Reconstructing the population dynamics of sprat (*Sprattus sprattus balticus*) in the Baltic Sea in the 20th century

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Long time-series of population dynamics are increasingly needed in order to understand human impacts on marine ecosystems and support their sustainable management. In this study, the estimates of sprat (*Sprattus sprattus balticus*) biomass in the Baltic Sea were extended back from the beginning of ICES stock assessments in 1974 to the early 1900s. The analyses identified peaks in sprat spawner biomass in the beginning of the 1930s, 1960s, and 1970s at around 900 kt. Only a half of that biomass was estimated for the late 1930s, for the period from the late 1940s to the mid-1950s, and for the mid-1960s. For the 1900s, fisheries landings suggest a relatively high biomass, similar to the early 1930s. The exploitation rate of sprat was low until the development of pelagic fisheries in the 1960s. Spatially resolved analyses from the 1960s onwards demonstrate changes in the distribution of sprat biomass over time. The average body weight of sprat by age in the 1950s–1970s was higher than at present, but lower than during the 1980s–1990s. The results of this study facilitate new analyses of the effects of climate, predation, and

anthropogenic drivers on sprat, and contribute to setting long-term management strategies for the Baltic Sea.

Keywords: Baltic Sea, historical data, population dynamics, sprat (*Sprattus sprattus balticus*).

Introduction

The developments towards practical implementation of an ecosystem-based approach to human use of marine resources (Backer and Leppänen, 2008; Siron *et al*., 2008; Garcia and Prouzet, 2009) are setting increasing demands on our understanding of the marine ecosystem functioning and the impacts of multiple drivers on the ecosystems (Curtin and Prellezo, 2010; Samhouri *et al*., 2011). Long-term datasets are recognized as valuable to improve our understanding of the ecosystem dynamics and possibly predict its future developments (O'Dor and Yarincik, 2003; Ainsworth and Pitcher, 2008; Poloczanska *et al*., 2008). This is because longer time-series usually include larger contrasts and cover different combinations of natural conditions and human pressures, which may facilitate disentangling the effects of individual drivers and identifying how they interact (Rose, 2004; Eero *et al*., 2011). Understanding past dynamics could indicate how the system might respond to future changes in particular drivers as a result of policy developments or expected changes in the environment (Hansson *et al*., 2007; MacKenzie *et al*., 2011a).

In order to gain understanding of the ecosystem, historical information is most useful when it simultaneously covers the performance of multiple key components and external drivers of the ecosystem. This could be the case for the central Baltic Sea, where a century-scale or longer-term information on several abiotic and biotic variables is available (e.g. Fonselius and Valderrama, 2003; Schneider and Kuss, 2004; Hagen and Feistel, 2005; Zillen *et al*., 2008). For the upper trophic level, the abundance of marine mammals and the population dynamics of a major predatory fish, i.e. cod (*Gadus morhua*), have been reconstructed back to the 1900s (Harding and Härkönen, 1999) and the 1920s (Eero *et al*., 2007; 2008), respectively. Additionally, some quantitative fishery information on cod is available since the 16th century (MacKenzie *et al*., 2007a). However, information on stock sizes of forage fish, i.e. sprat (*Sprattus sprattus balticus*) and herring (*Clupea harengus membras*), is currently available only from 1974 onwards, estimated from ICES stock assessments.

Sprat currently constitutes the largest biomass (ICES, 2011a) and is one of the most important fish species in the food web of the open Baltic Sea. It interacts with cod through predator–prey relations (Sparholt, 1994; Köster and Möllmann, 2000), competes with herring for food resources (Möllmann *et al*., 2005; Casini *et al*., 2011), and has important structural roles in the Baltic ecosystem, for example via trophic cascades down the food web (Möllmann *et al*., 2008; Casini *et al*., 2009). Present knowledge of sprat dynamics in the Baltic Sea is largely based on a pronounced increase in biomass from a very low level in the 1980s to a record-high stock size in the mid-1990s, due to reduced cod predation and favourable temperature conditions for sprat reproduction (Köster *et al*., 2003a; MacKenzie and Köster, 2004). It is largely unknown how the population would develop under different combinations of climate, predator abundance, and human pressures.

