levels in different salinites. ICES Mar. Sci. Symp. 198: 626-631.

Nissling, A., Larsson, R., Vallin, L. & K. Frohlund 1998: Assessment of egg and larval viability in cod, Gadus morhua - methods and results from an experimental study. Fish. Res. 38: 169-186.

Patokina, F.A. 1996: Feeding pecularities and interrelations of abundant fishes from the Baltic Sea. ICES C.M. 1996/J:5.

Petersen, G.I., Gerup, J., Nilsson, L., Larsen, J.R. & R. Schneider 1997: Body burdens of lipophilic xenobiotics and reproductive success in Baltic cod (Gadus morhua). ICES C.M. 1997/U:10.

Plikshs, M., Kalejs, M. & G. Graumann 1993: The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES C.M. 1993/J:22.

Rohlf, N. 1997: Behaviour studies of Baltic cod (Gadus morhua) larvae originating from Bornholm Basin. ICES C.M. 1997/S:14 (Poster).

Schnack, D. & F.W. Köster 1998: Baltic Cod Recruitment Project: Summary of results 1994-97. ICES C.M. 1998/R:21.

Shapiro, L.A. 1988: Correlation between the quantity and quality of the gonads in the Baltic cod. Fischerei-Forschung, vol. 26 (2): 66-69.

Sparholt, H. 1994: Fish species interactions in the Baltic Sea. Dana, vol. 10: 131-162.

Sparholt, H. 1996: Causal correlation between recruitment and spawning stock size of central Baltic cod? ICES J. mar. Sci. 53: 771-779.

Sparholt, H. & J. Tomkiewicz 1998: A robust way of compiling trawl survey data for the use in the Central baltic cod stock assessment. ICES C.M. 1998/B:1.

Sparre, P. 1993: Discussion of the estimation of suitability coefficients from more than one years stomach content data. Working Doc. presented to Working Group on Multispecies Assessment of Baltic Fish 1993.

Tomkiewicz, J., Eriksson, M., Baranova, T., Feldman, V. & H. Müller 1997: Maturity ogives and sex ratios for Baltic cod: establishment of a database and time series. ICES CM 1997/CC:20.

Tomkiewicz, J., Lehmann, K.M. & M.A. St.John 1998: Oceanographic influences on the distribution of of Baltic cod (Gadus morhua) during spawning in the Bornholm Basin of the Baltic Sea. Fisheries Oceanography, 7 (1): 48-62.

Uzars, D., & Plikshs, M. 1999. Cod (Gadus morhua callarias L.) cannibalism in the Central Baltic: Interannual variability and influence of recruitment abundance and distribution. ICES Journal of Marine Science, 56: 000-000 (in press).

Vallin, L. & A. Nissling 1999: Implications of stock structure on recruitment success of Baltic cod - related to hydrographic conditions. (submitted).

Voss, R. 1996. Horizontale Verteilung und Drift von Dorschlarven in der südlichen zentralen Ostsee in Abhängigkeit vom mesoskaligen Strömungssystem. Dipl. thesis, Institute of Marine Sciences, Kiel, 112pp.

Voss, R., Hinrichsen, H.-H. & M. St. John 1999: Variations in the drift of larval cod (Gadus morhua L.) in the Baltic Sea: combining field observations and modelling. Fish. Oceanogr. 8, 3: 199-211.

Westin, L. & A. Nissling 1991: Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod Gadus morhua, and implications for cod stock fluctuations in the Baltic. Marine Biology, 108: 5-9.

Wieland, K. 1995: Einfluß der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (Gadus morhua callarias) im Bornholmbecken, südliche zentrale Ostsee. Ber. Inst. f. Meeresk., Kiel, 266: 114pp.

Wieland, K. & A. Jarre-Teichmann 1997: Prediction of vertical distribution and ambient development temperature of Baltic cod (Gadus morhua L.) eggs. Fish. Oceanogr. 6 (3): 172-187.

Wieland, K., Waller, U. & D. Schnack 1994: Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana vol. 10: 163-177.

Wieland, K., Jarre-Teichmann, A. & Horbowa, K. 1999: Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES J. mar Sci., 56 (in press).

Tab. 1   Sum and average of salinity (psu) and oxygen concentration (in ml/l) in reproductive volume in the Bornholm Basin as well as depths at which 2ml/l oxygen concentration was reached. Given is also an indication which scenario has been applied to determine the relative vertical distribution of cod eggs: a) stagnation / early spawning b), stagnation / late spawning, c) inflow / early spawning, d) inflow / late spawning.

year	salinity (psu)		oxygen (ml/l)			scenario
	sum	average	sum	average	depths (m) at 2ml/l	
1976	465	14.08	215	6.53	bottom	c
1977	435	15.01	119	4.09	85	c
1978	184	13.13	74	5.28	79	a
1979	230	13.50	75	4.40	79.5	a
1980	493	14.95	194	5.69	bottom	c
1981	60	12.03	28	3.44	75	a
1982	113	12.60	26	2.86	73.5	a
1983	257	14.26	68	3.75	79	a
1984	214	13.38	69	4.50	73	a
1985	256	13.50	85	4.46	81	a
1986	345	13.79	84	3.37	bottom	c
1987	113	12.52	33	3.68	73.5	a
1988	48	11.88	49	3.37	74.5	a
1989	41	11.67	9	2.71	67	a
1990	115	12.12	30	3.11	72	a
1991	368	13.15	105	3.77	bottom	a
1992	254	13.52	46	2.83	bottom	c
1993	496	15.02	138	4.18	bottom	d
1994	286	15.08	72	3.78	bottom	d
1995	106	13.25	32	3.97	64	b
1996	147	13.38	43	3.92	62	b

Tab. 2 Exploratory correlations and regressions performed to etablish stock recruitment relationships for different Subdivisions. Parameter estimates and their significance level are given for the incorporated independent variables as well as the r2 and the Durban-Watson statistics indicating serial correlation in the residuals.

Dependent variable	Subdivision	Time series	Independent variables	Parameter estimates	p	r²	Durban Watson statistics (*: signif. at 5%)
egg production stage IA	25	1986-96	intercept	-2.42E+10	0.089		
			egg production by SSB	2.80E-03	0.001	0.74	1.3
egg production stage III	25	1986-96	intercept	-1.08E+09	0.453		
			egg production by SSB	1.89E-04	0.011	0.527	1.99
egg production stage III per egg production by SSB	25	1986-96	intercept	5.53E-05	0.156		
			oxygen survival factor	2.08E-04	0.040	0.39	2.3
egg production stage III per egg production by SSB	25	1986-96	intercept	1.88E-04	0.001		
			egg predation factor	-4.77E-06	0.088	0.29	2.7
egg production stage III	25	1986-96	intercept	9.67E+08	0.206		
			(egg prod. by SSB-egg predation)*oxygen survival factor	3.15E-04	0.003	0.657	2.38
larval abundance	25	1976-96	intercept	1.44E+09	0.933		
			egg production by SSB	1.15E-03	0.027	0.23	1.06*
larval abundance	25	1986-96	intercept	2.03E+10	0.127		
			egg production by SSB	-1.38E-04	0.799	0.01	1.47
larval abundance per egg production by SSB	25	1976-96	intercept	1.13E-03	0.031		
			oxygen survival factor	1.96E-04	0.839	<0.01	1.45
larval abundance per egg production by SSB	25	1986-96	intercept	1.72E-03	0.032		
			oxygen survival factor	-1.84E-03	0.293	0.12	2.5
larval abundance per egg production by SSB	25	1976-96	intercept	1.21E-03	0.002		
			egg predation index	1.92E-06	0.952	<0.01	1.49
larval abundance per egg production by SSB	25	1986-96	intercept	5.14E-04	0.442		
			egg predation index	4.39E-05	0.346	0.1	2.42
larval abundance	25	1986-96	intercept	1.77E+10	0.051		
			egg production stage III	-7.32E-02	0.972	<0.01	1.43
larval abundance per egg production stage III	25	1986-96	intercept	2.02E+01	0.007		
			oxygen survival factor	-2.91E+01	0.068	0.32	2.12
larval abundance per egg production stage III	25	1986-96	intercept	2.59E-01	0.963		
			egg predation index	7.63E-01	0.071	0.32	2.62
larval abundance per egg production by SSB	25	1976-96	intercept	6.86E-04	0.071		
			sum of oxygen in reproductive volume	7.10E-06	0.084	0.15	1.21
larval abundance	25	1976-96	intercept	-2.23E+09	0.873		
			egg prod. by SSB-egg predation	2.39E+08	0.085	0.38	
			sum of oxygen in reproductive volume	9.11E-04	0.062	adj. 0.31	0.74*
recruitment at age 0	25	1976-95	intercept	1.43E+08	0.004		
			larval abundance	4.70E-03	<0.001	0.65	0.99
recruitment at age 0 per larval abundance	25	1976-91	intercept	1.00E-02	0.001		
			sum of oxygen in reproductive volume	-1.16E-05	0.625	0.02	1.73
recruitment at age 0 per larval abundance	25	1976-91	intercept	9.78E-03	<0.001		
			larval transport index	-6.41E-05	0.586	0.02	1.75
recruitment at age 0	25	1976-95	intercept	9.51E+07	0.074		
			larval abundance	3.97E-03	<0.001	0.7	
			sum of oxygen in reproductive volume	9.96E+05	0.106	adj. 0.66	1.39
recruitment at age 0	25	1976-91	intercept	8.77E+07	0.188		
			larval abundance	3.75E-03	0.007	0.68	
			sum of oxygen in reproductive volume	1.24E+05	0.109	adj. 0.63	1.43
recruitment at age 0	25	1976-95	intercept	1.07E+08	0.067		
			larval abundance	3.83E-03	<0.001		
			sum of oxygen in reproductive volume	1.09E+06	0.095	0.7	
			larval transport index	-9.55E+05	0.549	adj. 0.65	1.45
predation mortality at age 0	25	1977-96	intercept	7.74E-03	0.874		
			spawning stock biomass	3.08E-09	<0.001	0.68	1.55
recruitment at age 0	25	1976-95	intercept	1.89E+07	0.747		
			egg prod. by SSB-egg predation	8.39E-06	<0.001	0.69	
			sum of oxygen in reproductive volume	1.39E+06	0.022	adj. 0.66	0.96*
recruitment at age 0	25	1976-95	intercept	4.40E+07	0.452		
			egg prod. by SSB-egg predation	8.34E-06	<0.001		
			sum of oxygen in reproductive volume	1.51E+06	0.012	0.74	
			larval transport index	-2.36E+06	0.118	adj. 0.69	1.38
LOG(recruitment at age 0)	25	1976-95	intercept	6.56E+00	0.016		
			LOG(egg prod. by SSB-egg predation)	3.98E-01	<0.001	0.7	
			LOG(sum of oxygen in reproductive volume)	1.88E-01	0.155	adj. 0.66	0.74*
LOG(recruitment at age 0)	25	1976-95	intercept	6.97E+00	0.010		
			LOG(egg prod. by SSB-egg predation)	3.84E-01	<0.001		
			LOG(sum of oxygen in reproductive volume)	2.23E-01	0.091	0.74	
			LOG(larval transport index)	-8.43E-02	0.151	adj. 0.69	0.94*

Tab. 2 cont.

