International Council for the
Exploration of the Sea

CM1996/C + J: 4
Hydrography Committee
Baltic Fish Committee

Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea

B. R. MacKenzie[1], M. A. St. John[1], M. Plikshs[2], H.-H. Hinrichsen[3], K. Wieland[3]

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

[2]Latvian Fisheries Research Institute, 6 Daugavgrivas str., LV-1007 Riga, Latvia

[3]Institut für Meereskunde an der Universität Kiel, Dusternbrooker Weg 20, D-24105 Kiel, Germany

Abstract

The volume of water with suitable oxygen and salinity conditions for survival and development of cod eggs in the eastern Baltic Sea varies significantly within and among years. It has recently been shown that this volume of water ("reproductive volume"), in addition to spawning stock biomass, is a major factor determining recruitment success in this cod population. However, it is unclear which oceanographic mechanisms are responsible for variability in reproductive volume, and how these processes interact on a seasonal and interannual basis. In this study, we use time series observations to identify inter-relationships between hydrographic and biological processes (e. g., inflows of North Sea water, winter mixing processes, production and decomposition of organic matter) influencing reproductive volumes from 1952-1992. A frequent pattern of seasonal variability in 4 eastern Baltic spawning areas includes a spring maximum which decreases during the summer, followed by an increase during the fall-winter months. However, this general pattern is violated in many years, and the magnitude of the seasonality is more pronounced, in some spawning areas than others. We have begun to analyse these patterns and interpret them in the context of other fluctuating components of the eastern Baltic pelagic ecosystem. Preliminary results show that reproductive volumes decrease by an average of 9 - 39% between May and August, and that the decrease in the spawning area most important to long-term recruitment (Bornholm Basin) is temperature-dependent. The seasonal decline in the Bornholm Basin also tends to be larger and more variable after 1964 than in the previous 12-year period. These patterns of reproductive volume variability may be important to cod reproductive success because of a long and variable spawning period.

Keywords: Baltic Sea, cod reproduction, oxygen, plankton, recruitment, salinity

Introduction:

The interaction between oxygen concentration and cod egg buoyancy is important for the survival of cod eggs in the Baltic Sea (Nissling et al. 1994, Wieland et al. 1994). This interaction is important because cod eggs can be neutrally buoyant at depths where oxgyen concentrations are so low that successful egg development is not possible (Wieland et al. 1994). In the Baltic Sea, the areas with the appropriate salinity and oxygen conditions are limited to the deep basins. Hydrographic conditions within these areas have been recorded for decades as part of various sampling and monitoring programmes (e. g., HELCOM). As a result, it is now possible to derive direct estimates of the volume of water available for successful cod spawning ("reproductive volume"; Plikshs et al. 1993, Hinrichsen and Wieland 1996).

Estimates of reproductive volume have been observed to vary both within and between years (Plikshs et al. 1993, Hinrichsen and Wieland 1996), and between spawning sites (Plikshs et al. 1993). Plikshs et al. (1993) have shown that the interannual variabililty in reproductive volume estimates can explain a significant portion of the variance in cod recruitment, after allowing for the effect of spawning stock size.

However, the way in which reproductive volumes vary over time (e. g., interannually, seasonally) and space (i. e., between areas) has not yet been described, nor have factors associated with this variability been identified quantitatively. Since this variability is related to the success of cod reproduction and recruitment, a lack of understanding of how reproductive volumes vary makes it difficult to anticipate how Baltic cod might react to variability that might arise due to, for example, changing nutrient loads or climate.

In this report, we quantify certain aspects of the temporal and spatial variability in reproductive volumes, and attempt to identify general relationships between key oceanographic processes and reproductive volume variability. Some candidate processes include the seasonal pattern of plankton production and decomposition typical for this region (Smetacek et al. 1978, Schulz et al. 1978, Bodungen et al. 1981), and inflows of saline North Sea water (Matthaus and Franck 1992). Eutrophication (*sensu* Nixon 1995), and decomposition of organic matter (Elmgren 1989, Sidrevics et al. 1993, Jonsson and Carman 1994), may also be responsible for some of the variability. As a result, it has been suggested that periods of favorable oxygen conditions (e. g., due to inflows) are now shorter than in the past (Nissling et al. 1994).

Our approach in this paper is empirically based, and will involve comparisons of reproductive volumes with other environmental variables. Although our analyses are incomplete and ongoing, we find that the variability in reproductive volumes has distinct non-random seasonal components, and that the degree of seasonality is temperature-regulated, possibly via rates of plankton production and organic matter decomposition. We have also found evidence suggesting that eutrophication has detrimentally impacted reproductive volumes.

Methods:

General:

We conducted statistical analyses of reproductive volumes within the main cod spawning areas in the eastern Baltic Sea. These analyses involved comparisons of reproductive volumes within sites, and also comparisons of volumes between sites within years. The within-site comparisons focussed mainly on seasonal variability, and how this seasonality varied over years.

We conducted additional analyses to identify potential processes responsible for the within-site seasonal variability. For these analyses, we considered only the Bornholm Basin because this area tends to have better oxygen conditions at the depths where cod eggs are neutrally buoyant, than the other spawning areas.

The processes we considered as being most influential on reproductive volumes were those related to the consumption and renewal of oxygen. These included rates of organic matter production and decomposition by both phytoplankton and zooplankton, as well as other factors (i. e., water temperature, plankton abundance) likely affecting such rates. Additional details about the choice of variables and their configuration are described at appropriate locations in the Results section. We note that the reproductive volumes used in our analyses also depend on salinity; however in this presentation we have chosen to postpone analysis of this variable (e. g., freshwater runoff: Bergström and Carlsson 1994; Viitasalo et al. 1995) until a later occasion.

Data sets and analyses:

Reproductive volume data for each spawning area were obtained from Plikshs et al. (1993). These data represent the volume of water in each area whose salinity exceeded 11 ppt and oxygen exceeded 2 ml l^{-1}. These estimates of reproductive volume are broadly consistent with those estimated using different methods and to some extent different data sources (Hinrichsen and Wieland 1996). The time series covers the period 1952-1992, and in most of our analyses we use the observations made in May and August, although observations for several other months of the year were available. We chose May and August instead of other months because this period coincides with the time of year when cod eggs are most likely to be present in spawning areas (Wieland 1995, MacKenzie et al. 1996). In addition, the seasonal distribution of major inflows to the Baltic during the last 100 years is in the period August-May, with the peak occurring between November and January (Matthaus and Franck 1992). Hence analysis of changes in reproductive volume during the overwintering period August to May may identify the role of major inflow events on these estimates.

Additionally, hydrographic (temperature) data were obtained from ICES, ice coverage data were obtained from Seina and Palosuo (1993) and J. Haapala (pers. comm.), and inflow intensities were provided by W. Matthaus (pers. comm.). Zooplankton data were assembled from the literature and archived institutional sources (Plikshs/Kostrichkina unpubl.).

Data analyses consisted of pairwise comparisons of time series of different variables. Comparisons were first conducted visually using bivariate scatterplots; if a pattern was evident, linear regression analyses were conducted. In some cases, the residuals from significant relationships were further analysed for major outliers and time patterns.

Results:

The long-term seasonal pattern of reproductive volume fluctuations for the Bornholm Basin shows that reproductive volumes tend to decrease from February to August and then increase again between October and February (Fig. 1). In the Bornholm Basin the May-August decrease in reproductive volume is about 9% whereas it is larger in the other cod spawning areas (Figure 2A; Table 1). However, the magnitudes of the declines among areas were not inter-correlated (Fig. 3). In the Bornholm Basin, there was a significant time trend in the residuals from a regression model of August reproductive volume vs. May reproductive volume: the seasonal decrease is larger since 1964 than during the previous 12 years (Fig. 2B). This pattern was not evident for the other areas.

We have analysed the seasonal patterns in the Bornholm Basin in further detail to identify potential mechanisms responsible for this variability. For example, vertical profiles of the change in oxygen concentration during early summer in the Bornholm Basin in 1993 and 1994 show that oxygen concentrations decrease during the spring/early summer period (Fig. 4). It is also evident that the decrease varies between years because the decrease in oxygen content was larger in 1994 than in 1993.

The decrease in oxygen concentrations and reproductive volume between spring and summer may be partly related to the decomposition of organic matter by microplankton. If this is true, the size of the decrease (i. e., deltaRV) may be related to factors such as water temperature, which infuences production and decomposition of plankton biomass, and the productivity of the plankton food web.

We tested this hypothesis by first comparing the seasonal change in reproductive volume in the Bornholm Basin with water temperatures measured in this area. The temperature data we chose for testing this hypothesis were those potentially responsible for controlling the rate of decomposition of settling organic matter following the spring phytoplankton bloom. In the Bornholm Basin, the spring bloom usually starts in mid-April and continues into May (Smetacek et al. 1978, Bodungen et al. 1981). Since particulate organic matter in the Baltic can be mineralized by bacteria while sedimenting (Iturriga 1979, Rheinheimer et al. 1989), we compared the change in reproductive volume between May and August with temperatures in May above, within and below the halocline (i. e., 25-35, 56-65 and 83-98 m).

The results of these analyses show that reproductive volumes in the Bornholm Basin decrease between May and August by a greater amount in warm years than in cold years (Fig. 5A), and that temperatures above and within the halocline are more strongly associated with the seasonal decrease than temperatures below the halocline (Fig. 5A). There is also some evidence that the spring to summer change in reproductive volume, after having removed the influence of temperature, has a temporal trend (Fig. 5B). After 1964, the variability in the time series is significantly larger (Fig. 5B), and the mean residual is significantly more positive (indicating a larger decrease between May and August).

We note that mean monthly temperatures at various depths in the Bornholm Basin are significantly associated with the severity of the previous winter (expressed as areal ice coverage of the Baltic Sea; Fig. 6, 7). Hence the relationships between (1) spring to summer reproductive volume variability and May water temperature, and (2) areal ice coverage and May water temperature suggest that ice coverage itself may be able to explain some of the variability in the spring-to-summer decline of reproductive volumes. This hypothesis is also supported by the available data (Fig. 8).

In addition to the role of temperature on decomposition of organic matter, temperature may also affect the rate at which various types of organic matter (e. g., phytoplankton, zooplankton, fecal pellets) are produced. If this is true, the abundance of organic matter itself may directly be related to the seasonal decline in reproductive volume. We therefore made two additional comparisons: (1) zooplankton abundances (as a proxy indicator of organic matter abundance) were compared with May water temperatures at 56-65 m depth (which is strongly associated with areal ice coverage; Fig. 6), and (2) zooplankton abundances were compared directly with the spring to summer decline in reproductive volumes.