Relative fluctuations in sprat biomass in the Baltic Sea in the 20th century have previously been addressed (e.g. Ojaveer and Kalejs, 2010), however mostly qualitatively. The first objective of this study was to gather the information scattered in various national and international publications and reports, in different languages, that could be used to quantify sprat stock dynamics in the Baltic Sea prior to 1974. The compiled data included sprat landings and their age compositions, individual weight-at-age, and sprat egg abundance. In a second step, these data were used to produce quantitative estimates of stock size from the 1970s back to the early decades of the 20th century. From the 1960s onwards, the analyses were conducted separately for three subregions in the Baltic Sea in order to resolve area-specific developments in sprat biomass over time.

Material and methods

Extended analytical stock assessment

Sprat in the Baltic Sea is currently assessed in ICES as one stock unit, covering ICES Subdivisions (SD) 22–32 (see Figure 1). In the years 1977–1988, the ICES Baltic Pelagic Working Group assessed the sprat in three units, corresponding to SD 22–25, 26 and 28, and SD 27 + 29–32 (ICES, 1990). In this study, both the aggregated as well as the area-specific developments in the sprat stock were addressed. Accordingly, the input data for standard age-based analytical stock assessment were compiled by the three subregions, i.e. SD 22–25, SD 26 and 28, and SD 27 + 29–32, which were subsequently combined for the assessment covering the entire stock. The input data included total landings, landings in numbers-at-age, weight-at-age, maturity ogives, and tuning information. The analytical assessment covered the years from 1956 to the present.

Commercial landings-at-age

Sprat landings in 1956–1969 were extracted from national statistics by country (Supplementary material, Table S1) and were thereafter combined with data on age compositions (Supplementary material, Table S2) to obtain annual landings in numbers-at-age. For the years 1970–1976, landings-at-age data were available from a former ICES Working Group on Assessment of Pelagic Stocks in the Baltic (ICES, 1990), for the three assessment units. From 1977 onwards, landings-at-age by SD were extracted from the multispecies assessment database (ICES, 1997), updated with data from the ICES Baltic Fisheries Assessment Working Group reports.

Weight-at-age

Data on sprat mean weight-at-age were compiled for the years 1953–1976 for the three assessment units (Supplementary material, Table S3). For the years 1977–2010, weight-at-age data were extracted from the multispecies assessment database (ICES, 1997) and from the ICES Baltic Fisheries Assessment Working Group reports. To obtain the average annual weights-at age-for the entire assessment area (SD 22–32), data for the three assessment units were averaged within a year, weighted by respective landings. Weight-at-age in the stock was assumed equal to the weight-at-age in the landings, which is a common practice for this stock in the assessments performed by ICES (ICES, 2011a).

Natural mortality

Natural mortality (M) of sprat in the Baltic Sea is dependent on the abundance of its main predator, i.e. cod (Sparholt, 1994). Annual predation mortalities of sprat from 1974 onwards have been estimated by the ICES Working Group on Multispecies Assessment Methods (ICES, 2009). The average M of sprat for age groups 1–7 in SD 22–32 in 1974–2007 was highly correlated with the eastern Baltic cod spawning-stock biomass (SSB) (r^2=0.835, p<0.01). This regression was used to derive M values for SD 22–32 for the years 1956–1973 and 2008–2010, as cod SSB for these years was available (Eero *et al.* 2007; ICES, 2011a). The area-specific information on sprat M was extrapolated from the area-disaggregated multispecies assessments conducted for SD 25, 26, and 28 for the period 1976–2003 by the ICES Study Group on Multispecies Assessment in the Baltic (ICES, 2005), described in detail in Section B of the Supplementary material.

Maturity ogives

The constant age-specific maturity ogives used in ICES assessments (ICES, 2011a) were applied for all years and assessment units.

Assessment runs

The assessments were performed using the standard XSA (Extended Survivors Analyses) method, which is used in ICES to assess sprat in the Baltic Sea. Four assessments were conducted, which included (i) a combined run for the entire Baltic Sea (SD 22–32) and three separate runs for (ii) SD 22–25, (iii) SD 26 and 28, and (iv) SD 27 + 29–32. The tuning information for the assessment for SD 22–32 was from the acoustic surveys in autumn and spring in 1991–2010 and 2001–2010, respectively, as used by ICES (ICES, 2011a). In separate runs by subregions, the sum of the acoustic indices for respective SDs was used (ICES, 2011b). The assessment for SD 27 + 29–32 used the indices only from the autumn surveys, as the acoustic data for spring were unavailable for this area.