Dependent variable	Subdivision	Time series	Independent variables	Parameter estimates	p	r²	Durban Watson statistics (*: signif. at 5%)
egg abundance	26	1976-96	intercept	1.64E+10	0.903		
			egg production by SSB	6.19E-03	0.106	0.13	0.59*
egg abundance	28	1976-96	intercept	2.82E+10	0.813		
			egg production by SSB	1.18E-02	0.012	0.29	2.07
egg abundance per egg production by SSB	26	1976-96	intercept	3.18E-03	0.853		
			reproductive volume	1.10E-03	<0.001	0.55	1.34
egg abundance per egg production by SSB	28	1976-96	intercept	7.65E-03	0.005		
			reproductive volume	1.50E-04	0.001	0.44	2.11
larval abundance	26	1976-96	intercept	-1.33E+09	0.916		
			egg production by SSB	7.61E-04	0.039	0.2	0.62*
larval abundance	28	1976-96	intercept	7.19E+09	0.773		
			egg production by SSB	1.56E-03	0.094	0.14	1.43
larval abundance per egg production by SSB	26	1976-96	intercept	5.56E-06	0.950		
			reproductive volume	1.30E-05	<0.001	0.58	1.26
larval abundance per egg production by SSB	28	1976-96	intercept	4.87E-04	0.400		
			reproductive volume	3.26E-05	0.002	0.41	1.69
recruitment at age 0	26	1976-95	intercept	1.95E+08	0.044		
			larval abundance	7.80E-03	0.003	0.4	1.25
recruitment at age 0	28	1976-95	intercept	1.32E+08	0.009		
			larval abundance	7.67E-04	0.150	0.11	0.55*
predation mortality at age 0	26	1977-96	intercept	-1.15E-01	0.095		
			spawning stock biomass	5.64E-09	<0.001	0.82	2.56
predation mortality at age 0	28	1977-96	intercept	-4.90E-02	0.381		
			spawning stock biomass	1.09E-08	<0.001	0.82	1.65
recruitment at age 0	26	1976-95	intercept	-8.07E+07	0.523		
			egg prod. by SSB	1.08E-05	0.005	0.6	
			reproductive volume	2.78E+06	0.032	adj. 0.55	1.4
LOG(recruitment at age 0)	26	1976-95	intercept	-5.44E+00	0.467		
			LOG(egg prod. by SSB)	7.92E-01	0.004	0.65	
			LOG(reproductive volume)	1.42E-01	0.044	adj. 0.61	0.80*
recruitment at age 0	28	1976-95	intercept	-3.59E+07	0.383		
			egg prod. by SSB	8.18E-06	<0.001	0.7	
			reproductive volume	7.45E+05	0.088	adj. 0.66	1.47
LOG(recruitment at age 0)	28	1976-95	intercept	-1.80E+01	0.001		
			LOG(egg prod. by SSB)	1.19E+00	<0.001	0.81	
			LOG(reproductive volume)	1.15E-01	0.137	adj. 0.78	0.79*

Tab. 3   Parameter estimates, their significance level, r^2-values and Durban Watson statistics (significant on 95% level: *) of multiple linear regressions relating recruitment at age 0 in different Subdivisions with egg production by the spawning stock and different environmental variables (final model configurations), utlizing different data sub-sets of the time series for estimation of the parameters.

Time-series	Subdivision	Independent variable	Parameter estimates	p	r^2	Durban Watson statistics
1976-95	25	intercept	4.396E+07	0.4517		
		egg prod. by SSB-egg predation	8.340E-06	<0.001		
		sum of oxygen in reproductive volume	1.511E+06	0.0115	0.74	
		larval transport index	-2.361E+06	0.1178	adj. 0.69	1.38
1980-95	25	intercept	4.326E+07	0.4004		
		egg prod. by SSB-egg predation	6.900E-06	<0.001		
		sum of oxygen in reproductive volume	1.473E+06	0.0118	0.75	
		larval transport index	-1.625E+06	0.1894	adj. 0.69	1.27
1981-95	25	intercept	1.149E+08	0.0225		
		egg prod. by SSB-egg predation	5.679E-06	<0.001		
		sum of oxygen in reproductive volume	2.446E+05	0.6551	0.66	
		larval transport index	-7.210E+05	0.4496	adj. 0.57	1.73
1976-90	25	intercept	6.683E+07	0.3373		
		egg prod. by SSB-egg predation	7.491E-06	0.0078		
		sum of oxygen in reproductive volume	1.857E+06	0.0197	0.76	
		larval transport index	-3.533E+06	0.33	adj. 0.69	1.6
1976-91	25	intercept	6.660E+07	0.3373		
		egg prod. by SSB-egg predation	7.511E-06	0.0078		
		sum of oxygen in reproductive volume	1.856E+06	0.0197	0.77	
		larval transport index	-3.575E+06	0.33	adj. 0.71	1.61
1976-95	26	intercept	-8.070E+07	0.523		
		egg prod. by SSB-egg predation	1.078E-05	0.005	0.58	
		reproduction volume	2.778E+06	0.032	adj. 0.53	1.98
1980-95	26	intercept	-7.559E+07	0.1147		
		egg prod. by SSB-egg predation	8.726E-06	<0.001	0.87	
		reproduction volume	2.887E+06	0.0015	adj. 0.85	0.93 *
1981-95	26	intercept	-2.442E+07	0.6076		
		egg prod. by SSB-egg predation	7.558E-06	<0.001	0.73	
		reproduction volume	1.251E+06	0.2344	adj. 0.69	1.24
1976-90	26	intercept	-8.609E+07	0.6572		
		egg prod. by SSB-egg predation	1.082E-05	0.0479	0.54	
		reproduction volume	2.973E+06	0.0637	adj. 0.47	2.15
1976-91	26	intercept	-5.895E+07	0.7216		
		egg prod. by SSB-egg predation	1.027E-05	0.0371	0.56	
		reproduction volume	2.954E+06	0.0552	adj. 0.49	2.1
1976-95	28	intercept	-3.592E+07	0.383		
		egg prod. by SSB-egg predation	8.184E-06	<0.001	0.70	
		reproduction volume	7.454E+05	0.088	adj. 0.66	1.47
1980-95	28	intercept	-2.269E+07	0.5181		
		egg prod. by SSB-egg predation	7.071E-06	<0.001	0.71	
		reproduction volume	-2.625E+04	0.9612	adj. 0.69	1.24
1981-95	28	intercept	-1.256E+07	0.71		
		egg prod. by SSB-egg predation	6.021E-06	<0.001	0.62	
		reproduction volume	-3.099E+04	0.9518	adj. 0.56	1.29
1976-90	28	intercept	-4.643E+07	0.4309		
		egg prod. by SSB-egg predation	8.263E-06	<0.001	0.66	
		reproduction volume	1.149E+06	0.0584	adj. 0.61	1.52
1976-91	28	intercept	-5.976E+07	0.3925		
		egg prod. by SSB-egg predation	8.592E-06	<0.001	0.64	
		reproduction volume	1.191E+06	0.063	adj. 0.58	1.58

Tab. 4   Explained variance (adjusted for degree of freedoms) in recruitment at age 0
by multiple linear regressions (final model configurations, untransformed) starting
respectively ending the analysis at different years, including the Durban Watson
statistics indicating significant autocorrelation in the residuals at the 95% level*.

Model fit with time period	Sub-division	adjusted r^2	Durban Watson statistics	Model fit with time period	adjusted r^2	Durban Watson statistics
1976-95	25	0.69	1.38	1976-89	0.65	1.61
1977-95	25	0.64	1.37	1976-90	0.69	1.6
1978-95	25	0.61	1.37	1976-91	0.71	1.61
1979-95	25	0.57	0.98*	1976-92	0.73	1.53
1980-95	25	0.69	1.27	1976-93	0.69	1.23
1981-95	25	0.57	1.73	1976-94	0.69	1.42
1982-95	25	0.6	1.4	1976-95	0.69	1.38
1976-95	26	0.53	1.98	1976-89	0.42	2.17
1977-95	26	0.53	1.93	1976-90	0.46	2.15
1978-95	26	0.51	1.99	1976-91	0.49	2.1
1979-95	26	0.5	1.1	1976-92	0.51	2.06
1980-95	26	0.85	0.93*	1976-93	0.52	2.07
1981-95	26	0.69	1.24	1976-94	0.53	2.03
1982-95	26	0.56	1.28	1976-95	0.53	1.98
1976-95	28	0.66	1.47	1976-89	0.53	1.67
1977-95	28	0.72	1.52	1976-90	0.58	1.58
1978-95	28	0.72	1.43	1976-91	0.61	1.52
1979-95	28	0.72	1.13	1976-92	0.64	1.48
1980-95	28	0.69	1.24	1976-93	0.66	1.45
1981-95	28	0.56	1.29	1976-94	0.65	1.41
1982-95	28	0.48	1.4	1976-95	0.66	1.47

(a)

$\log(y) = -341109 + 675.546x - 0{,}334471x^2$

$r^2 = 0.73$

log (relative egg stage IA abundance)

0.7
-1.3
-3.3
-5.3
-7.3

1006   1008   1010   1012   1014
density (in kg/m^3)

(b)

$\log(y) = -375834 + 744.314x - 0{,}3685x^2$

$r^2 = 0.73$

log (relative egg stage IA abundance)

0.9
-1.1
-3.1
-5.1
-7.1

1006   1008   1010   1012   1014
density (in kg/m^3)

(c)

$\log(y) = -269100 + 532.326x - 0{,}26326x^2$

$r^2 = 0.72$

log (relative egg stage IA abundance)

-1
-3
-5
-7
-9

1006   1008   1010   1012   1014   1016
density (in kg/m^3)

(d)

$\log(y) = -160207 + 317.089x - 0{,}1569x^2$

$r^2 = 0.82$

log (relative egg stage IA abundance)

-1.1
-2.1
-3.1
-4.1
-5.1

1006   1008   1010   1012   1014   1016
density (in kg/m^3)

Fig. 1:   Vertical distribution of cod eggs in Subdivision 25:

Logarithmic relative abundance of egg stage IA in relation to the ambient density in stagnation periods during spring/early summer (a) and summer (b) as well as inflow periods during spring/early summer (c) and summer (d) together with fitted parabolic functions.
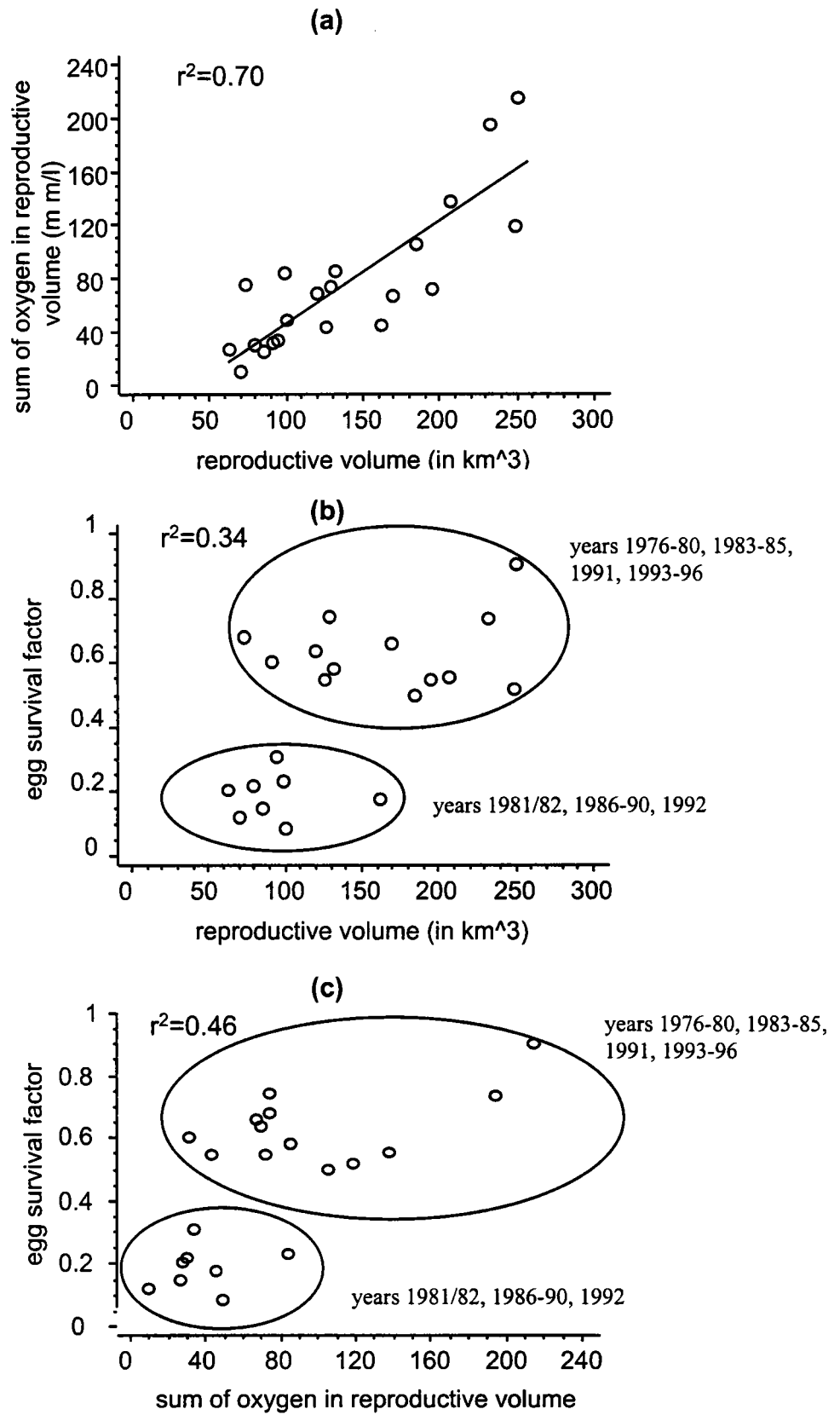
Fig. 2 Relationships between the reproductive volume, the sum of oxygen in the reproductive volume and the oxygen related egg survival factor in Subdivision 25.