These analyses showed that cold years (as expressed either by our water temperature or ice coverage variables) tend to be characterized by a lower biomass of crustacean zooplankton in the spring (Fig. 9). This pattern is consistent among three separate areas of the Baltic and for different time periods within the last 40 years. In addition, for two of the three zooplankton series tested, the decrease in reproductive volume was greater in years when there was more zooplankton than in zooplankton-poor years (Fig. 10); in the case which was the exception, there was no significant relationship.

Our statistical comparisons clearly identify anomalous situations as well as interrelationships among variables. For example, in 1959 and 1974, there were large *increases* in reproductive volume between May and August, and in 1986 there was an anomalously high abundance of zooplankton in the Gulf of Riga (Fig. 9B).

The second part of the long-term seasonality in reproductive volumes is characterized by a mean increase during the fall/winter months (Fig. 1). However, this pattern is not consistent across years; there is no obvious correspondance between the late summer (August) and following spring (May) reproductive volumes (Fig. 11) as one might expect if processes for renewing and consuming oxygen were in balance. Some of the large outliers may be years when specific oceanographic processess (e. g., inflow events, winter mixing intensity) occurred (or failed to occur).

We checked this possibility for the particular case of inflow events for which an extensive time series is available (Matthaus and Franck 1992). Inflow events can renew oxygen levels in deep Baltic basins, if they are derived from saline, oxygen-rich water masses and if they are of sufficient duration and volume. Inflows of strong intensity should have large effects on oxygen and salinity characteristics in the Bornholm Basin, and consequently on cod reproductive volumes. We therefore compared the intensity of inflow events (as expressed by the factor Q derived by Matthaus and Franck 1992) in each winter with the change in reproductive volume between August and May. This comparison showed that several of the large outlier years in Fig. 11 (i. e., 1968, 1971, 1975, 1979) were years when there were major inflows to the Bornholm Basin (Fig. 12). However, there were also some winters when reproductive volumes increased by large amounts without intense inflows (e. g., 1958, 1966), and conversely several winters when there were intense inflows which did not substantially increase reproductive volumes (e. g., 1963, 1969, 1973, 1982; Fig. 12).

Discussion:

Implications for cod reproductive and recruitment success:

Earlier investigations in the Baltic have shown that it is possible to quantify the size of cod spawning habitat on the basis of abiotic factors controlling successful development of eggs (Plikshs et al. 1993). These estimates of cod reproductive volume are significant correlates of cod recruitment after adjusting for spawning stock biomass (Plikshs et al. 1993).

We have now shown that reproductive volumes vary systematically, and that significant amounts of this variation are associated with other processes in the pelagic ecosystem. Reproductive volumes in all 4 eastern Baltic spawning sites typically decrease by on average 9-39% between May and August. In the Bornholm Basin, the extent of the decrease is related to both spring water temperatures and the maximal area of ice coverage in the preceding winter. Our results suggest that cold years during the last 4 decades were favorable for cod egg development, possibly via the effect of temperature on the production, consumption and decomposition of organic matter (see details below).

The seasonal and interannual variations in reproductive volume are probably important for the reproductive and recruitment success of this population because of its variable spawning behaviour (Bagge et al. 1994, Baranova 1995) and egg buoyancy (Nissling et al. 1994). Egg surveys show that spawning typically occurs over at least three months, and that the peak in spawning can vary by at least two months (Wieland and Horbowa 1996, MacKenzie et al. 1996). Adult cod therefore potentially expose their eggs to a wide range of oxygen conditions within a given year, depending on the timing of spawning relative to the seasonality in reproductive volume.

Biological oceanographic processes affecting spring to summer variability in the size of cod spawning habitat:

One way in which temperature could affect reproductive volume seasonality in the Bornholm Basin is its potential influence on the functioning and structure of the pelagic food web. Townsend et al. (1994) have used modelling studies to show that the fate of organic matter produced during spring blooms in coastal waters in temperate latitudes depends on temperature: in cold years (< 3-5 C), metabolic and grazing rates of metazoan consumers, and bacterial decomposition rates are both suppressed (Pomeroy and Diebel 1986, Townsend et al. 1994). Temperatures in this range are typical for depths above and within the halocline in the Bornholm Basin during spring (MacKenzie et al. 1996; also Fig. 6). In such years, the consumption and decomposition of new organic matter will likely be low, resulting in maintenance of high oxygen conditions for longer periods of the year, and the growth and abundance of metazoans will be low. Our findings that spring zooplankton abundance is higher in warmer years (see also Sidrevics et al. 1993), and that zooplankton abundance itself tends to be related to the seasonal decline in reproductive volume is consistent with this interpretation.

In this context we note that particulate and dissolved organic matter in the Bornholm Basin, and elsewhere in the Baltic, undergoes bacterial mineralization during sedimentation (Iturriga 1979; Larsson and Hagström 1982; Lahdes et al. 1988; Rheinheimer et al. 1989). For example, at an offshore station in the northern Baltic Proper, 45% of the primary production of the spring bloom was mineralized by bacteria, with most (70%) occurring in the upper 30 m of the water column (Lahdes et al 1988). In addition, bacterial activity in the Baltic during summer was nearly 100-fold higher in the warm surface layer compared to rates below the thermocline in cold winter water (Rheinheimer et al. 1989), activity levels are higher in summer than in winter (Iturriga 1979) and laboratory experiments show that bacterial mineralization of phytoplankton is about 10-fold faster at 20C than at 5C (Iturriga 1979). The mineralization and consumption of organic matter by bacteria, ciliates and other zooplankton (Leppanen and Bruun 1988; Nielsen and Kiørboe 1994), consume oxygen and are temperature-dependent. Hence temperature effects on these processes may partly explain why reproductive volumes tend to decrease more in warm years than in cold years.

The influence of temperature on reproductive volume seemed to be strongest for depths above and within the halocline. Apparently temperatures in the deepest part of the Bornholm Basin play a subordinate role to other factors. One such factor could be the amount of organic material sedimenting from the upper layer. Graf et al. (1982) have shown that benthic microbial activity at a site in the western Baltic tripled in response to inputs of fresh phytodetritus even though temperatures remained stable.

We believe therefore that measures of organic matter abundance, that are themselves closely related to microbial activity, might explain more variability in reproductive volume seasonality than zooplankton abundances. Two such measures are primary production rates and chlorophyll a concentrations. We note that in pelagic aquatic ecosystems these variables are strongly related to rates of bacterial production (Cole et al. 1988), and chlorophyll a concentrations (Bird and Kalff 1984), respectively. Hence comparisons of primary production rates and chlorophyll a concentrations with reproductive volumes may improve the relationships found here.

The seasonal patterns which we analysed here are consistent with seasonal changes in oxygen concentration reported by Matthaus (1978) and Olesen (1993, 1995) for the Bornholm Basin and Kattegat. Both workers found that oxygen concentrations decreased throughout the water column after the spring bloom.

Our analyses suggest that the influence of oxygen renewal events (e. g. inflows: Matthaus and Franck 1992) on cod reproductive volumes in the Bornholm Basin is now shorter than in earlier times. This finding is based on the fact that the residuals from the seasonal change in reproductive volume vs. temperature relationship had a significant time pattern: reproductive volumes in recent decades decrease by larger amounts on a seasonal basis than in the 1950's to mid-1960's, and are more variable in recent decades.

The time pattern observed in our residuals is consistent with the general eutrophication pattern in the Baltic region. A number of authors have reported increased nutrient concentrations (Wulff and Rahm 1988, Sanden and Rahm 1993, Rahm et al. 1996) in the Baltic over the last 2-4 decades. The atmospheric load of nitrogen (nitrate and ammonia) increased most steeply between the mid-1960's and the late 1970's - early 1980's (Granat 1990). Other workers have shown in the same time period that chlorophyll a (Renk et al. 1992, Maske 1994), primary production rates (Renk et al. 1992), seston concentration (Maske 1994), Secchi depths (Sanden and Håkansson 1996), deposition of organic matter to the sediments (Jonsson and Carman 1994) and zooplankton abundances (Ciszewski 1985, Kostrichkina 1990, Sidrevics et al. 1993) in various areas of the Baltic have all changed in ways which are consistent with an increasing nutrient load. Our results are therefore not surprising, although they are among the few to quantify how eutrophication might be affecting cod reproductive success in at least one spawning area.

Physical oceanographic processes affecting fall-winter to spring seasonality:

Our comparisons of reproductive volume variability over the winter months showed less correspondance than with the spring to summer period. This may be due to the seasonal distribution of major Baltic inflows which peaks in the November-January period (Matthaus and Franck 1992). Several large outlier years could be traced to the intensity of major inflow events, but the occurrence or failure of such events could not account for the overwinter variation in reproductive volumes. In addition, there were two large *increases* in reproductive volume during the springs of 1959 and 1974 which are not seen in the time series of inflow events compiled by Matthaus and Franck (1992). Other processes must be involved, including the occurrence of smaller inflows which enter the Bornholm Basin but which do not propagate further into the Baltic. Events such as these occurred in the winters of 1989-90, 1990-91 and 1991-92 (Matthaus 1995) and can increase reproductive volumes in the Bornholm Basin (Fig. 12).

Another means by which reproductive volumes could increase during the winter months is via vertical mixing, which in the Baltic is mainly due to wind (Matthaus 1990). During the winter months the permanent halocline deepens by about 10 m every year due to mainly wind-driven vertical mixing (Stigebrandt and Wulff 1987). As a result, the salinity and nutrient concentration of the upper layer increases (Stigebrandt and Wulff 1987), and oxygen can be mixed to deeper levels. Storms at other times of year, and upwelling/downwelling events, will also cause mixing across the halocline (Matthaus 1990). For example, in a cold spring when thermal stratification is delayed, wind-induced mixing could penetrate deeper than during a warm spring, and therefore delay or reduce the seasonal decline in reproductive volumes discussed above. Strong winter cooling resulting in convective mixing might also contribute to cross-halocline mixing (Schulz et al. 1992; St. John et al. 1996). Interactions between inflows, vertical mixing and thermal stratification such as these may be responsible for the overwintering variability in reproductive volumes, and therefore deserve further study.

We also found little evidence that the spring to summer decline in reproductive volume was correlated among spawning areas. The lack of spatial correlation in reproductive volume seasonality could be associated with differences and lags in the advection of water masses between areas. For example, major inflows require several months before their effect on all areas is fully established (Matthaus and Lass 1996), and small inflows which reach the Bornholm Basin can improve oxygen conditions there but not elsewhere (Matthaus 1995). Hence reproductive volumes in specific areas may be regulated both by advective and local (e. g., food web) processes.