In the assessments, SSB was calculated for spawning time, i.e. applying a fraction of 0.4 of the natural and fishing mortality before spawning, as done in the assessments by ICES (2011a). The estimates of SSB from the analytical assessments are presented from 1960 onwards. This is because the information on age composition of landings for 1956–1959 was not fully representative for all areas (Supplementary material, Table S2) and only included information for age groups 1–6. The earliest cohort that was fully represented in the annual landings data for ages 1–10 was the 1955 year class, which allowed extending the recruitment (age 1) estimates back to 1956, based on the catch information for a particular cohort in respective years.

Spawner biomass based on egg abundance

Spawning areas for sprat in the Baltic Sea include the Baltic Proper and the western and central parts of the Gulf of Finland (Ojaveer and Kalejs, 2010). Among the different basins, the coverage of sprat egg abundance data for the years before the 1970s was best for the Gdansk Deep in SD 26. Earlier investigations have shown that sprat SSB in SD 26 and 28 is significantly correlated to the realized egg production in these areas (Köster *et al*., 2003b). In this study, the average sprat egg abundance during peak spawning (number of eggs m^{-2} in May–June) in SD 26 (STORE, 2003) was found to be significantly correlated to the total sprat SSB in the Baltic Sea (SD 22–32), based on data for 1974–1995 (r^2=0.414, p<0.01). This regression was used to derive proxies for sprat

SSB for selected years in the period 1931–1973, when egg abundance estimates for SD 26 were available (Supplementary material, Table S4). The historical sprat egg abundance estimates were mostly from Polish ichthyoplankton surveys, supplemented with data from German surveys in 1931 (Supplementary material, Table S4). Only the data from May until the first half of July were used, which correspond to peak spawning (Karasiova, 2002).

Results

Sprat dynamics in the Baltic Sea in the 1900s –1970s

The extended analytical assessment of sprat in the Baltic Sea (SD 22–32) identified peaks in SSB in the beginning of the 1960s and 1970s at around 900 kt (Figure 2a; Supplementary material, Table S5), which is similar to the SSB estimated for most of the 2000s. In the mid-1960s, the SSB was more than 50% lower, at about 400 kt. The proxies for SSB derived from egg abundance estimates confirmed the relatively higher sprat SSB in the early 1970s compared to the mid-1960s, although the absolute values for the early 1970s based on egg abundance estimates were lower than the estimates from the analytical assessment for these years. For the years 1945–1955, as well as for the late 1930s, egg abundance data suggest a relatively low SSB, at around 300–500 kt. The high average egg abundance in 1931 corresponds to a SSB at around 850 kt, i.e. similar to the analytical estimates for the early 1960s and 1970s (Figure 2a).

The estimates of sprat SSB relative to landings suggest a low overall exploitation rate of sprat in the Baltic Sea until the 1960s, when it gradually started to increase, corresponding to an increase in total landings (Figure 2b). In the period of low exploitation rate, sprat landings by both Germany and Poland, which were the leading sprat fishing countries in the Baltic Sea at that time, peaked in the first half of the 1930s (Figure 3). Polish landings in the early 1930s were comparable to those in the early 1960s (Figure 3), in line with a similar biomass estimated for the two time periods (Figure 2a). Sprat landings in the period from the late 1930s to the 1960s were low (Figure 3), in line with relatively low sprat egg abundance in these years (Figure 2a). Sprat landings in the beginning of the 1900s were comparable to those in the early 1930s, according to both Polish and German fisheries statistics (Figure 3).

In the years 1956–1974, the strongest year classes were formed in 1955, 1957, 1959, and 1967 (age 1 in subsequent years; Figure 2a; Supplementary material, Table S5). Average weight of sprat underwent an increasing trend from the 1950s to the 1990s in all age groups, after which weights dropped to their present low level (Figure 4). The average weight of young sprat (age groups 2–3) in the 1950s was as low as in the 2000s; however, the weight of older age classes (3+) was substantially higher in the 1950s compared to recent decades.