Subdivision 25

Subdivision 26
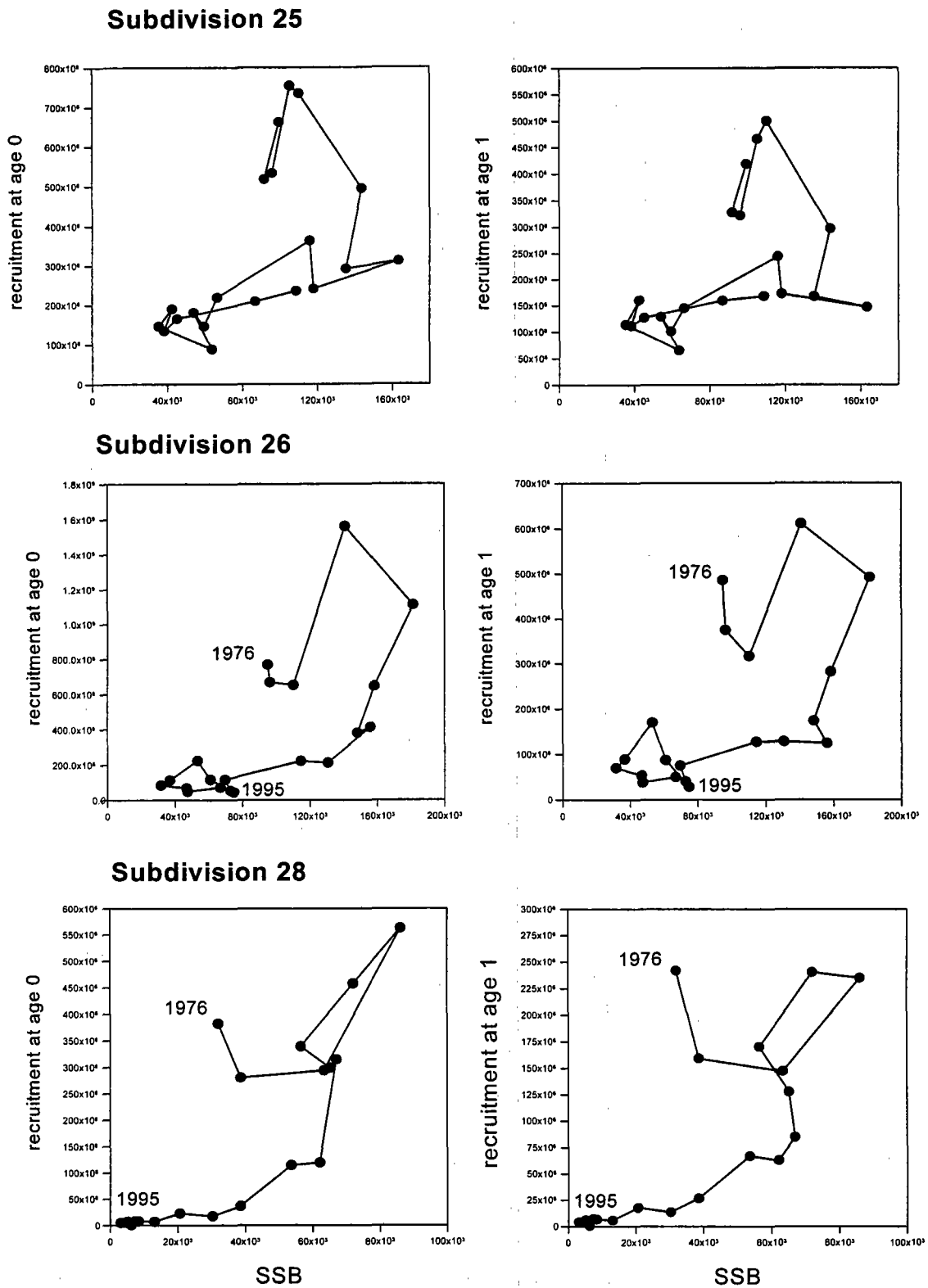
Subdivision 28

Fig. 3 Stock-recruitment relationships of cod in different Subdivisions
obtained from area dis-aggregated MSVPA runs
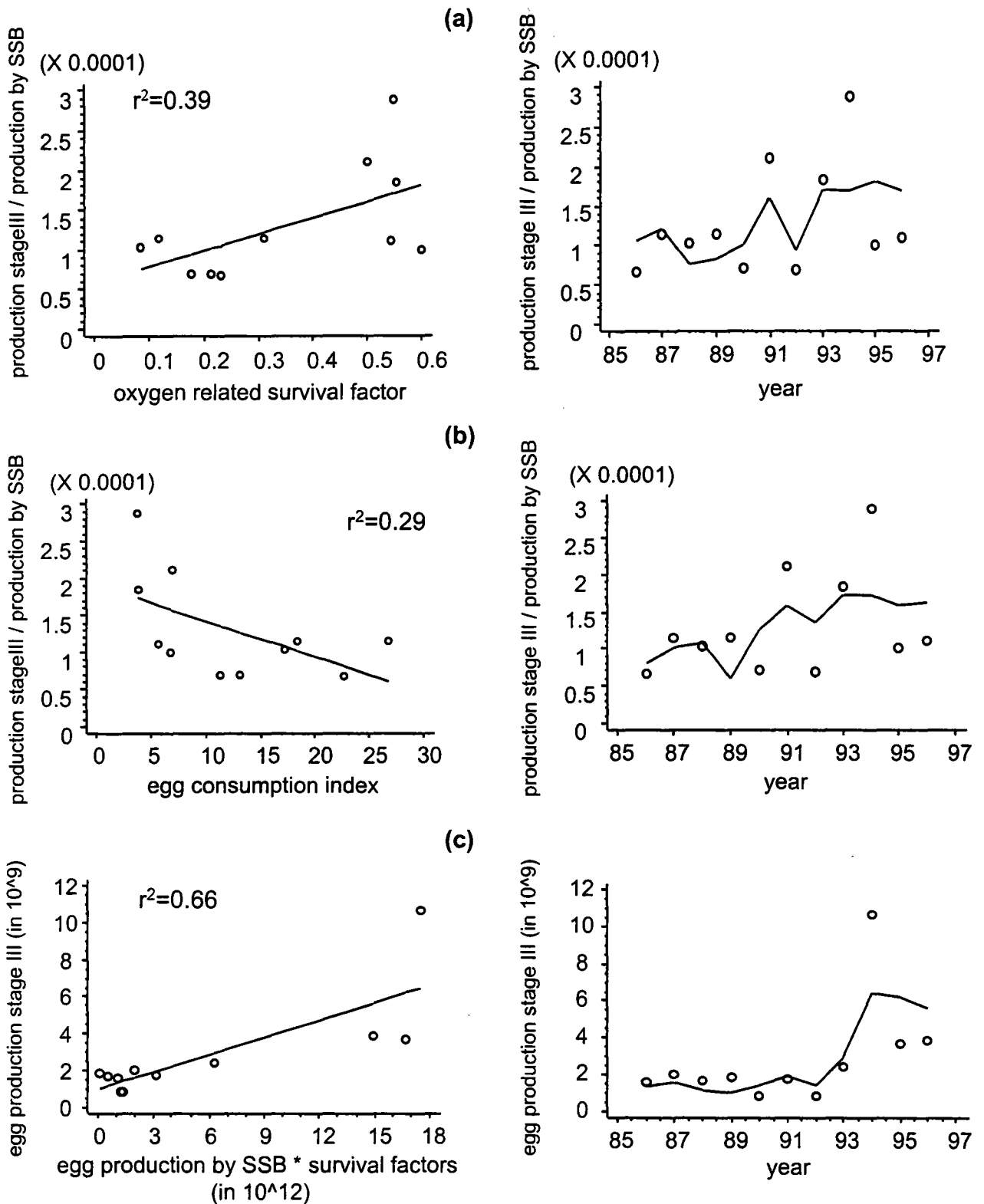
Fig. 4   Linear regressions of egg production at stage III per egg production by SSB in Subdivision 25 on oxygen related egg survival factor (a) and egg consumption index (b) as well as egg production at stage III on (egg production by SSB - egg consumption) * oxygen related survival factor (c). Note: observed values are dots while predicted values are shown as solid lines

(a)

(b)

(c)
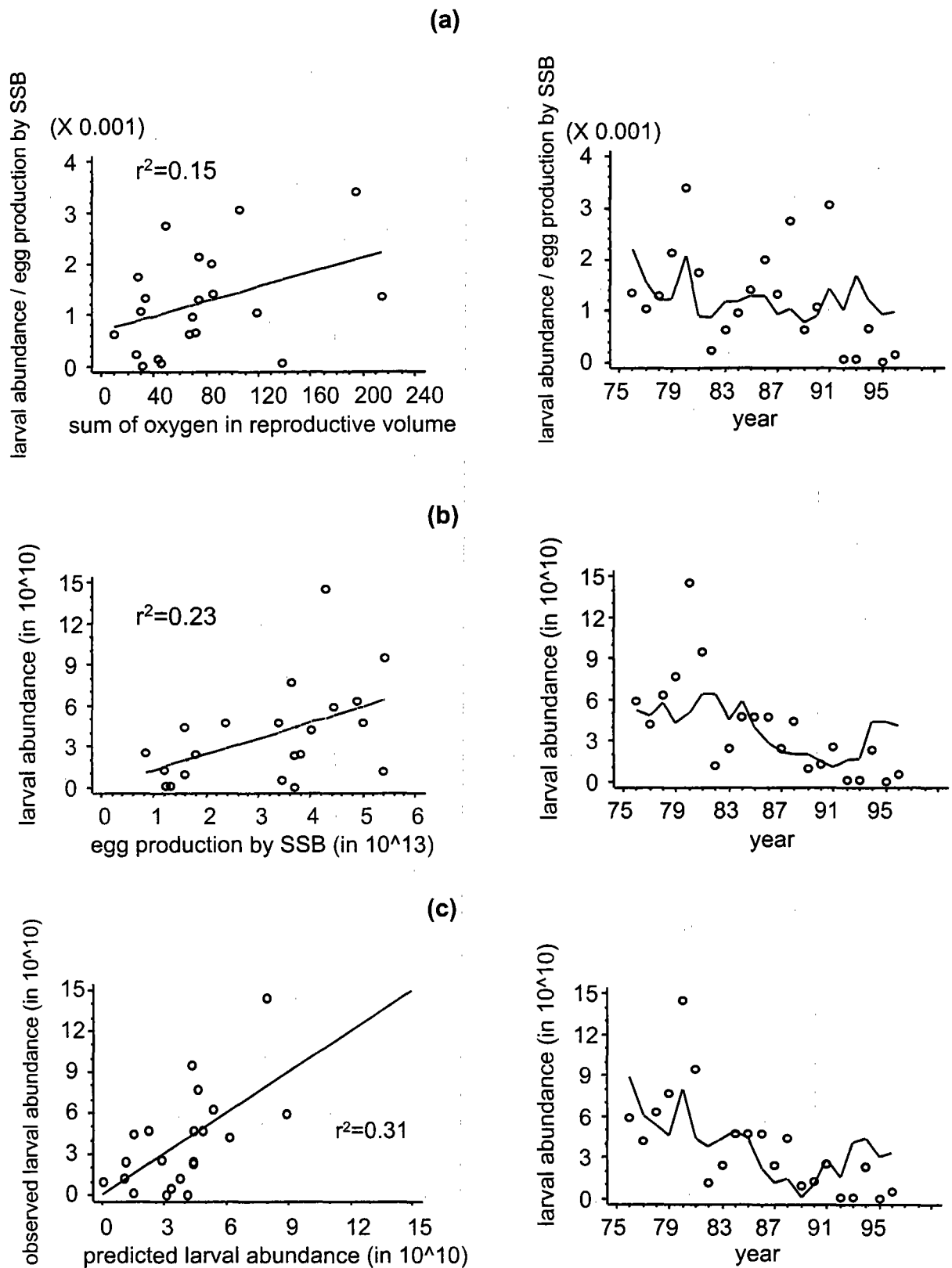
Fig. 5   Linear regressions of larval abundance per egg production by SSB on sum of oxygen in the reproductive volume (a), larval abundance on egg production by SSB (b) and a multiple linear regression on egg production and sum of oxygen as independent variables (c). Note: observed values are dots while predicted values are shown as solid lines

(a)