Patterns in ecosystem variability:

Many of our statistically significant relationships explain rather modest proportions (typically 20-30%) of the total variability in the dependent variables, and there are occasionally very large outliers. Reasons for such variability can be attributed both to natural and artifactual causes. Thus, within a given year, many other processes (e. g. patchiness, unusual mixing regimes) could occur to obscure the long-term response. Attempts should be made in the future to identify what is associated with this variability. In addition, artifacts such as insufficient sampling and different data processing methods will contribute to the unexplained variation. The patterns identified here are therefore average situations for the particular period covered by the time series; attempts to extrapolate to other time periods should be done cautiously because other processes may be dominant at different time scales.

However, we note that in some instances the same tendancy recurred with different data sets. For example, the abundance of zooplankton estimated by four different studies at different times and places of the Baltic and using different gears and different sample processing protocols, basically responded in the same general way (e. g. to temperature and ice coverage). This is reassuring and gives added confidence to patterns resolved from individual time series.

There is a strong effect of areal ice coverage in the Baltic on thermal conditions in the Bornholm Basin. This relationship varied with depth and by month, so that temperatures at some depths were more dependant on ice coverage than others. However, having established this relationship, it potentially allows reconstruction of historical thermal regimes (with error estimates) for the Bornholm Basin dating back to the earliest records of ice coverage (1720). This information could be valuable when interpreting biological data for which no other temperature data are available. In particular, the relationships of ice coverage to temperature, reproductive volume seasonality and zooplankton abundances could in principle enable one to re-construct some coarse features of the Bornholm Basin plankton food web for the last 275 years.

Conclusion:

We have begun to identify patterns and linkages between cod reproductive biology and seasonal environmental variability. Our preliminary results show that it is possible to quantify variations in the size of the spawning habitat of an important marine fish species to other ecosystem variables. Cod spawning habitats in the Baltic decrease in size by an average of 9-39% between spring and summer, depending on the spawning area and the year, and they sometimes increase during winter as a result of processes such as inflows and vertical mixing. The magnitude of the spring to summer decline in the Bornholm Basin is associated with spring water temperatures, and suggests a link to the rates of production and decomposition of organic matter, and therefore to eutrophication of the Baltic. Our future work will attempt to compare these findings with other data sets and analyses (e. g., primary production rates, chlorophyll a concentrations, reproductive volume estimates) and with the other Baltic spawning areas. Seasonal patterns such as these seem to be important to cod reproduction because cod in the Baltic spawn over unusually long and variable periods and therefore risk exposing their eggs to lethal conditions.

Acknowledgements:

We wish to thank Jari Haapala for ice coverage data, Wolfgang Matthaus for inflow data,

O. Vagn Olsen for extracting hydrographic data and Markku Viitasalo for discussions. This work was supported by a grant from the European Union (AIR2 94 1226).

Table 1. Relationships between August and May reproductive volume estimates for four cod spawning areas in the eastern Baltic Sea during the years 1952-1992. Reproductive volume data from Plikshs et al. (1993). * = residuals show significant decreasing trend from 1952-1992 (see Fig. 2B). Data analyses were restricted to only those years when reproductive volume in May was greater than zero. DeltaRV is defined as RV_{MAY} - RV_{AUGUST}, and the percentage value is defined as (100*deltaRV)/RV_{MAY}. All regression intercepts are not significantly different from zero ($P > 0.05$).

Basin	Regression Model	R^2	P	DeltaRV	%	N
Bornholm	Aug. = 0.79*May +19.2*	0.56	< 0.0001	13.7±55.9	9	41
Gdansk	Aug. = 0.57*May +5.0	0.34	< 0.0001	22.0±33.7	35	22
Southern Gotland	Aug. = 0.39*May +14.4	0.19	< 0.0249	25.5±44.6	39	26
Central Gotland	Aug. = 0.58*May +47.8	0.32	< 0.0540	59.3±201.3	23	12

Figure Captions

Fig. 1. Mean monthly reproductive volume estimates (± 2 standard errors) for the Bornholm Basin during 1952-1992. Data from Plikshs et al. (1993).

Fig. 2. A. The relationship between reproductive volumes measured in May and August of the same year for the Bornholm Basin. Reproductive volume is defined as the volume of water whose salinity exceeds 11 ppt and oxygen concentration exceeds 2 ml/l. Data from Plikshs et al. 1993. Symbols are years. B. The time trend in the residuals from the regression relationship shown in panel A.

Fig. 3. Spatial comparison of seasonal changes in reproductive volume between May and August for the Bornholm Basin and southern Gotland Basin for years when reproductive volume in May was greater than 0 km^3. Comparisons involving other pairs of basins were similar. Symbols are years.

Fig. 4. The depth-specific mean change in oxygen concentration in the central Bornholm Basin (55°17.5'N, 15°45'E) in summer 1993 (May 23 to July 7) and 1994 (May 31 to July 8).

Fig. 5. (A). The difference in reproductive volume (deltaRV) between May and August relative to mean May temperature at 56-65 m in the Bornholm Basin for the years 1952-1992. The regression model for all years is deltaRV = 15.7*T - 39.4 ($R^2 = 0.16$; $P = 0.0091$). If the years 1959 and 1974 are excluded from the calculation, the model becomes deltaRV = 18.8*T - 42.4 ($R^2 = 0.32$; $P = 0.0002$); this model is shown on the panel. Reproductive volume and temperature data from Plikshs et al. (1993) and ICES. Symbols are years. The relationship between deltaRV and temperatures at 26-35 m was deltaRV = 21.5*T - 67.3 ($R^2= 0.27$; $P =0.0006$; 1959 and 1974 excluded). There was no significant relationship between temperature at 83-98 m and deltaRV ($P = 0.7825$; 1959 and 1974 excluded). (B). The time trend in the residuals from the regression relationship shown in panel A. The vertical dashed line shows where the mean residual becomes significantly more positive (t-test for nonhomogeneous variances; $P = 0.02$) and where the variance in the series becomes significantly larger (variance ratio test; $P = 0.0074$).

Fig. 6. The relationship between May temperature at 56-65 m in the Bornholm Basin and area of ice coverage in the Baltic Sea. Temperature data from ICES and ice coverage data from Seina and Palosuo (1993) and Haapala (1996).

Fig. 7. Statistical significance levels, P, for the relationships between mean monthly temperature at 9-14 m and 56-65 m in the Bornholm Basin and area of ice coverage in the Baltic Sea for the years 1960-1994.

Fig. 8. A. The difference in reproductive volume (deltaRV) between May and August in the Bornholm Basin relative to the area of ice coverage of the Baltic Sea for the years 1952-1992. The regression model (excluding the years 1959 and 1974) is deltaRV = -0.20*Area + 60.2 ($R^2 = 0.17$; $P = 0.009$). Reproductive volume and ice coverage data from Plikshs

et al. (1993), and Seina and Palosuo (1993) and Haapala (1996) respectively. Symbols are years. B. The time trend in the residuals from the regression relationship shown in panel A. The vertical dashed line shows where variance in the series becomes larger.

Fig. 9. The influence of May temperature in the Bornholm Basin (56-65 m) on the abundance of crustacean zooplankton during May in different parts of the Baltic. **(A)** Southern Baltic, including Bornholm Basin, for the years 1979-1983. The fitted regression line is given by the equation Zoopl. = 11.4*Temp. - 2.51 ($R^2 = 0.86$; $P = 0.0232$). Zooplankton (depth-averaged; 0-bottom) data from Ciszewska (1990). **(B)** Gulf of Riga for the years 1956-1990 (no data for 1957). The fitted regression line is given by the equation Zoopl. = 2.61*temp - 0.24 ($R^2 = 0.66$; $P < 0.0001$; note that 1986 was excluded from the calculation). Zooplankton data (depth-averaged; 0-40 m) from Sidrevics et al. (1993). **(C)** ICES Subdivisions 26 (excluding Gulf of Gdansk), 28 and 29 (eastern and northern Baltic Proper) for the years 1960-1990 (no data for the years 1968, 1979, and 1983). The fitted regression line is given by the equation Zoopl. = 1.07*temp + 3.17 ($R^2 = 0.21$; $P < 0.0136$). Zooplankton data (depth-averaged; 0-100 m) from Pliksh s (unpubl.). Water temperature data from ICES. Symbols are years.

Fig. 10. The difference in reproductive volume (deltaRV) between May and August in the Bornholm Basin relative to the abundance of crustacean zooplankton in May in different parts of the Baltic. **(A)** Southern Baltic, including Bornholm Basin, for the years 1979-1983. The regression model et al. (1993) and is deltaRV = 1.8*zoo - 47.9 ($R^2 = 0.79$; $P = 0.0439$). Zooplankton data from Ciszewska (1990). **(B)** Gulf of Riga for the years 1956-1990 (no data for 1957). The regression model is deltaRV = 5.28*zoo - 18.2 ($R^2 = 0.24$; $P = 0.0037$). The regression model excluded the years 1959, 1974 and 1986. Zooplankton data from Sidrevics et al. (1993). **(C)** ICES Subdivisions 26 (excluding Gulf of Gdansk), 28 and 29 (eastern and northern Baltic Proper) for the years 1960-1990 (no data for the years 1968, 1979, and 1983). Reproductive volume and zooplankton data from Plikshs et al. (1993) and Plikshs (unpubl.), respectively. Symbols are years.

Fig. 11. The relationship between reproductive volumes measured in August of year t and in May of year t+1 for the Bornholm Basin. The 1:1 line is shown for reference, and large outliers are enclosed by polygons. Symbols are years according to August. Data from Plikshs et al. 1993.

Fig. 12. The difference in reproductive volume in the Bornholm Basin between May of year t+1 and August of year t for winters having different cumulative intensities of inflows of Belt Sea water. Inflow intensities are the sum of individual intensity (Q) values for each fall/winter period Sept. 1 - April 30. Symbols on panel are years according to August. Reproductive volume and inflow intensities from Plikshs et al. (1993), Matthaus and Franck (1992).