Area-specific developments in sprat spawner biomass

The magnitude and timing of changes in sprat SSB during the last five decades involve spatially distinct patterns, demonstrated by the area-disaggregated assessments conducted for three subregions in the Baltic Sea, i.e. SD 22–25, SD 26 and 28, and SD 27 + 29–32 (Figure 5). In the 1960s, the largest biomass of sprat was found in the northern Baltic Sea (SD 27 + 29–32), after which the SSB in this area drastically declined to a record-low level in the 1980s. In the period from the 1970s to the 1980s, SSB declined also in SD 26 and 28 and in SD 22–25, but less dramatically due to a previously relatively lower biomass in these areas. SSB in SD 22–25 and SD 26 and 28 started to recover in the second half of the 1980s, whereas in the northern Baltic Sea (SD 27 + 29–32), the biomass did not increase until the 1990s. In the mid-1990s, SSB reached a peak in all three subregions, resulting in a record-high overall stock level in the Baltic Sea. The biomass in SD 22–25 in the mid-1990s was particularly outstanding, being several-fold higher than in any other time-period from the 1960s to the present. From the second half of the 1990s to the 2000s, SSB in SD 22–25 rapidly declined. In contrast, the biomass in SD 26 and 28 and SD 27 + 29–32 has been relatively stable, exhibiting only a minor decline since the mid-1990s to the present (Figure 5).

Discussion

General uncertainties in historical fish biomass estimates

Estimates of historical fish biomass are almost always and inevitably associated with larger uncertainties compared to modern stock assessments. Modern assessments of fish stock status involve international systematic data collection programmes designed to support scientific advice on the management of the stocks. Data for pre-assessment years are most often fragmentary and incomplete, collected for different purposes and potentially difficult to interpret due to issues such as technological developments in fisheries and changes in data collection methods (Ojaveer and MacKenzie, 2007; Engelhard, 2008; Alexander *et al*., 2011). Nevertheless, there is a growing interest worldwide to recover evidence of the historical biomass of marine animal populations, and dedicated scientific programmes and expert groups have been formed to tackle this task (Pitcher, 2001; Holm, 2003; ICES, 2010). Despite the challenges involved, empirical evidence from the past is extremely valuable for developing baselines for population abundance and distribution (Van Keeken *et al*., 2007; Hardt, 2009; Lotze and Worm, 2009). Furthermore, a long-term perspective can help to gain knowledge of the ecosystem responses to various combinations of anthropogenic pressures and environmental drivers, other than those observed during the few recent decades covered by routine stock assessments (Cardinale *et al*., 2010; Eero *et al*., 2011). In general, estimates of historical fish biomass are intended to mainly be used to understand broad ecosystem dynamics, while they may be less suited to provide point estimates of annual stock sizes, which is the purpose of modern stock assessments. It is important that differences in the quality and purpose of historical and modern stock estimates are recognized and that historical estimates are used for purposes that match the expected uncertainties in the estimates.

Sprat stock estimates from the extended analytical assessment

Input data used in the analytical assessment to extend the biomass and recruitment estimates of the Baltic sprat from 1974 back to 1960 and 1956, respectively, covered the main distribution area of the stock (Supplementary material, Tables S2 and S3). Information on age composition of landings was available only from Poland, and the former Soviet Union and German Democratic Republic; however, these countries combined took from 65 to >90% of the total sprat landings in the Baltic Sea at that time. The Baltic sprat fishery in the 20th century has been conducted using a variety of fishing gears including nets, purse-seines, and bottom trawls. In the early 1960s, the pelagic trawls became dominant (Thurow, 1974). Therefore, the age structure of sprat landings in the years included in the analytical assessment is not expected to be seriously influenced by differences in gear selectivity. A general problem for estimating fish biomass using commercial catches is the accuracy of the reported catch statistics, which generally do not include discards, recreational catch, and unreported landings, which combined can, in some cases, form a substantial component of the total removals. For the Baltic Sea, a recent attempt to reconstruct total fish removals back to 1950 did not reveal substantial unreported landings or discards of sprat in the 1950s–1970s (Zeller *et al*., 2011), which would change the perception of stock size in these years.