(b)
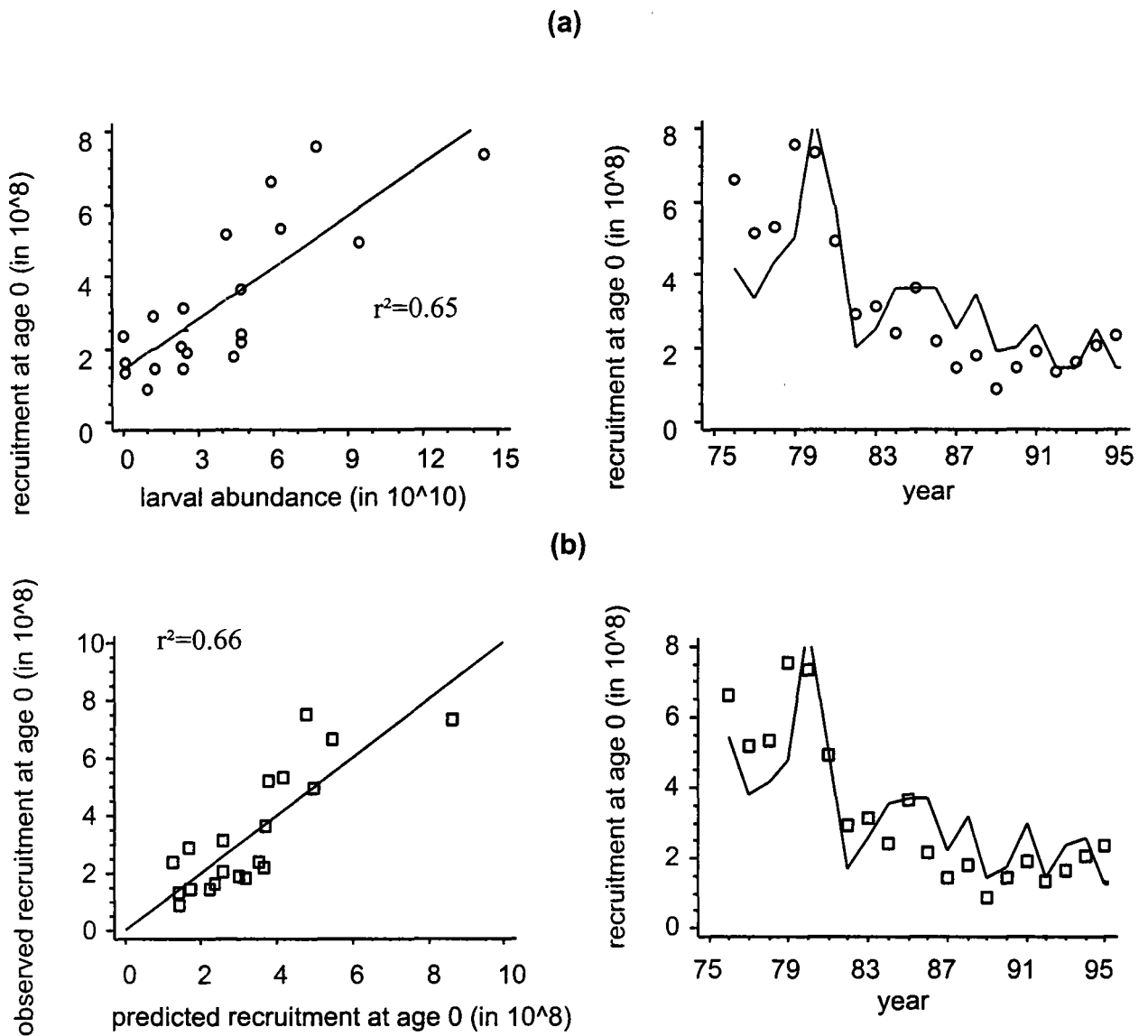
Fig. 6   Linear regression of recruitment at age 0 in Subdivision 25 on larval abundance (a) and multiple linear regression on larval abundance, sum of oxygen in the reproductive volume (b). Note: observed values are dots while predicted values are shown as solid lines
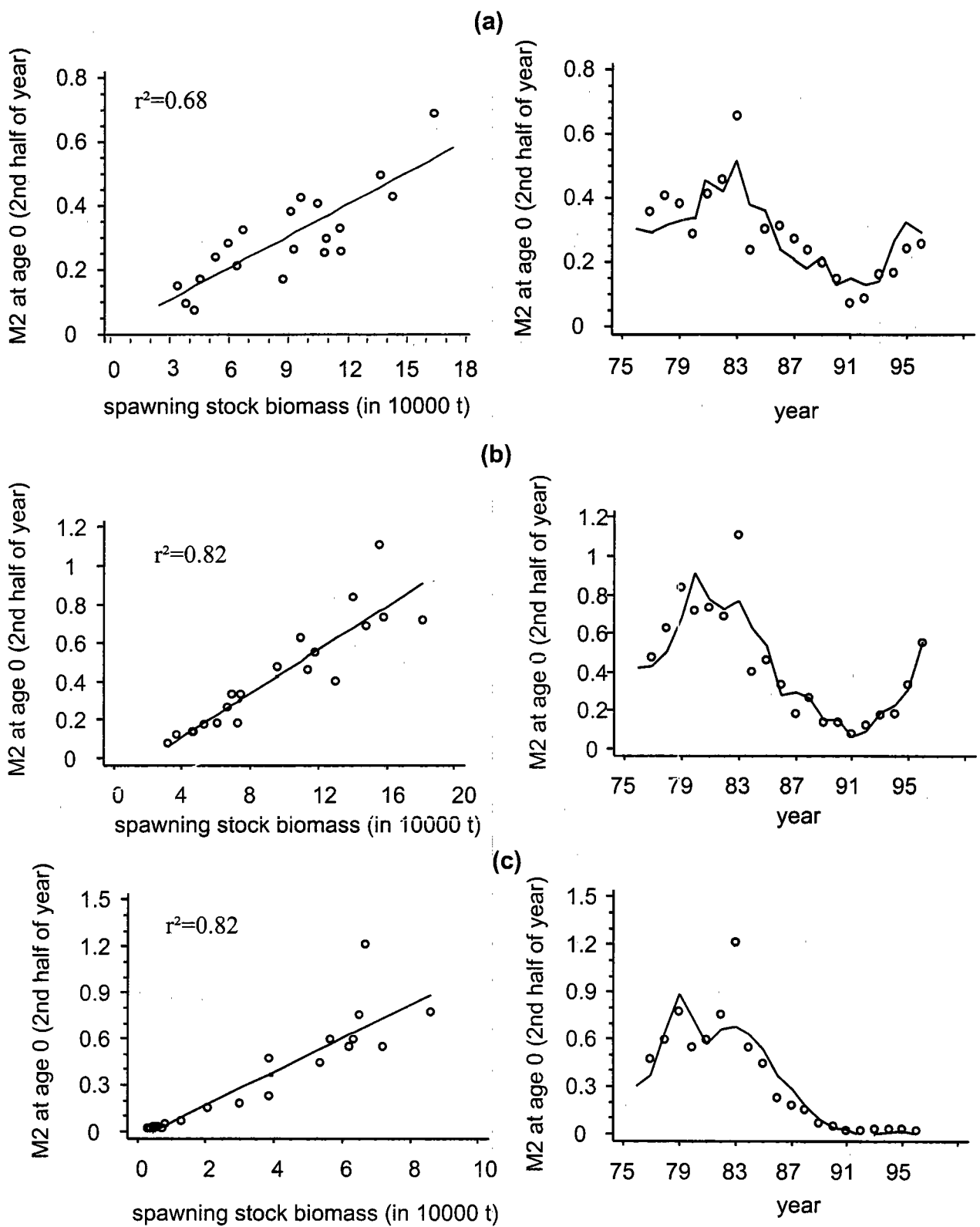
Fig. 7   Linear regression of predation mortality coefficients (M2) of cod age-group 0 (2nd half of year) on cod spawning stock biomass for Subdivision 25 (a), 26 (b) and 28 (c). Note: observed values are dots while predicted values are shown as solid lines.
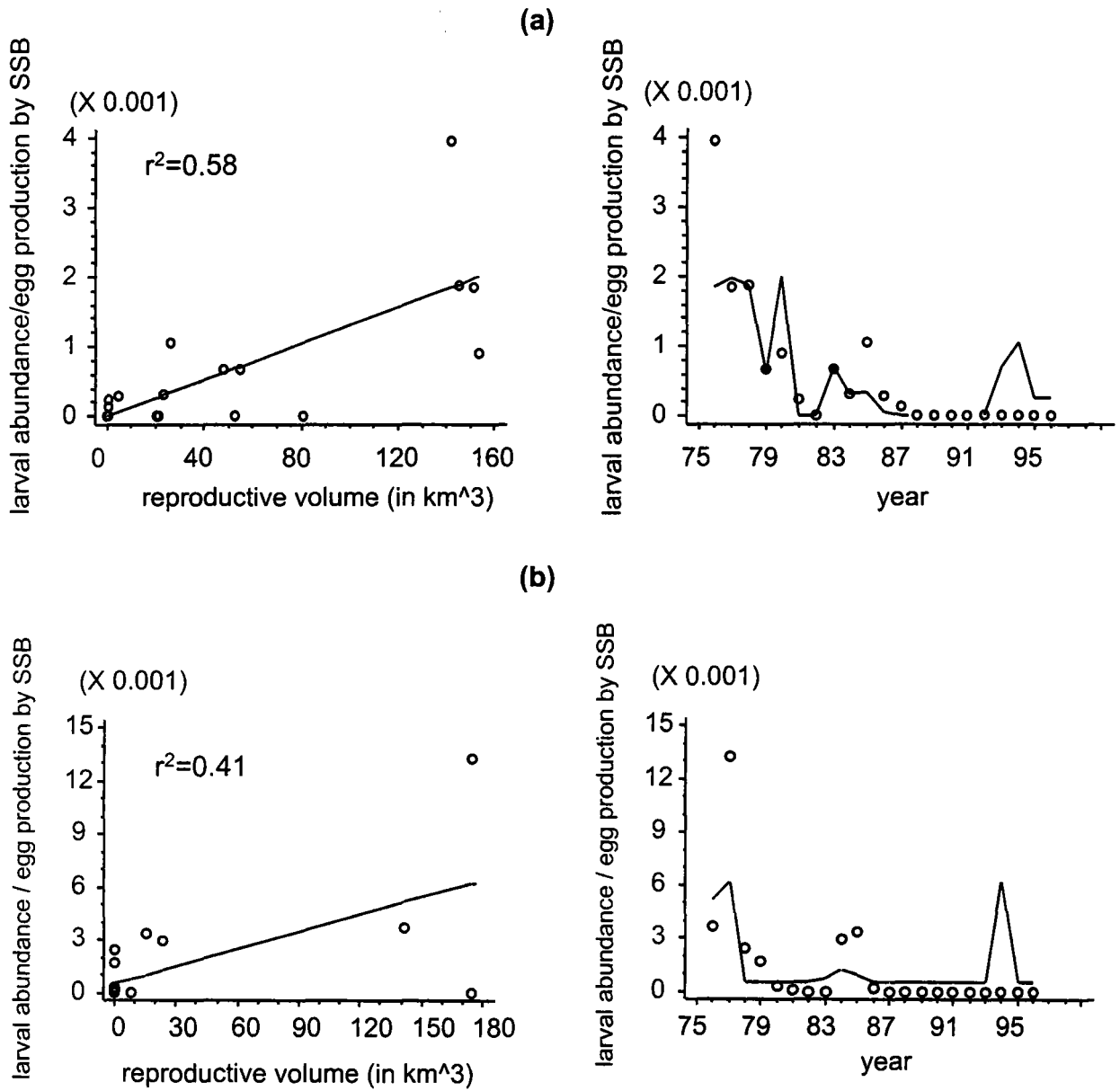
Fig. 8 Linear regression of larval abundance per egg production by SSB to reproductive volume in Subdivision 26 (a) and 28 (b). Note: observed values are dots while predicted values are shown as solid lines.