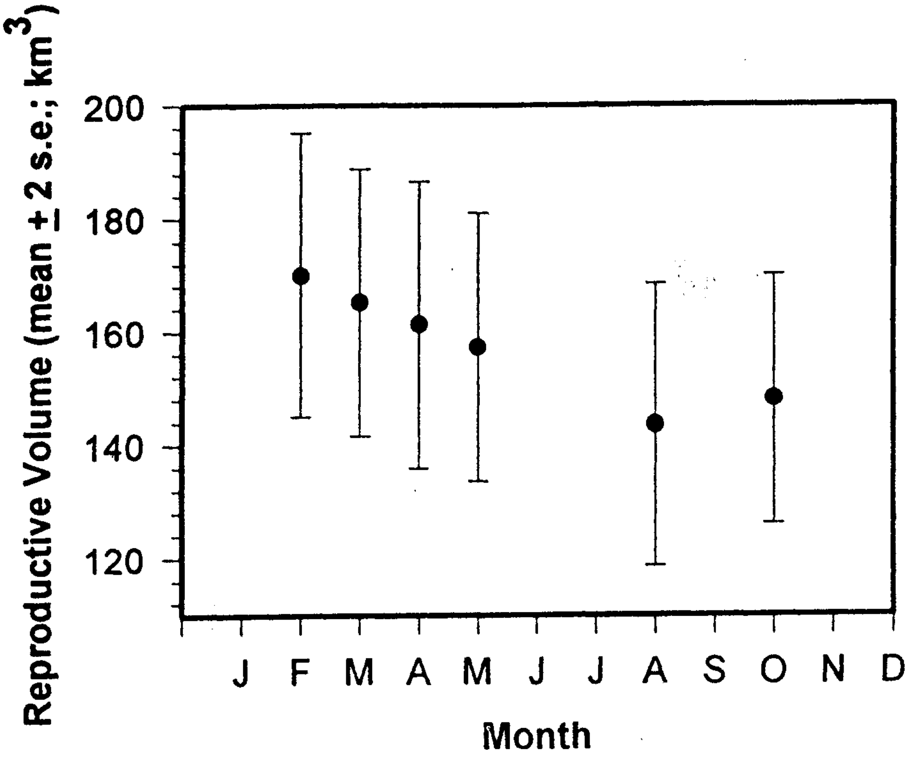

Reproductive Volume (mean ± 2 s.e.; km^3)
200
180
160
140
120
J
F
M
A
M
J
J
A
S
O
N
D
Month

Fig. 1

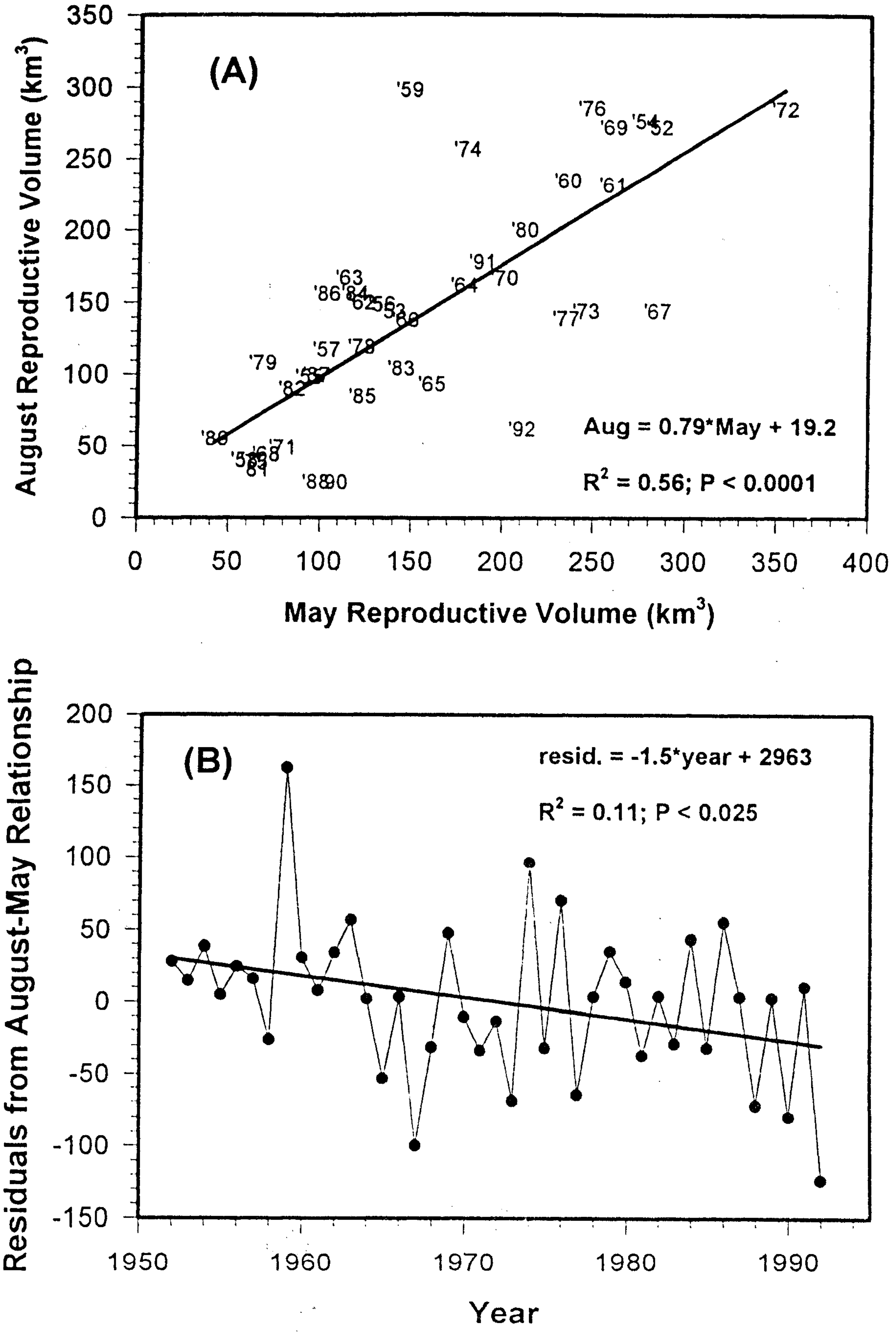
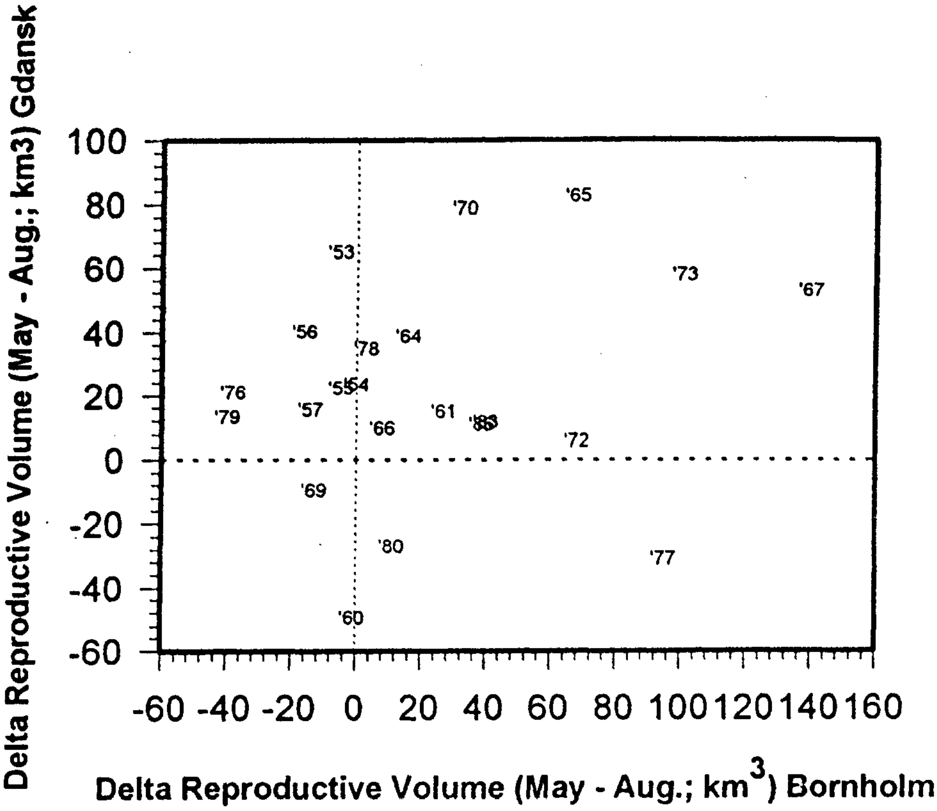

(A)
August Reproductive Volume (km³)
May Reproductive Volume (km³)
350
300
250
200
150
100
50
0
0
50
100
150
200
250
300
350
400
'59
'76
'69
'54
'52
'72
'74
'60
'61
'80
'91
'70
'64
'63
'86
'84
'62
'55
'56
'53
'66
'77
'73
'67
'57
'78
'79
'83
'65
'82
'87
'85
'92
'89
'71
'68
'58
'81
'88
'90
Aug = 0.79*May + 19.2
R² = 0.56; P < 0.0001
(B)
Residuals from August-May Relationship
Year
resid. = -1.5*year + 2963
R² = 0.11; P < 0.025
200
150
100
50
0
-50
-100
-150
1950
1960
1970
1980
1990

Fig. 2



Delta Reproductive Volume (May - Aug.; km3) Gdansk
Delta Reproductive Volume (May - Aug.; km^3) Bornholm
100
80
60
40
20
0
-20
-40
-60
-60 -40 -20 0 20 40 60 80 100 120 140 160
'53
'70
'65
'73
'67
'56
'78
'64
'76
'79
'55
'54
'57
'61
'83
'85
'66
'72
'69
'80
'77
'60