A usual source of uncertainty in most fish stock assessments is natural mortality, which is often assumed constant over time. In the Baltic Sea, natural mortality of sprat used in ICES assessments is estimated based on the diet composition of cod, i.e. the main predator of sprat, and the resulting M values are strongly correlated with cod biomass in the eastern Baltic Sea. The M values used in the extended assessment for the 1950s–1970s are based on the assumption that cod was also the main predator of sprat at that time. Other potential predators of the Baltic sprat include seals, whose abundance in the 1950s–1970s was higher compared to the 1970s–1990s, although at a similar level as in recent years (MacKenzie *et al*., 2011b), and much lower compared to their abundance before the 1940s (Harding and Härkönen, 1999). The seal-induced natural mortality on Baltic sprat is thus not considered to have been substantially higher in the 1950s–1970s than at present. In the area-disaggregated assessments, additional uncertainty is introduced by the spatially explicit relative natural mortality rates, which were assumed similar in the 1950s–1970s to those estimated for the 1970s–2000s. Further, the approach of performing separate assessments for different subregions does not explicitly take into account redistribution of the stock during the year in relation to spawning and feeding migrations (Köster *et al*., 2001), as stock distribution back in time is determined only by catch-at-age data. Nevertheless, this approach has been shown to reasonably capture the major area-specific developments in the Baltic sprat (Köster *et al*., 2001).

Indications of sprat stock size from egg abundance and fishery landings

Proxies for sprat spawning-stock biomass derived from egg abundance data are probably associated with relatively larger uncertainties compared to the analytical estimates. The egg production method (Parker, 1980; Lasker, 1985) has frequently been used to estimate spawning-stock biomass of short-lived pelagic species. However, the method generally uses detailed information on parameters such as daily egg production rate, total seasonal egg production, and fecundity (Kraus and Köster, 2004), which were not available for the Baltic sprat for the historical time-period. Consequently, average egg abundance during peak spawning was used as a proxy for spawning stock size. Egg abundance estimates included in the analyses were only from the Gdansk Deep (SD 26), and the resulting SSB estimates may thus not be fully representative of stock size in the entire Baltic Sea. However, the SSB in SD 26 and 28 was strongly correlated with the SSB in the entire Baltic Sea (SD 22–32) ($r^2=0.804$, $p<0.001$) in the years covered by the analytical assessment (1960–2010). Another source of uncertainty in the SSB estimates based on egg abundance is the relatively low number of sampling stations for some years. The SSB estimate for 1931 should particularly be treated with caution as it is based on data from only four stations (Supplementary material, Table S4). However, the approximate SSB corresponding to average egg abundance in 1931 is supported by fisheries landings in the early 1930s.

In general, care should be taken when interpreting changes in fish landings, as these can be due to changes in fishing effort, technological developments, or market demand, in addition to changes in stock size. However, for stocks characterized by large fluctuations in recruitment production, such as sprat in the Baltic Sea, the many-fold fluctuations in landings (Figures 2b and 3) at short time-scales can hardly be explained by fishery developments alone (Elwertowski, 1979). The longest time-series of sprat landings were available for Germany and Poland, countries that took, by far, the largest proportion of the relatively high sprat landings in the first half of the 1930s. In the early 1930s, after the introduction of pair trawls (Meyer, 1942), both German and Polish fishers started to target sprat schools offshore (Kändler, 1949). A similar level of landings reported in the early 1930s as in the early 1960s in the Polish fisheries suggest that stock size in the two time-periods was similar, or could have been larger in the 1930s, when taking into account technological developments in these decades. Furthermore, sprat landings per vessel per day in the Polish fisheries in winter 1932/1933 were more than tenfold higher than in the mid-1950s (Elwertowski, 1957, 1979), which supports a relatively high sprat stock in the early 1930s.

Both German and Polish sprat landings were also relatively high in the early 1900s, when fishing technology was much less developed. Major technological developments in German sprat fisheries took place in 1918 with the introduction of the purse-seine. Before that, sprat was caught with nets (Meyer, 1947), whereas from the 1930s onwards, the fishery was mainly conducted with trawls (Meyer, 1942). Levels of landings in the early 1900s similar to those in the early 1930s suggests that stock size in these two periods was at least similar, or could have been larger in the early 1900s; however, no additional information is available to validate this.

Potential applications for the extended time-series of sprat dynamics

Previous studies addressing the development of sprat in the Baltic Sea in pre-assessment years have identified differences in year-class strength (Elwertowski, 1960), suggested time-periods of relative fluctuations in stock size (e.g. Elwertowski, 1957, 1979), and estimated biomass in parts of the Baltic Sea (Aps, 1989). The results of this study support the previous findings concerning (i) strong year classes formed in 1955, 1957, 1959, and 1967 (Kalejs and Ojaveer, 1989); (ii) a large biomass in the northeastern Baltic Sea in the early 1960 (Aps, 1989); and (ii) relatively high sprat landings in the early 1930s (Elwertowski, 1960). The main contribution of this study is integrating the fragmentary and qualitative information on historical stock developments into quantitative estimates covering the entire Baltic Sea, including the spatially resolved estimates, when possible.