(a)

(b)
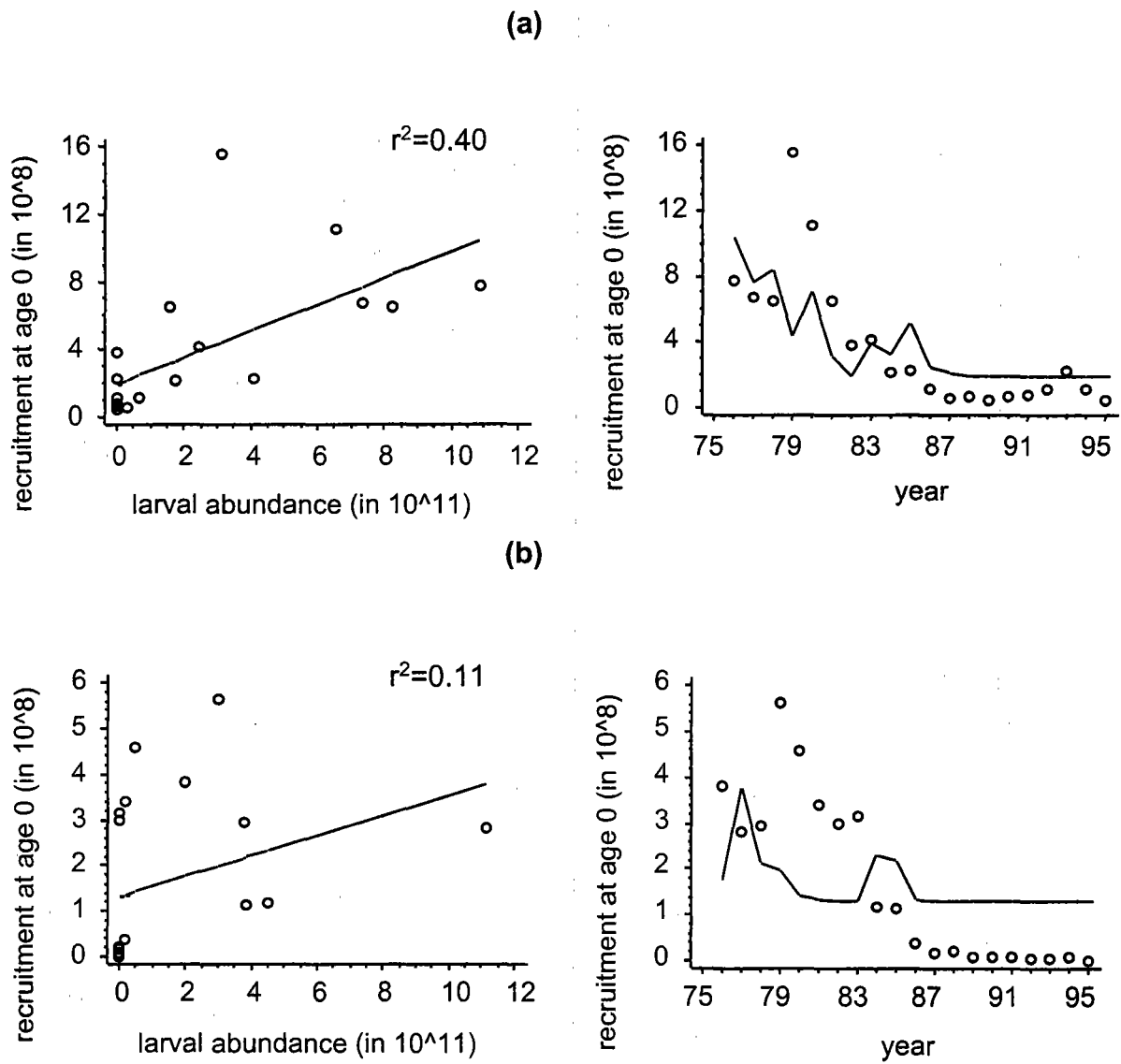
Fig. 9   Linear regression of recruitment at age 0 to larval abundance in subdivision 26 (a) and 28 (b). Note: observed values are dots while predicted values are shown as solid lines.
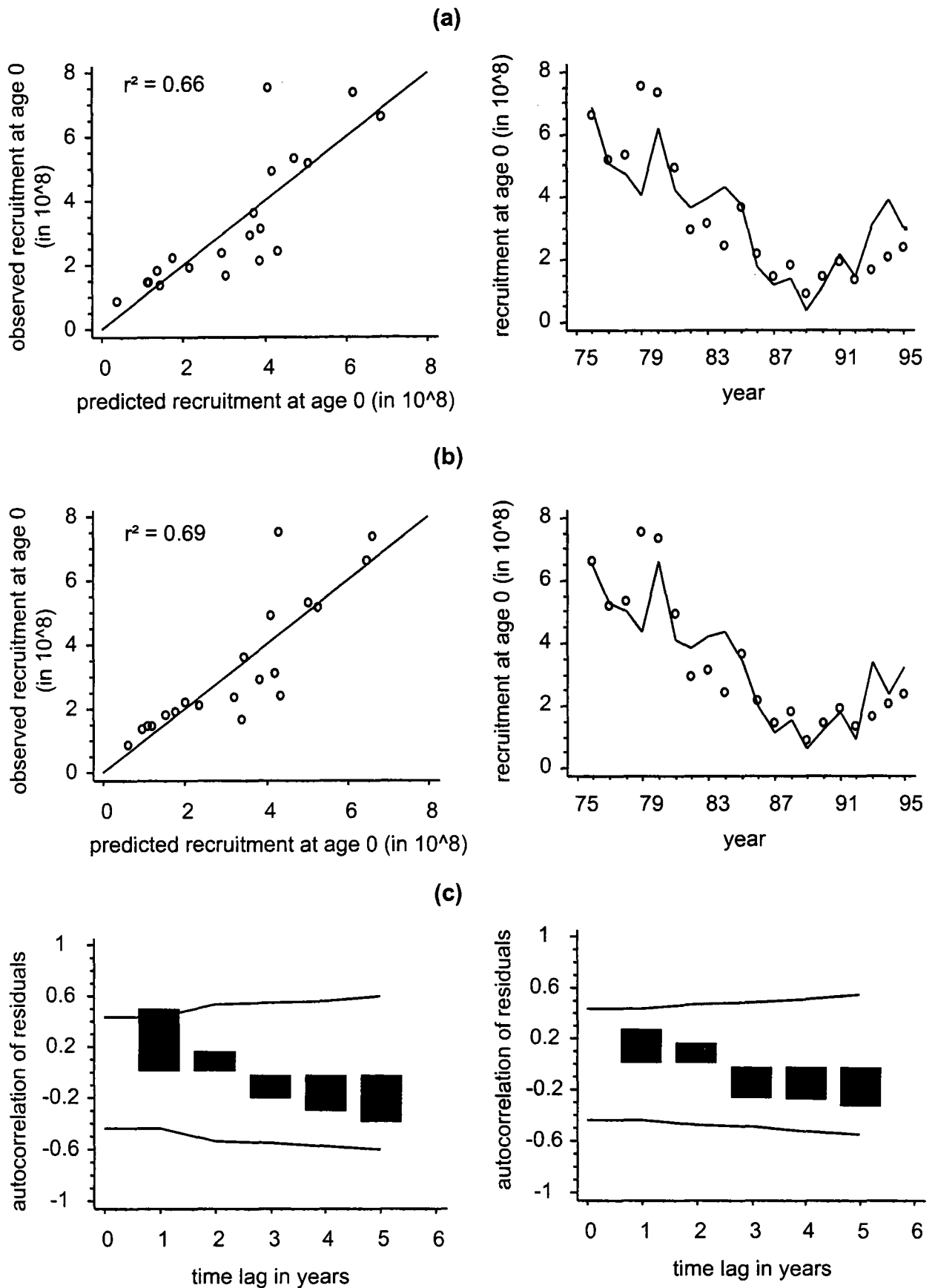
Fig. 10   Multiple linear regression of recruitment at age 0 in Subdivision 25 on egg production by SSB
- egg consumption and sum of oxygen in the reproductive volume: observed versus predicted
recruitment as well as time trend of observed (points) and predicted values (lines) (a). Same
statistical model including the larval transport index as a further independent variable (b) and
autocorrelation of residuals of the first (left) and second model (right) including the 95%
confidence limits (c).
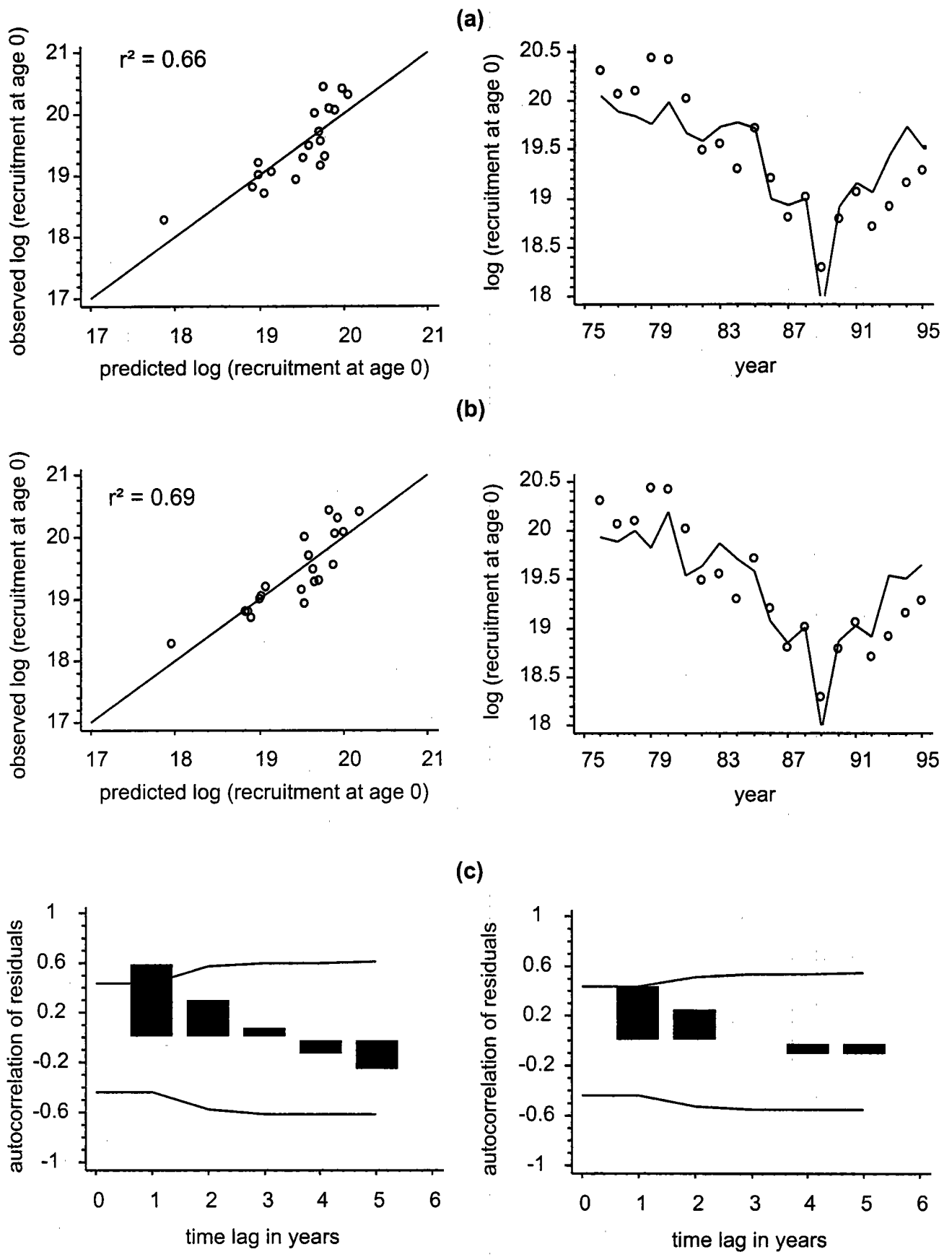
Fig. 11   Multiple linear regression of log (recruitment at age 0) in Subdivision 25 on independent
variables described in Fig. 10 but log transformed (a) and (b) observed versus
predicted recruitment as well as time trend of observed (points) and predicted values
(lines); autocorrelation of residuals of the first (left) and second model (right) including
the 95% confidence limits (c).