Fig. 3

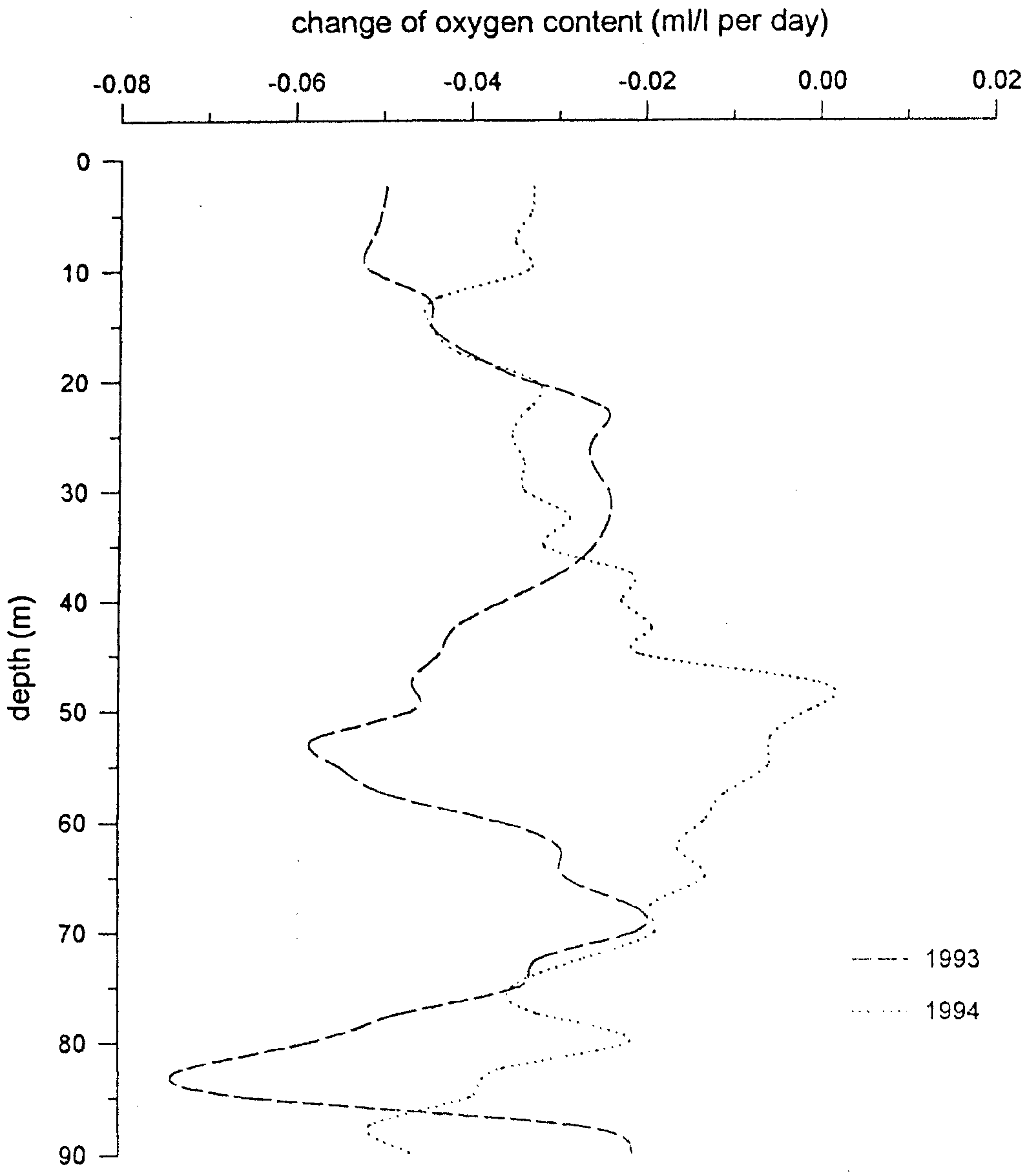

change of oxygen content (ml/l per day)
-0.08
-0.06
-0.04
-0.02
0.00
0.02
depth (m)
0
10
20
30
40
50
60
70
80
90
1993
1994

Fig. 4

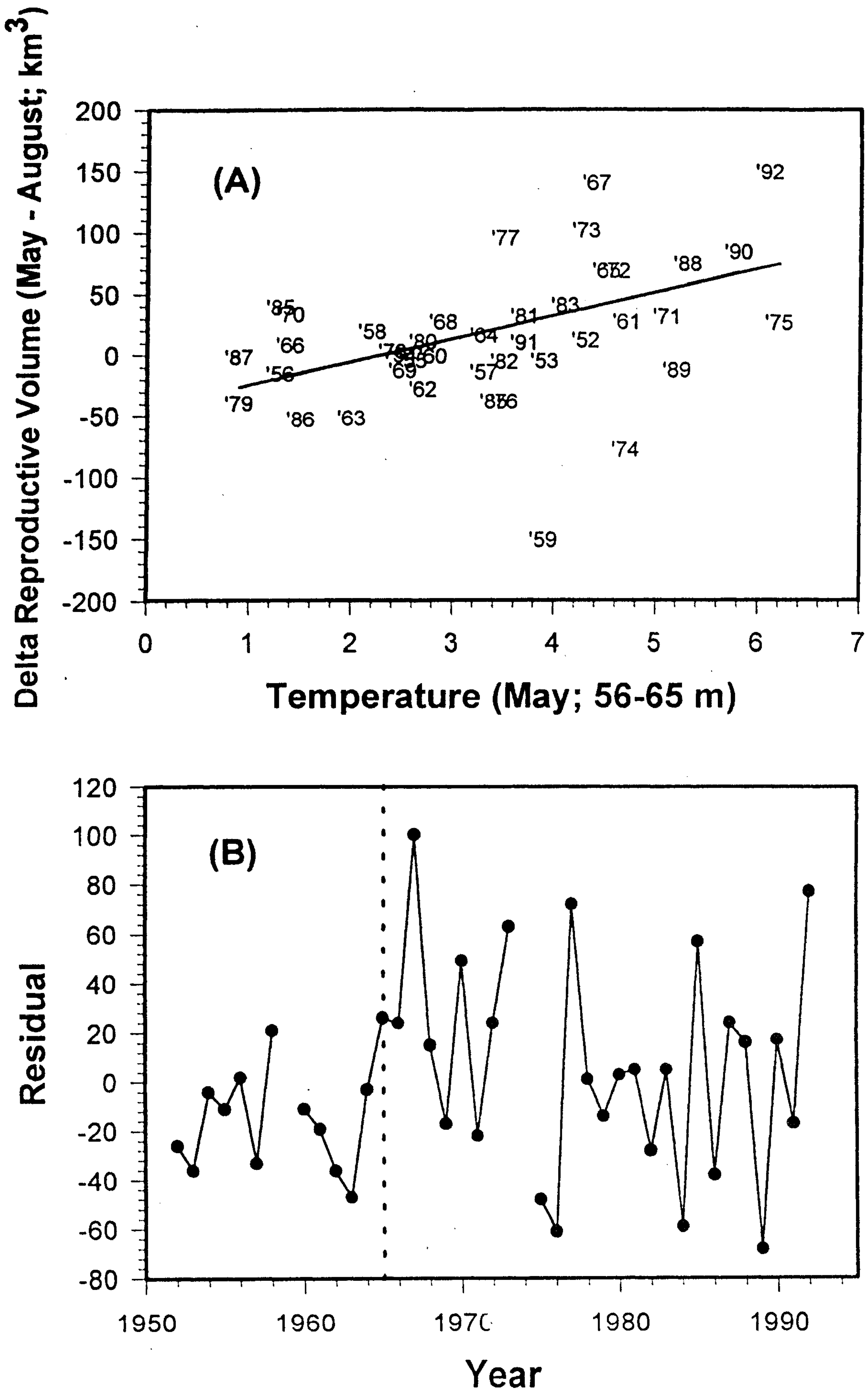

(A)
Delta Reproductive Volume (May - August; km^3)
200
150
100
50
0
-50
-100
-150
-200
0
1
2
3
4
5
6
7
Temperature (May; 56-65 m)
'92
'67
'73
'77
'90
'88
'65'72
'85
'70
'83
'81
'71
'61
'75
'58
'68
'64
'66
'91
'52
'78
'80
'84
'65
'60
'87
'82
'53
'56
'69
'57
'89
'62
'79
'85'76
'86
'63
'74
'59
(B)
Residual
120
100
80
60
40
20
0
-20
-40
-60
-80
1950
1960
1970
1980
1990
Year

Fig. 5

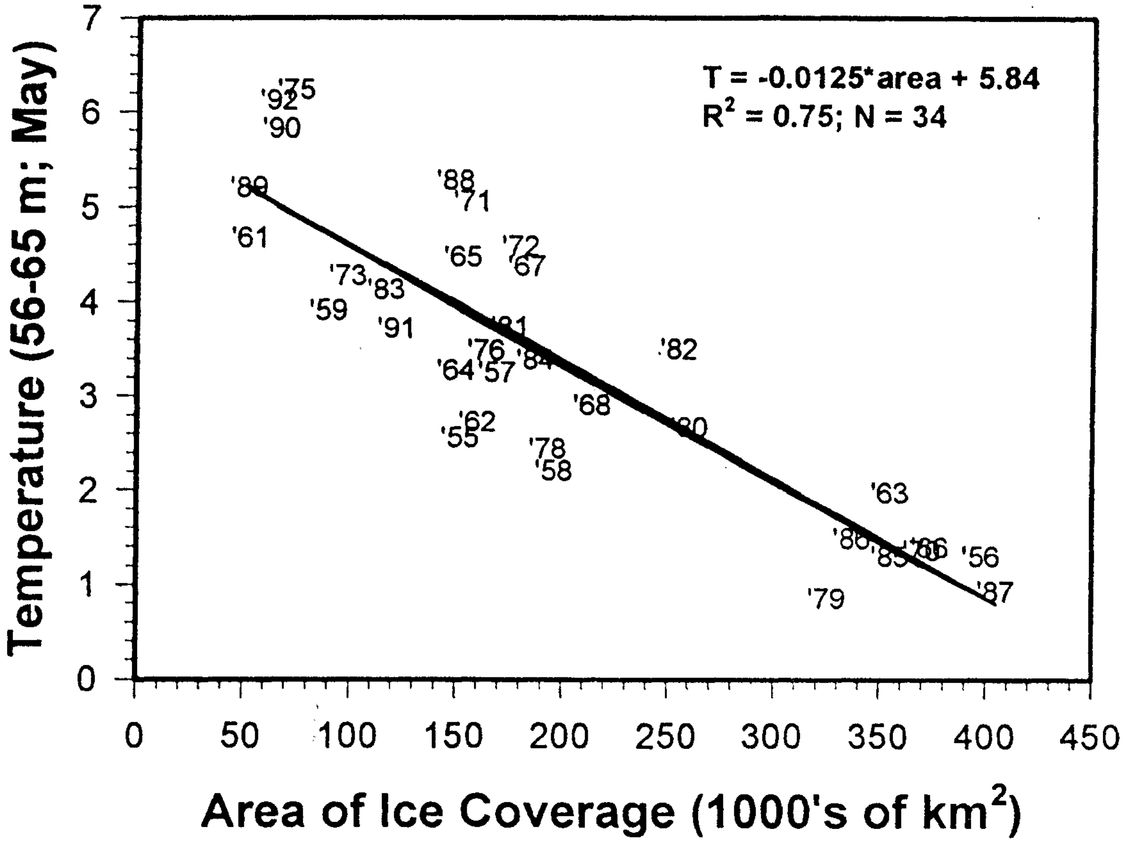

T = -0.0125*area + 5.84
R² = 0.75; N = 34
Temperature (56-65 m; May)
Area of Ice Coverage (1000's of km²)
0
1
2
3
4
5
6
7
0
50
100
150
200
250
300
350
400
450
'75
'92
'90
'89
'61
'88
'71
'65
'72
'67
'73
'83
'59
'91
'81
'76
'84
'64
'57
'82
'68
'62
'55
'78
'58
'80
'63
'86
'85
'66
'56
'79
'87