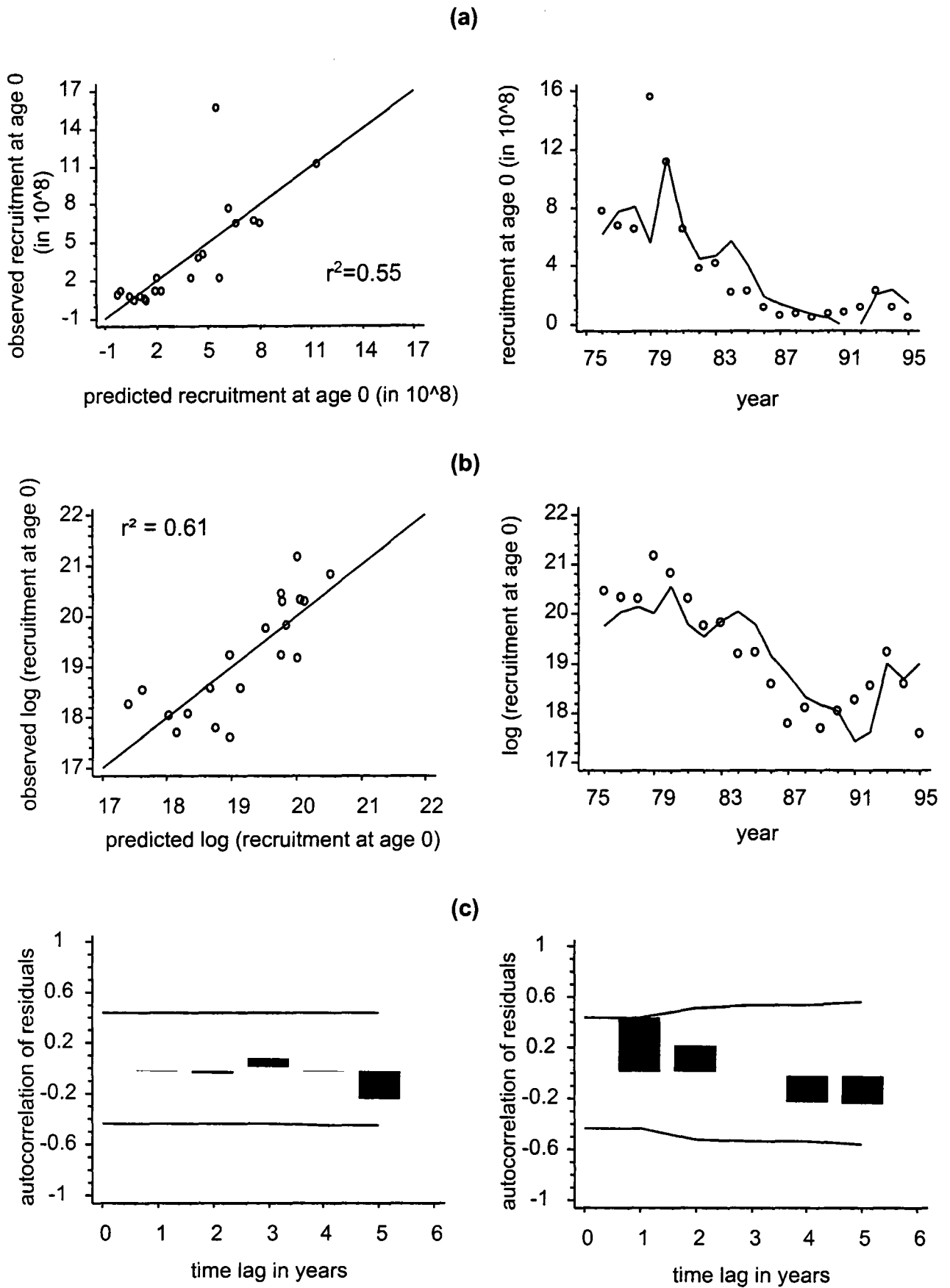
Fig. 12   Multiple linear regression of recruitment at age 0 in Subdivision 26 on egg production by SSB and reproductive volume (a), same model with log-transformed data (b) observed versus predicted recruitment as well as time trend of observed (points) and predicted values (lines); autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits (c).
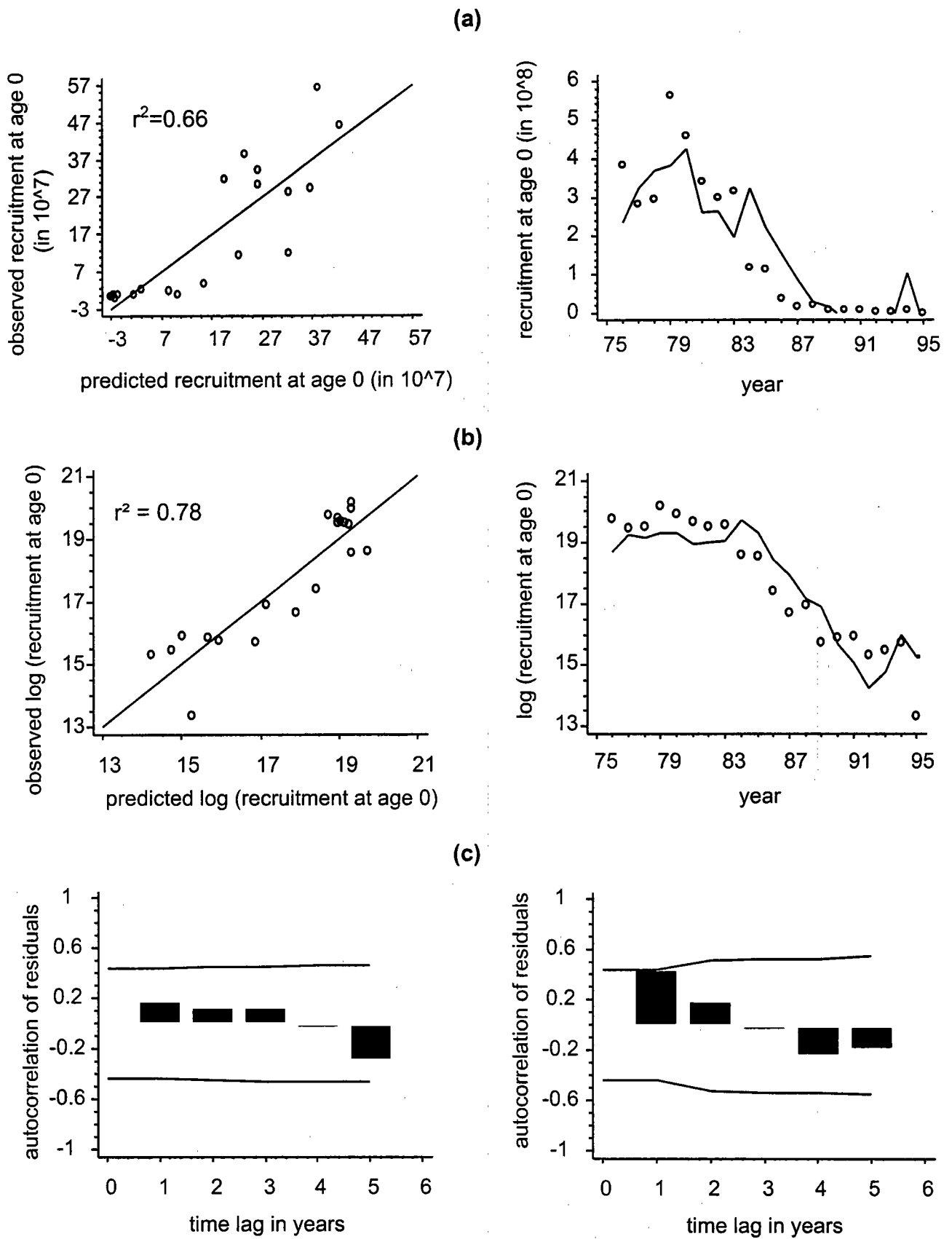
Fig.13   Multiple linear regression of recruitment at age 0 in Subdivision 28 on egg production
          by SSB and reproductive volume (a), same model with log-transformed data (b):
          observed versus predicted recruitment as well as time trend of observed (points) and
          predicted values (lines); autocorrelation of residuals of the first (left) and second
          model (right) including the 95% confidence limits (c).
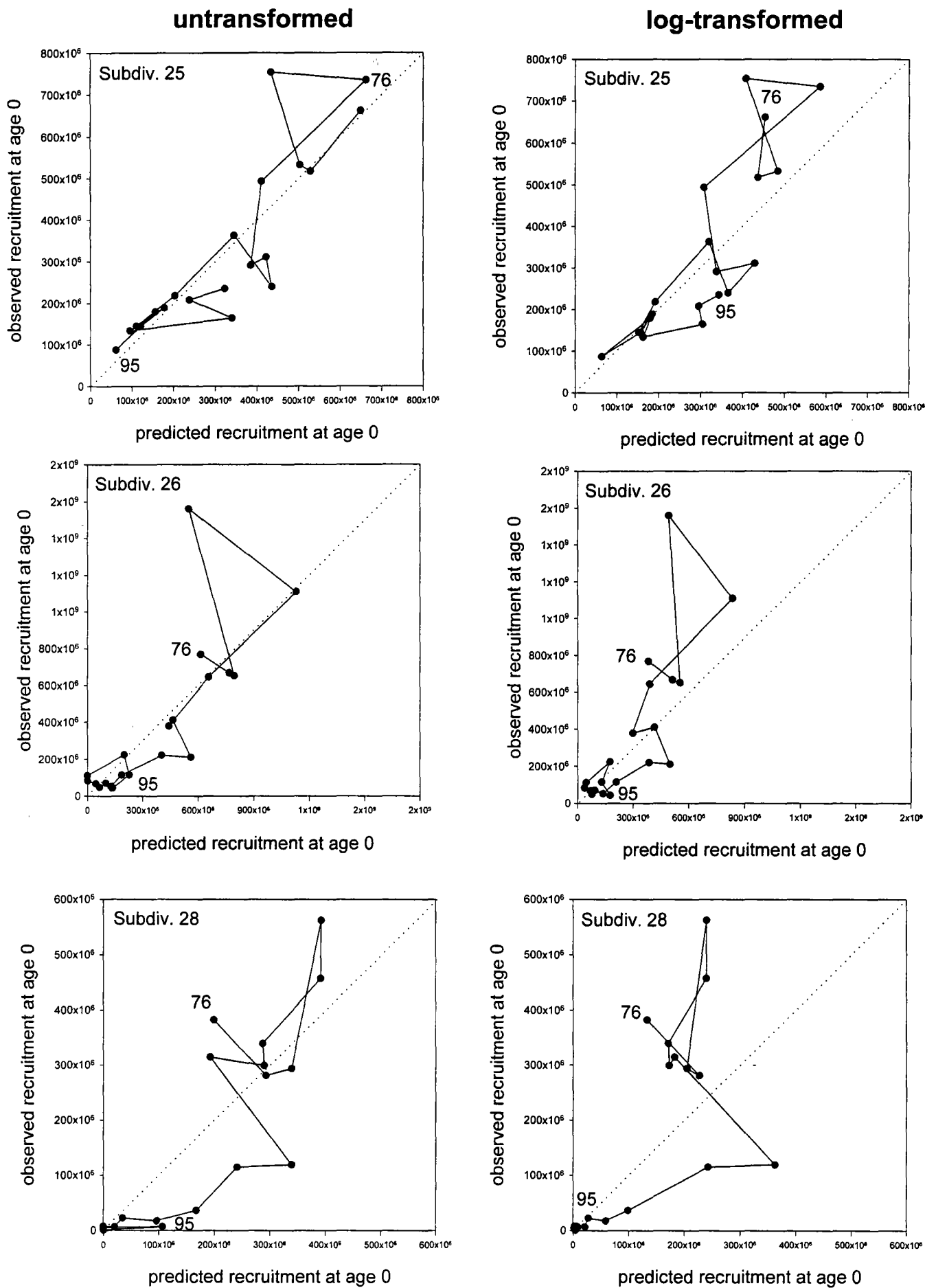
Fig. 14   Observed vs. predicted recruitment at age 0 for Subdiv. 25, 28 & 28 derived by multiple linear regression models - untransformed (left) and log-transformed versions (right).
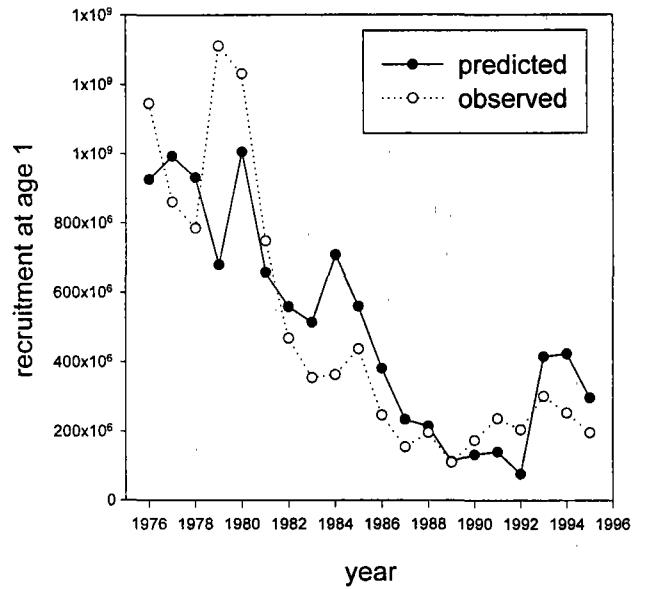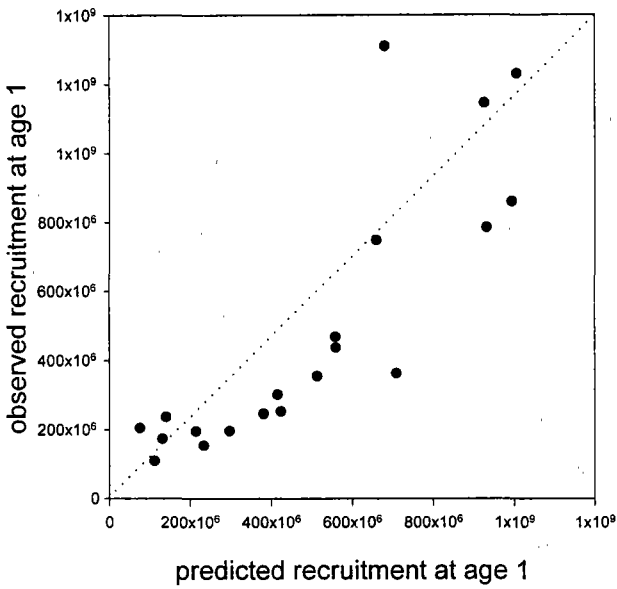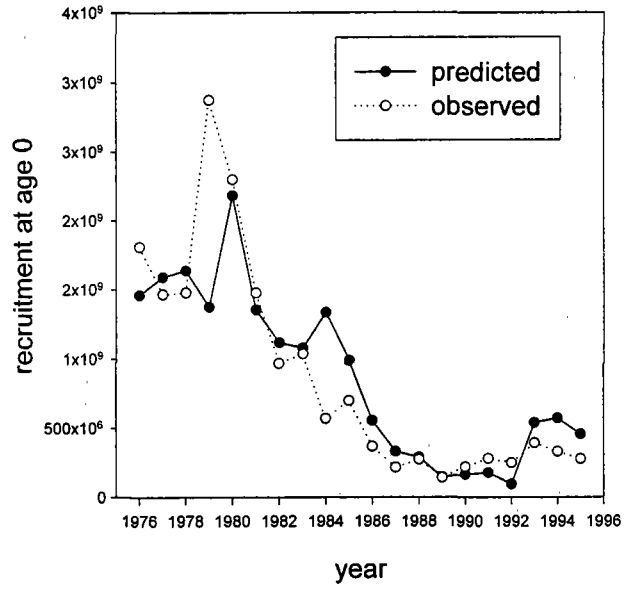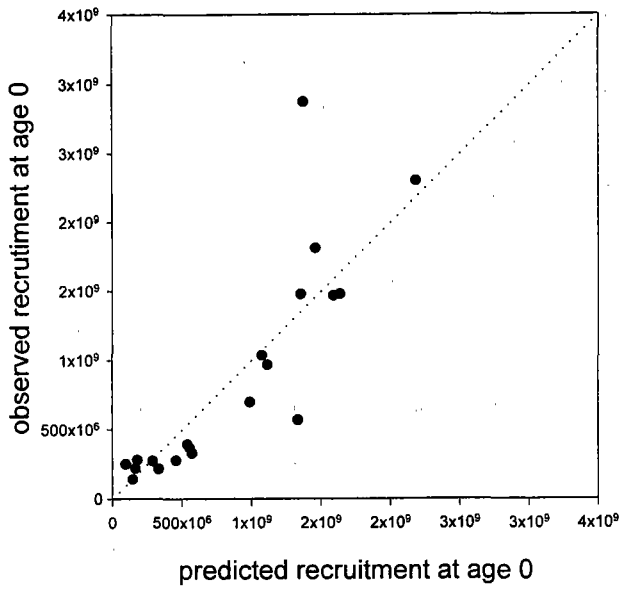