Fig. 6

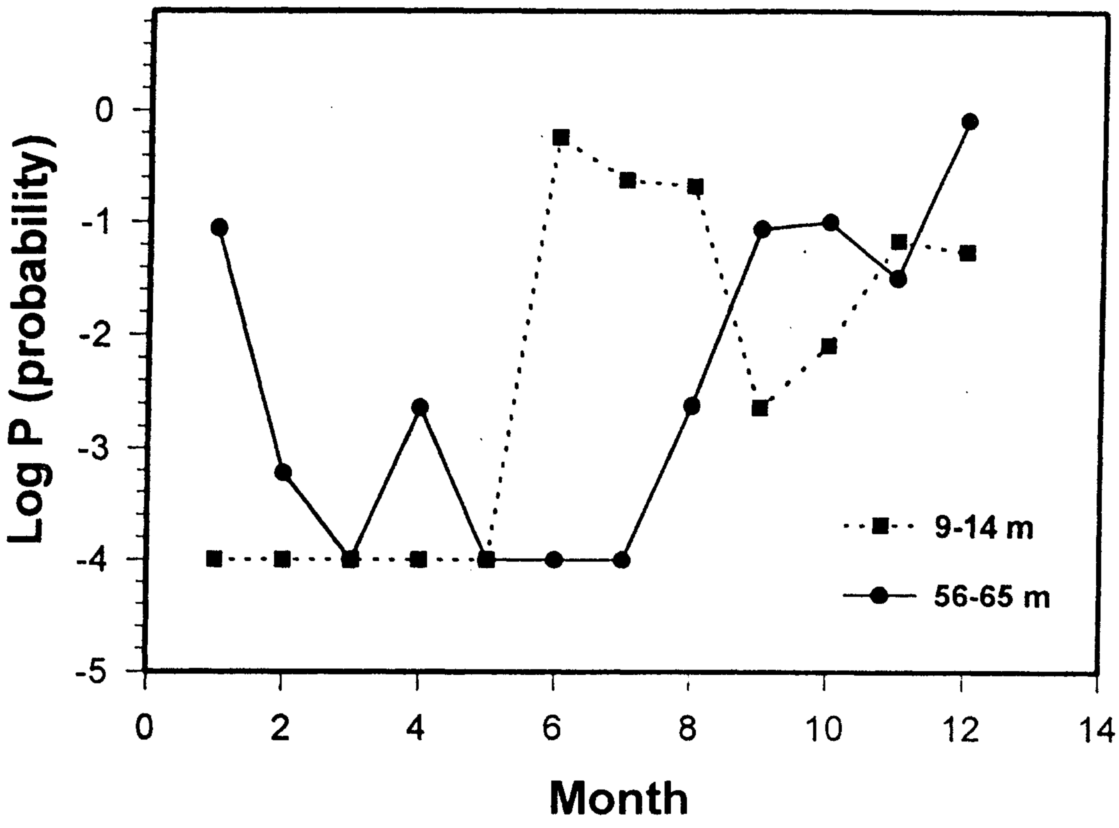


Fig. 7

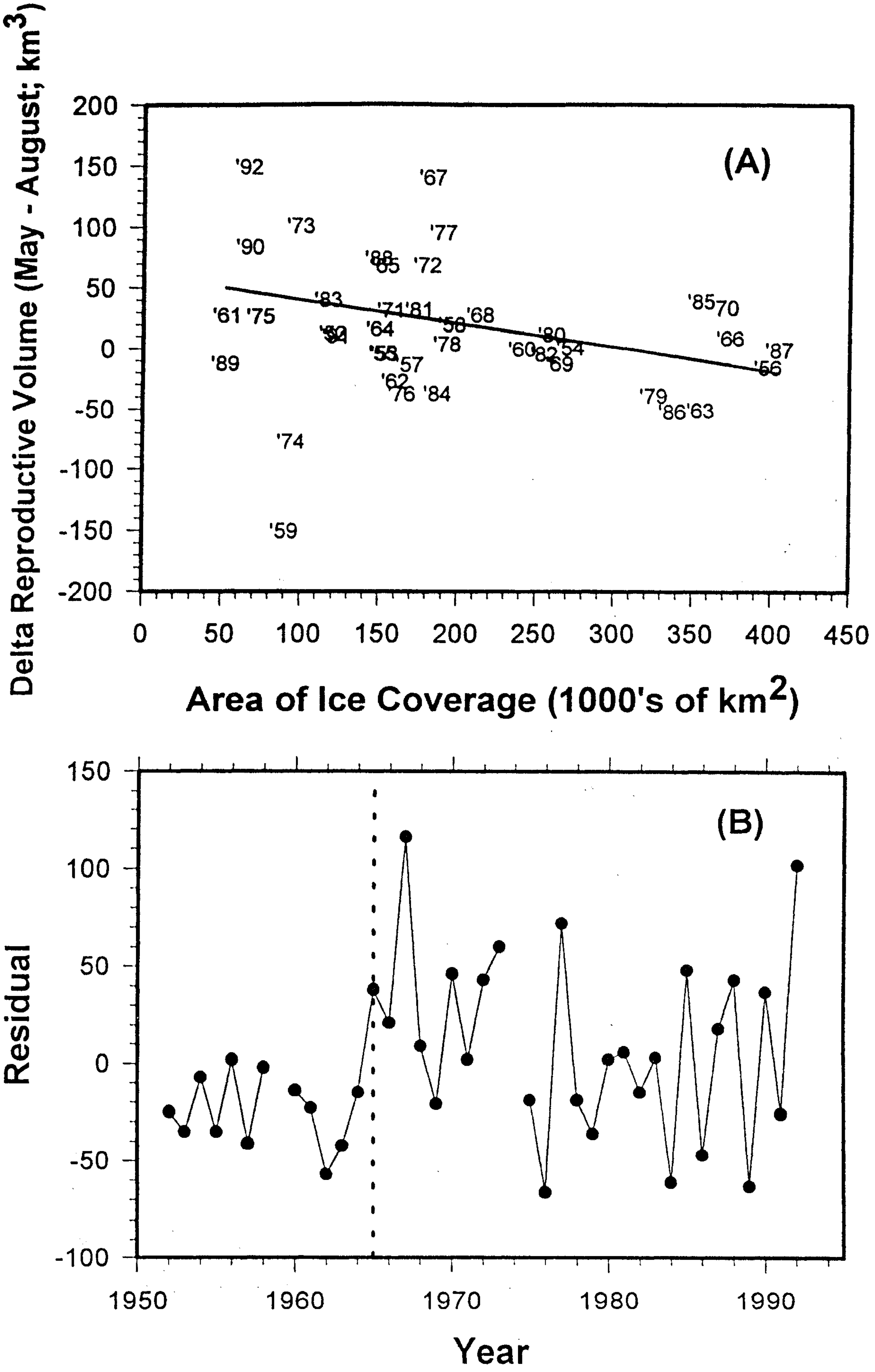

(A)
Delta Reproductive Volume (May - August; km^3)
Area of Ice Coverage (1000's of km^2)
200
150
100
50
0
-50
-100
-150
-200
0
50
100
150
200
250
300
350
400
450
'92
'67
'73
'77
'90
'88
'65
'72
'83
'71
'81
'68
'85
'70
'61
'75
'58
'64
'80
'66
'87
'78
'60
'82
'54
'55
'57
'69
'56
'89
'62
'76
'84
'79
'86
'63
'74
'59
(B)
Residual
Year
150
100
50
0
-50
-100
1950
1960
1970
1980
1990

Fig. 8

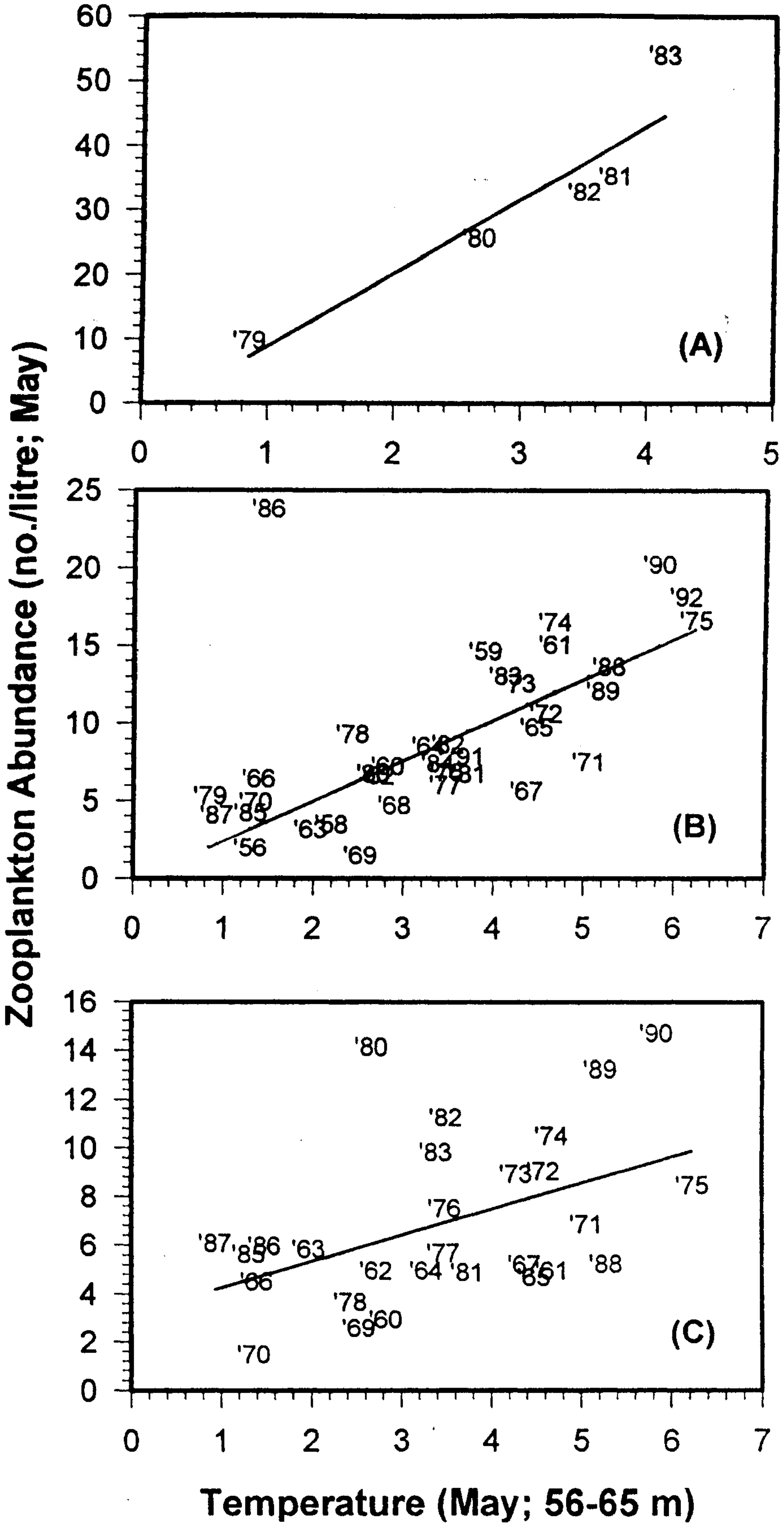

Zooplankton Abundance (no./litre; May)
Temperature (May; 56-65 m)
(A)
0
10
20
30
40
50
60
0
1
2
3
4
5
'83
'81
'82
'80
'79
(B)
0
5
10
15
20
25
0
1
2
3
4
5
6
7
'86
'90
'92
'75
'74
'61
'59
'83
'73
'88
'89
'72
'65
'78
'64
'62
'91
'84
'76
'81
'77
'71
'67
'66
'79
'70
'87
'85
'80
'60
'82
'68
'63
'58
'56
'69
(C)
0
2
4
6
8
10
12
14
16
0
1
2
3
4
5
6
7
'80
'90
'89
'82
'74
'83
'73
'72
'75
'76
'71
'87
'85
'86
'63
'77
'62
'64
'81
'67
'65
'61
'88
'66
'78
'69
'60
'70

Fig. 9

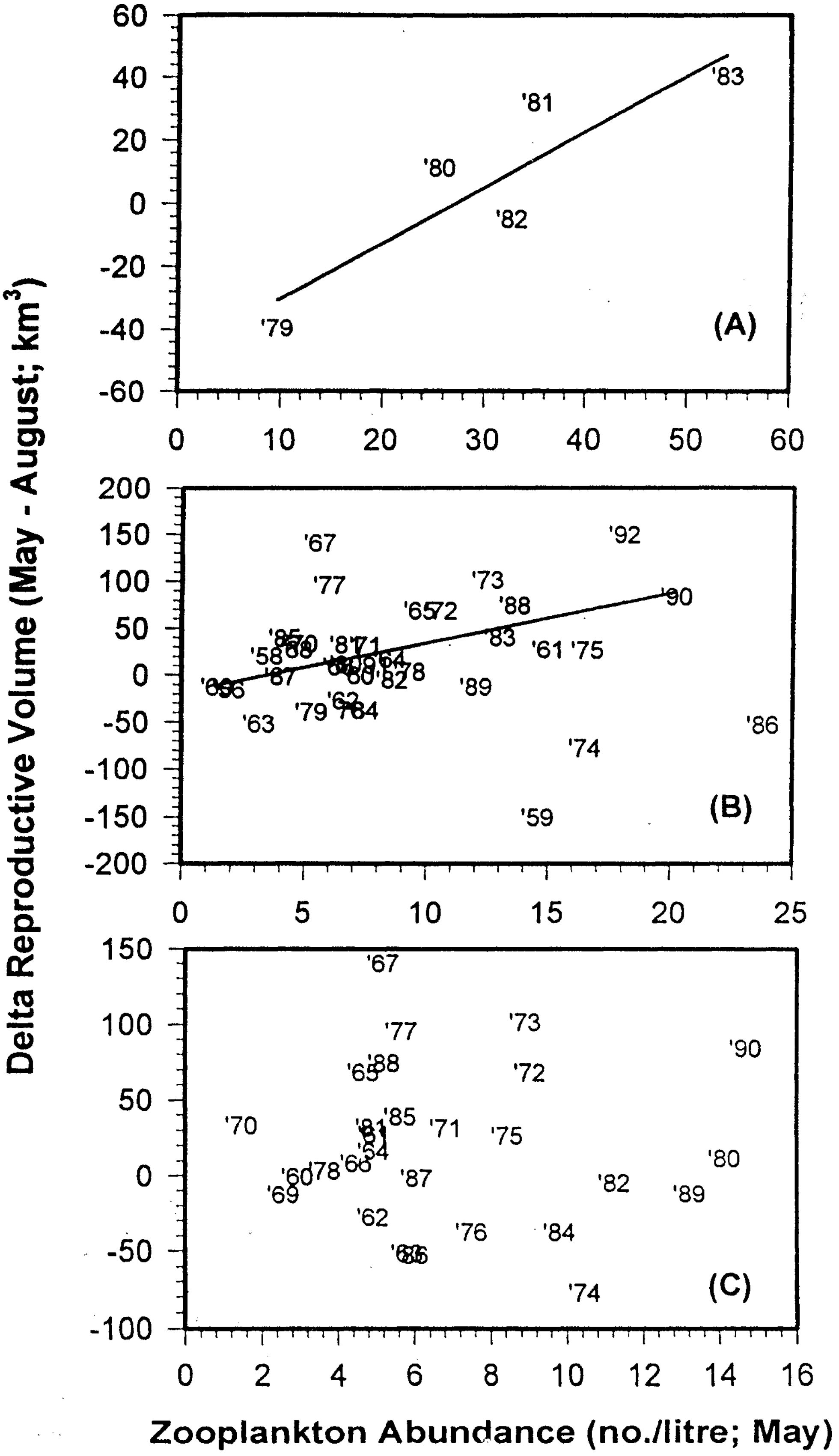

Delta Reproductive Volume (May - August; km³)
Zooplankton Abundance (no./litre; May)
(A)
'79
'80
'81
'82
'83
(B)
'67
'77
'92
'73
'88
'90
'65
'72
'83
'61
'75
'89
'63
'79
'62
'74
'86
'59
(C)
'67
'77
'73
'90
'65
'88
'72
'70
'85
'71
'75
'80
'82
'89
'87
'69
'62
'76
'84
'74

Fig. 10

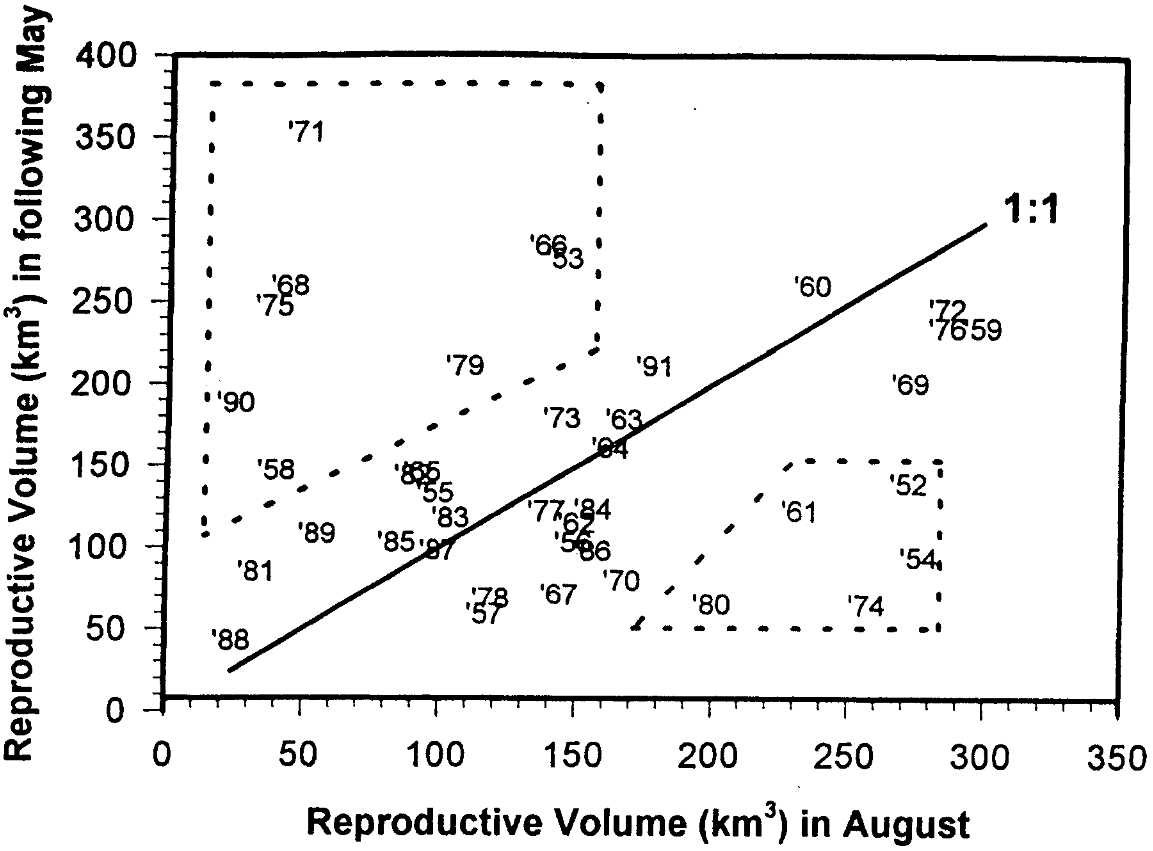

Reproductive Volume (km^3) in following May
Reproductive Volume (km^3) in August
1:1
0
50
100
150
200
250
300
350
400
'71
'66
'53
'68
'75
'60
'72
'76
'59
'79
'91
'90
'69
'73
'63
'64
'58
'82
'65
'55
'52
'83
'77
'62
'84
'61
'89
'85
'87
'56
'86
'54
'81
'70
'78
'57
'67
'80
'74
'88