Fig. 15 Observed vs. predicted recruitment at age 0 (above) and age 1 (below) in combined Subdiv. 25, 26 & 28 based on egg production by SSB, environmental factors (reproductive volume, larval transport index) and species interaction (egg predation by clupeids and cannibalism on 0-group) (final model versions).
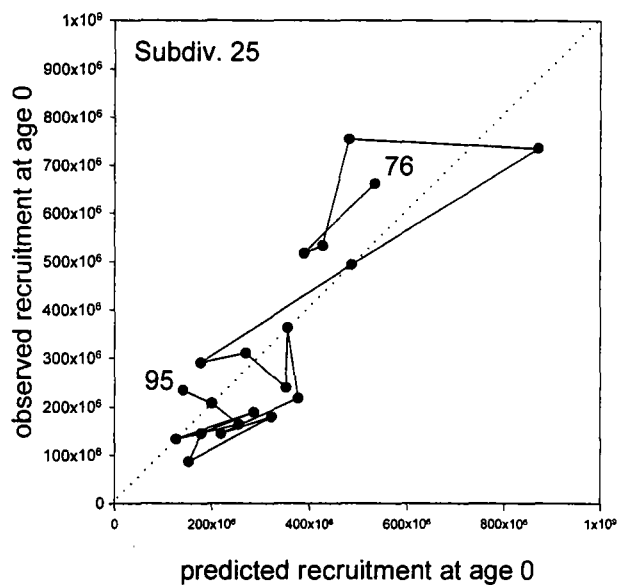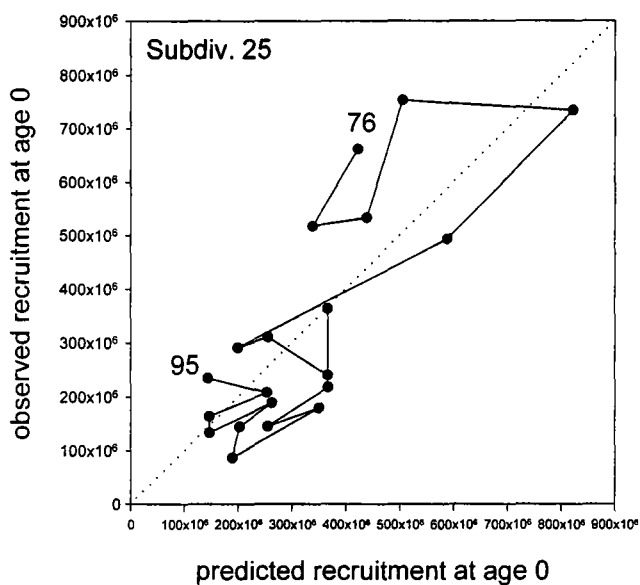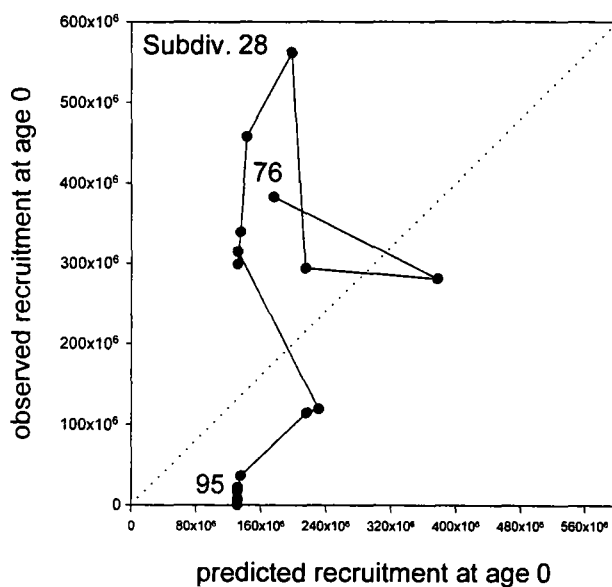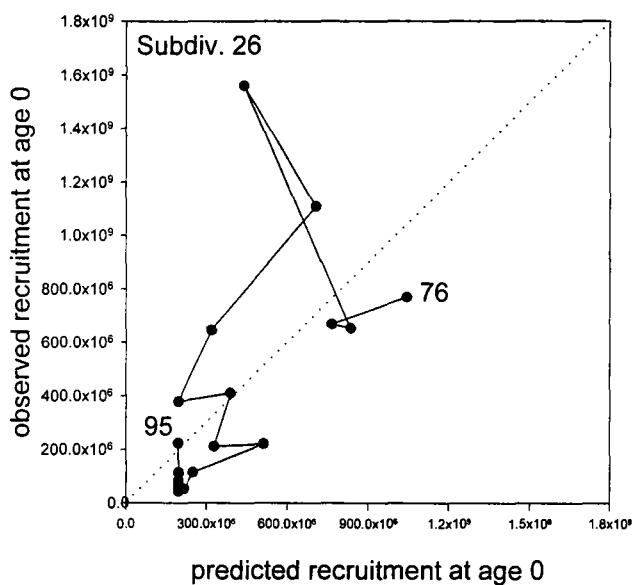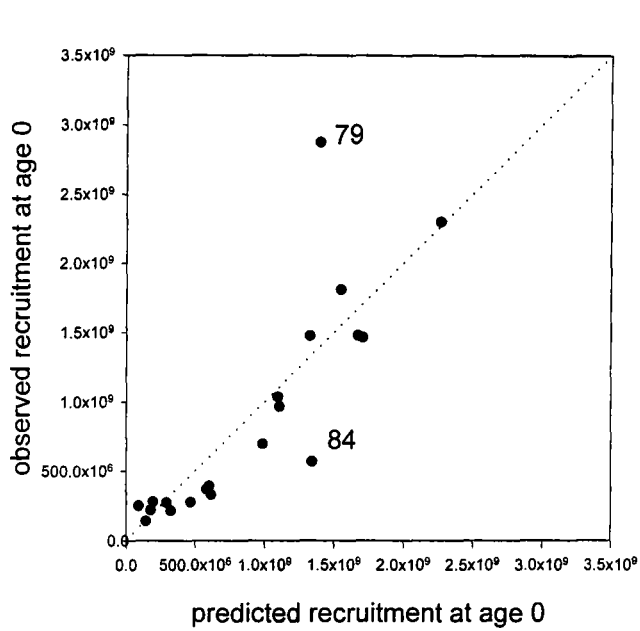
Fig. 16 Observed vs. predicted recruitment at age 0 in Subdiv. 25 (a) based on linear regression of recruitment on larval abundance (left) and multiple linear regression with larval abundance, sum of oxygen in the reproductive volume and larval transport index as independent variables (right), in Subdiv. 26 & 28 (b) based on linear regression of recruitment on larval abundance.
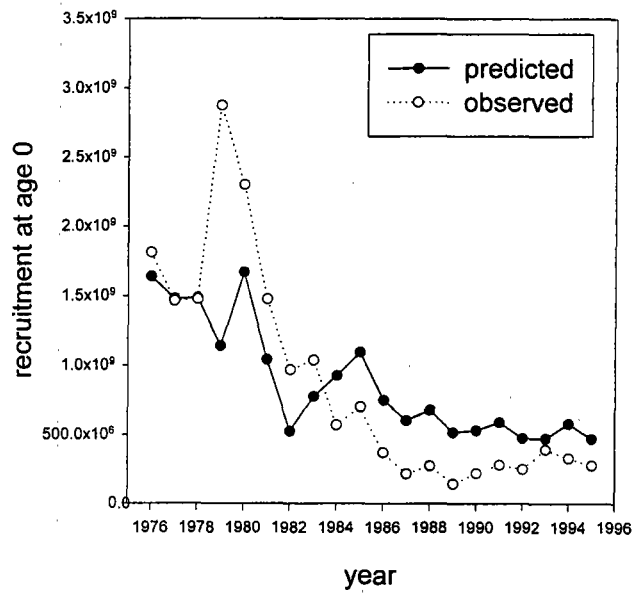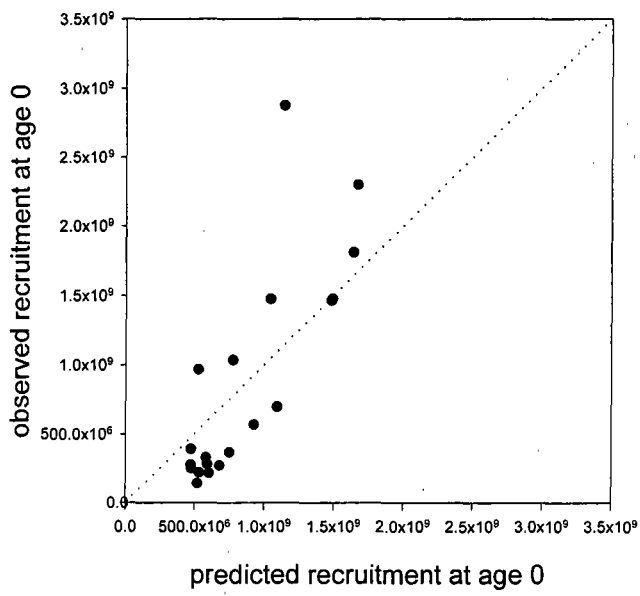
Fig. 17 Observed vs. predicted recruitment at age 0 in combined Subdiv. 25, 26 & 28 obtained from model utilizing larval abundance as independent variable.
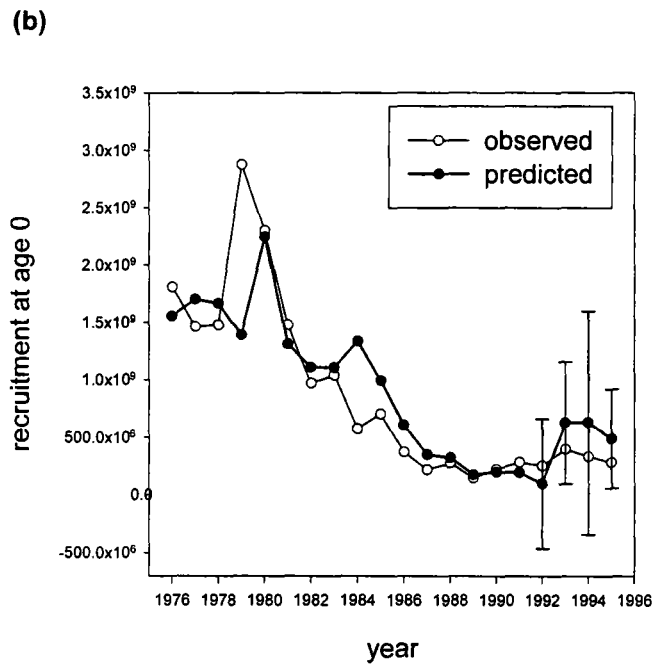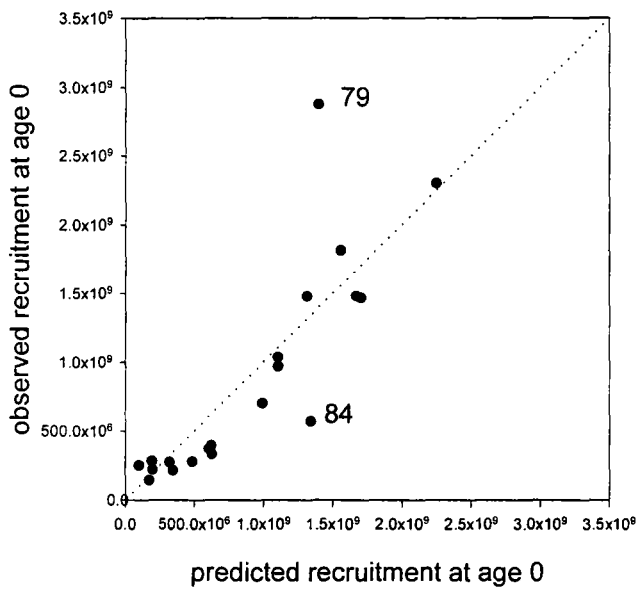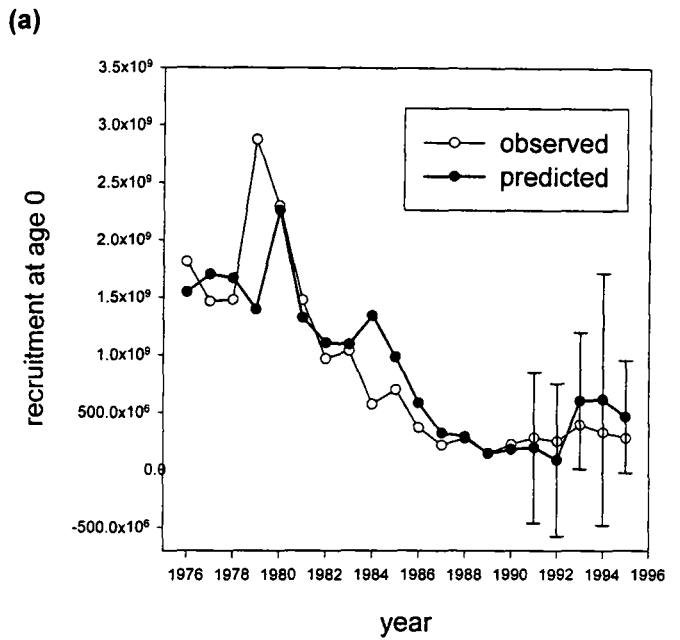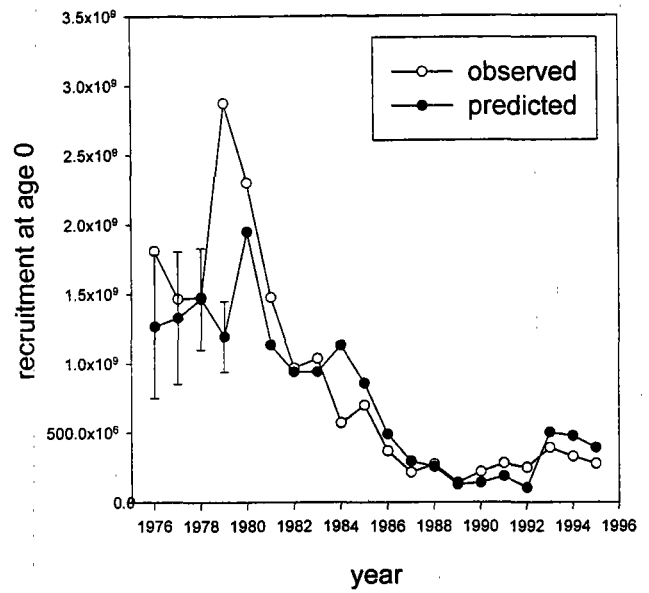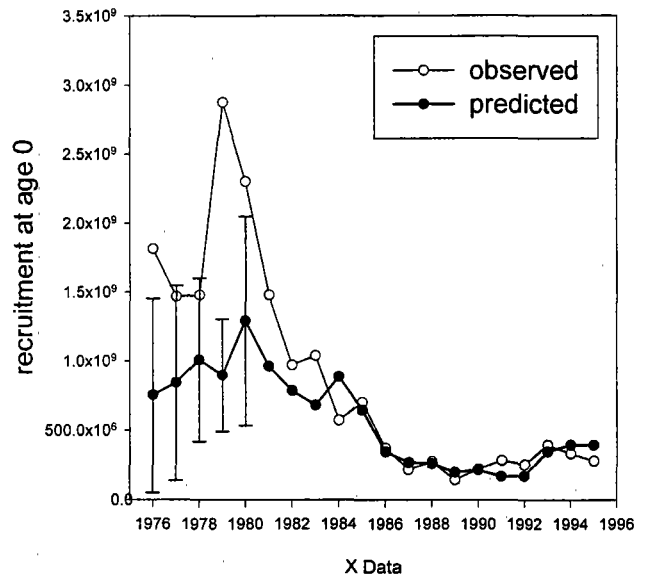
Fig. 18   Observed vs. predicted recruitment at age 0 in combined Subdiv. 25, 26 & 28 based on egg production
by SSB including environmental factors utilizing subsets of data: 1976-90 (a) and 1976-91 (b). Shown
are the 95% condidence limits of the predicted means for recruitment in 1991-95 and 1992-95.
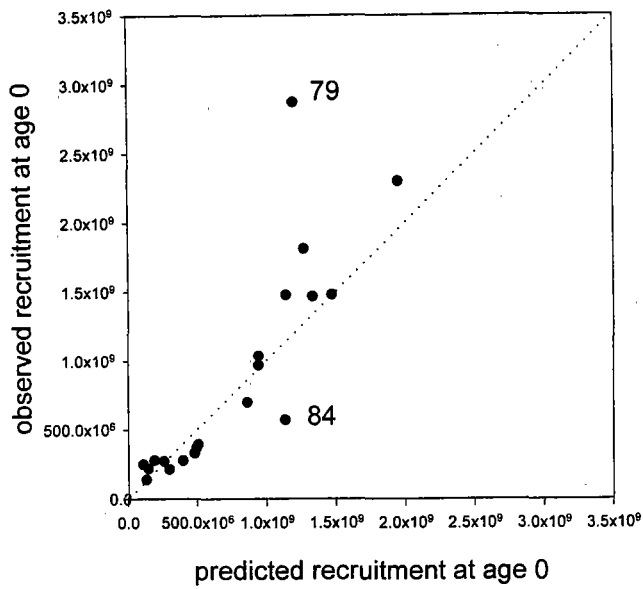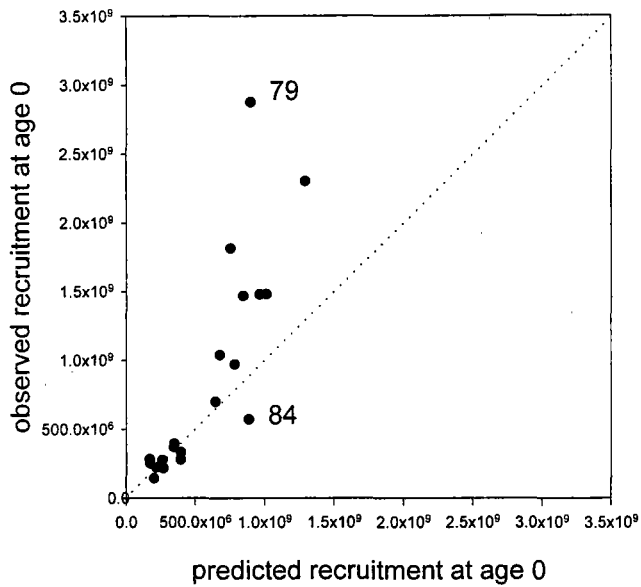
Fig. 19 Observed vs. predicted recruitment at age 0 in combined Subdiv. 25, 26 & 28 based on egg production by SSB including environmental factors utilizing subsets of data: 1980-95 (a) and 1981-95 (b). Shown are the 95% confidence limits of the predicted means for predicted recruitment in 1976-79 and 1976-80.
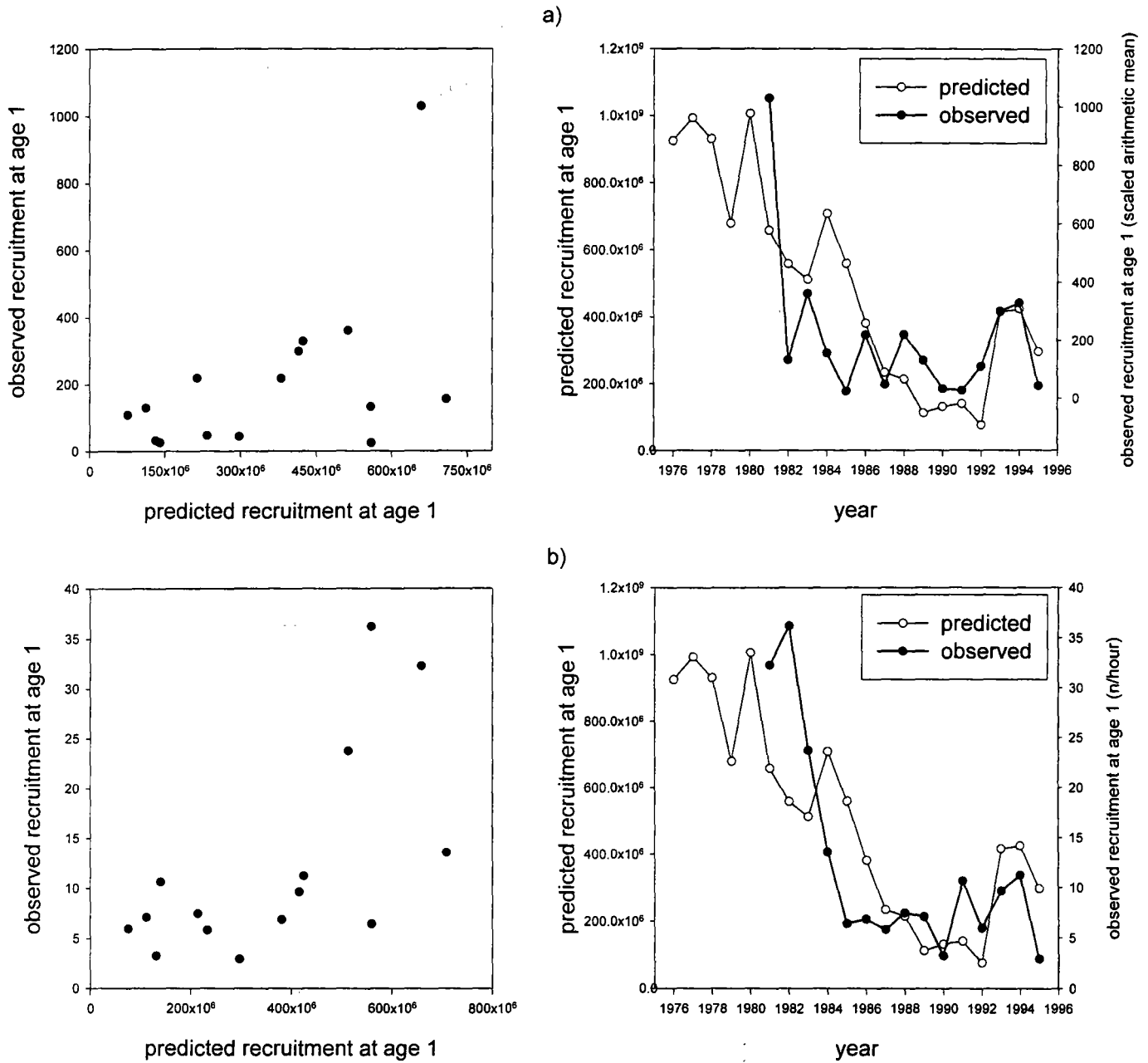
Fig. 20 Observed vs. predicted recruitment at age 1 in combined Subdiv. 25, 26 & 28. Observed recruitment: a) scaled arithmetic mean, b) GLM-output of catch rates obtained by the international trawl survey. Predicted recruitment obtained by final models as in Fig. 15.