Fig. 11

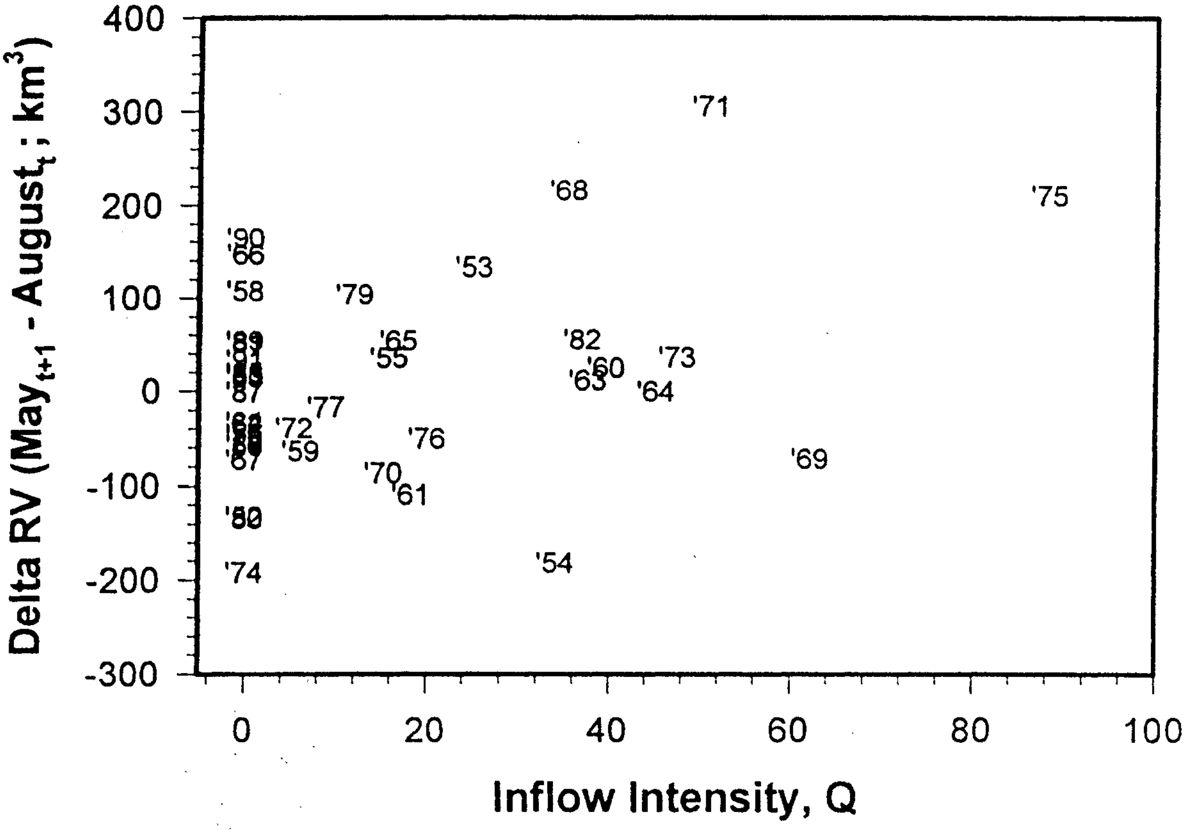

Delta RV (May$_{t+1}$ - August$_t$; km^3)
400
300
200
100
0
-100
-200
-300
0
20
40
60
80
100
Inflow Intensity, Q
'71
'68
'75
'90
'66
'53
'58
'79
'65
'55
'82
'73
'60
'63
'64
'87
'77
'72
'76
'59
'69
'67
'70
'61
'80
'74
'54

Fig. 12

References:

BAGGE, O., F. THUROW, AND E. STEFFENSEN. 1994. The Baltic cod. Dana 10: 1-28.

BARANOVA, T. 1995. The structure of spawning cod stock in the eastern Baltic during 1972-1995. ICES CM 1995/J: 9.

BERGSTRÖM, S., AND B. CARLSSON. 1994. River Runoff to the Baltic Sea: 1950-1990. Ambio 23(4-5): 280-287.

BIRD, D., AND J. KALFF. 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can. J. Fish. Aquat. Sci. 41: 1015-1023.

BODUNGEN, B. V., K. V. BROCKEL, V. SMETACEK, AND B. ZEITZSCHEL. 1981. Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea). Kieler Meeresforsch., Sonderh. **5**: 49-60.

CISZEWSKA, I. 1990. Quantitative changes in the Baltic mesozooplankton on the basis of monitoring within the 1979-1983 period. Oceanologia **29**: 77-90.

CISZEWSKI, P. 1985. Long-term trends in mesozooplankton biomass development in the southern Baltic. Oceanologia **22**: 63-70.

COLE, J. C., S. FINDLAY, AND M. L. PACE. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar. Ecol. Prog. Ser. **43**: 1-10.

ELMGREN, R. 1989. Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. Ambio **18**(6): 326-332.

FRANCK, H., AND W. MATTHAUS. 1992. The absence of effective major inflows and the present changes in the hydrographic conditions of the central Baltic deep water. Proc. 12th Symp. Baltic Mar. Biologists, Helsingør 1991. *In* Intern. Symp. Series, Olsen & Olsen, Fredensborg, 53-60.

GRAF, G., W. BENGTSSON, U. DIESNER, R. SCHULZ AND U. THEEDE. 1982. Benthic response to sedimentation of a spring phytoplankton bloom: process and budget. Mar. Biol. 67: 201-208.

GRANAT, L. 1990. Estimating atmospheric nitrogen loading to the Baltic Sea. Ambio Special Report 7, 20-21.

HAAPALA, J. 1996. Pers. comm. Dept. Geophysics, University of Helsinki, Helsinki, Finland.

HINRICHSEN, H.-H., AND K. WIELAND. 1996. Reproduction volume of Baltic cod in the Bornholm Basin estimated from single point measurements. ICES C.M. 1996/C+J:7. ICES CM 1996.

Iturriaga, R. 1979. Bacterial activity related to sedimenting particulate matter. Marine Biology **55**: 157-169.

Jonsson, P., and R. Carman. 1994. Changes in deposition of organic matter and nutrients in the Baltic Sea during the twentieth century. Marine Pollution Bulletin **28**(7): 417-426.

Kostrichkina, E. M. 1990. Zooplankton dynamics associated with changes of water regimes in the Baltic Sea during the recent 40 years (1949-1989). Plenary reports of VIII All-Union Conference on Fisheries Oceanology, Moscow; UNRO 1990.

Kullenberg, G., and T. S. Jacobsen. 1981. The Baltic Sea: an outline of its physical oceanography. Marine Pollution Bulletin **12**(6): 183-186.

Lahdes, E., K. Kononen, L. Karjala, and J-M. Leppänen. 1988. Cycling of organic matter during the vernal growth period in the open Northern Baltic Proper. V. Community respiration and bacterial ecology. Finnish Marine Research **255**: 79-95.

Leppänen, J-M., and J-E. Bruun. 1988. Cycling of organic matter during the vernal growth period in the open Northern Baltic Proper. IV. Ciliate and mesozooplankton species composition, biomass, food intake, respiration, and production. Finnish Marine Research **255**: 55-78.

Larsson, U., and Å. Hagström. 1982. Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophicated gradient. Mar. Biol. 67: 57-70.

MacKenzie, B. R., M. A. St. John, and K. Wieland. 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Mar. Ecol. Prog. Ser. **134**: 265-281.

Maske, H. 1994. Long-term trends in seston and chlorophyll *a* in Kiel Bight, Western Baltic. Cont. Shelf Res. **14**(7-8): 791-801.

Matthaus, W. 1978. Kieler Meeresforschungen 4.

Matthaus, W. 1990. Mixing across the primary Baltic halocline. Beitr. Meereskd., Berlin **61**: 21-31.

Matthaus, W. 1995. Natural variations and human impacts reflected in long-term changes in the Baltic deep water. ICES CM 1995/C:9.

Matthaus, W., and H. Franck. 1992. Characteristics of major Baltic inflows - a statistical analysis. Contl. Shelf Res. **12**: 1375-1400.

Matthaus, W., and H. U. Lass. 1996. The recent salt inflow into the Baltic Sea. J. Phys. Oceanogr. 25: 280-286.

Nielsen, T. G., and T. Kiorboe. 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. Limnol. Oceanogr. 39(3): 508-519.

NISSLING, A., H. KRYVI, AND L. VALLIN. 1994. Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. Mar. Ecol. Prog. Ser. **110**: 67-74.

NIXON, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia **41**: 199-219.

OLESEN, M. 1993. The fate of an early diatom spring bloom in the Kattegat. Ophelia **37**(1): 51-66.

OLESEN, M. 1995. Comparison of the sedimentation of a diatom spring bloom and of a subsurface chlorophyll maximum. Marine Biology **121**: 541-547.

PLIKSHS, M., M. KALEJS, AND G. GRAUMAN. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic Baltic cod. ICES CM 1993/J:22.

POMEROY, L. R., AND D. DEIBEL. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science **233**: 359-361.

RAHM, L., D. CONLEY, P. SANDÉN, F. WULFF, AND P. STÅLNACKE. Time series analysis of nutrient inputs to the Baltic Sea and changing DSi:DIN ratios. Mar. Ecol. Prog. Ser. **130**: 221-228.

RENK, H., J. NAKONIECZNY, S. OCHOCKI, AND S. GROMISZ. 1985. Long-term changes of phytoplankton and zooplankton biomass in southern Baltic. ICES CM 1985/L:28.

RENK, H., J. M. BRALEWSKA, Z. LORENZ, J. NAKONIECZNY, AND S. OCHOCKI. 1992. Primary production of the Baltic Sea. Bulletin of the Sea Fisheries Institute 3(127): 35-42.

RHEINHEIMER, G., K. GOCKE, AND H-G. HOPPE. 1989. Vertical distribution of microbiological and hydrographic-chemical parameters in different areas of the Baltic Sea. Mar. Ecol. Prog. Ser. **52**: 55-70.

ST. JOHN, M. A., H.-H. HINRICHSEN, A. LEHMANN, AND B. R. MACKENZIE. 1996. Oxygen in the deep basins of the Baltic Sea: the influence of convective mixing. ICES CM 1996/C + J: 2

SANDÉN, P., AND B. HÅKANSSON. 1996. Long-term trends in Secchi depth in the Baltic Sea. Limnol. Oceanogr., **41**(2): 346-351.

SANDÉN, P., AND L. RAHM. 1993. Nutrient Trends in the Baltic Sea. Environmetrics **4**(1): 75-103.

SCHULZ, S., W. KAISER, AND G. BREUEL. 1992. A comparison of biological data from 1976-1990 and 1991 - the influence of a warm winter. ICES CM 1992/L:19.

SEINA, A., AND E. PALOSUO. 1993. The classification of the maximum annual extent of of ice cover in the Baltic Sea 1720-1992. MERI No. 20. Fin. Inst. Mar. Res., Helsinki. 31 pp. (Finnish with English abstract).

SIDREVICS, L., R. LINE, V. BERZINSH, AND G. KORNILOVS. 1993. Long-term changes of zooplankton abundance in the Gulf of Riga. ICES CM 1993/L:15.

SMETACEK, V., K. V. BRÖCKEL, B. ZEITZSCHEL, AND W. ZENK. 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Mar. Biol. **47**: 211-226.

STIGEBRANDT, A., AND F. WULFF. 1987. A model for the dynamics of nutrients and oxygen in the Baltic proper. J. Mar. Res. **45**: 729-757.

TOWNSEND, D. W., L. M. CAMMEN, P. M. HOLLIGAN, D. E. CAMPBELL, AND N. R. PETTIGREW. 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms. Deep-Sea Research I, **41**(5-6): 747-765.

VIITASALO, M., I. VUORINEN, AND S. SAESMAA. 1995. Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. J. Plankton Res. **17**(10): 1857-1878.

WIELAND, K., U. WALLER, AND D. SCHNACK. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10: 163-177.

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 Nr. 266. 114 pp.

WIELAND, K. AND K. HORBOWA. 1996. Recent changes in peak spawning time and location of spawning of cod in the Bornholm Basin, Baltic Sea. ICES C.M. 1996/J:15.

WULFF, F., AND L. RAHM. 1988. Long-term, seasonal and spatial variations of nitrogen, phosphorus and silicate in the Baltic: an overview. Marine Environ. Res. **26**: 19-37.