The population structure of sprat in the Baltic Sea is not well understood (Ojaveer and Kalejs, 2010 and references therein). However, distinct developments in biomass and recruitment by subregions are apparent (Köster *et al.*, 2001). This was already recognized in the 1980s, when the Baltic sprat was assessed separately by three subregions, which was considered a compromise between the biological and practical aspects (Sjöstrand, 1989; Ojaveer and Kalejs, 2010). The extended time-series of sprat dynamics covers different environmental conditions (Fonselius and Valderrama, 2003) and cod abundance (Eero *et al.*, 2007, 2008), both in time and space. This facilitates new analyses of the relative importance of climate and cod predation and their interactions to determine sprat dynamics in the Baltic Sea. Resolving the impacts of climate and being able to predict future biomass is considered vital for the management of species with highly variable production rates, such as sprat in the Baltic Sea (MacKenzie *et al*., 2008). New information on sprat dynamics in the past could be useful for improving and validating the models of stock development under future climate change (MacKenzie *et al*., 2007b).

Several human pressures, which probably influence sprat in the Baltic Sea, have intensified during the 20th century. These include a substantial increase in nutrient loads from the 1950s to the 1980s (Wulff *et al*., 1990). Further, fishing pressure on sprat was low until the development of pelagic fisheries in the 1960s (Figure 2b). Little is known about how fishing interacts with other drivers on sprat. Also, it is unclear how increased nutrient concentrations influence the production of planktivorous fish in the Baltic Sea. New information on sprat stock dynamics extending back to the onset of these major human impacts could allow separating their effects from the impacts of climate and cod predation. Understanding the effects of anthropogenic drivers in combination with biological interactions and climate forcing is important in relation to the management goals for the Baltic Sea, which, amongst others, include a reduction in nutrient loads and implementation of sustainable fisheries (HELCOM, 2007).

In addition, the European Commission is currently aiming to take into account biological interactions in the new fisheries management plans being developed for the Baltic Sea. Sprat is one of the key species in the central Baltic foodweb as a major prey item for predatory fish, such as cod (Sparholt, 1994), and a predator on cod eggs (Köster and Möllmann, 2000). Further, through regulation of zooplankton and competition with the pelagic life stages of other species (such as herring, early life stages of cod) for zooplankton resources, sprat can be an important driver of the overall foodweb dynamic in the central Baltic Sea (e.g. Casini *et al*. 2009). In conclusion, new quantitative evidence of sprat dynamics under various combinations of natural and human drivers can contribute to developing an ecosystem-based approach and setting long-term management strategies for the Baltic Sea.

Supplementary material

Supplementary material is available at the ICESJMS online version of this paper. Section A provides information on literature sources and coverage of the input data used to extend the time-series of stock estimates of Baltic sprat. Section B provides details on the estimation of natural mortality of sprat, used in the extended analytical assessment. Section C includes the extended time-series of sprat spawner biomass and recruitment.

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Figure captions

Figure 1. Map of the ICES subdivisions in the Baltic Sea.

Figure 2. (a) Sprat spawning-stock biomass (SSB) and recruitment (R; numbers at age 1) in SD 22–32 estimated from the analytical assessment (VPA); and the estimates of SSB based on egg abundance. The error bars represent 0.95 confidence intervals of the SSB, predicted from a linear regression with the average egg abundance as a predictor variable. (b) International sprat landings (L) in the Baltic Sea (Hammer *et al.*, 2008 and updates from the Baltic Assessment Working Group) together with the estimated exploitation rate (landings divided by SSB). The vertical broken lines separate the time-period covered by ICES assessments (from 1974 onwards) from the historical estimates produced in this study.

Figure 3. Baltic sprat landings by Germany (SD 22–26; data from the annual national report series Jahresbericht über die Deutsche Fischerei) and Poland (SD 26; Laszczynski *et al.*, 1964; Elwertowski, 1979).

Figure 4. Annual mean weight of sprat in the Baltic Sea (SD 22–32) for age groups 2–6.

Figure 5. The spawning-stock biomass of sprat estimated from the area-disaggregated assessments for SD 22–25, 26 and 28, and 27 + 29–32.

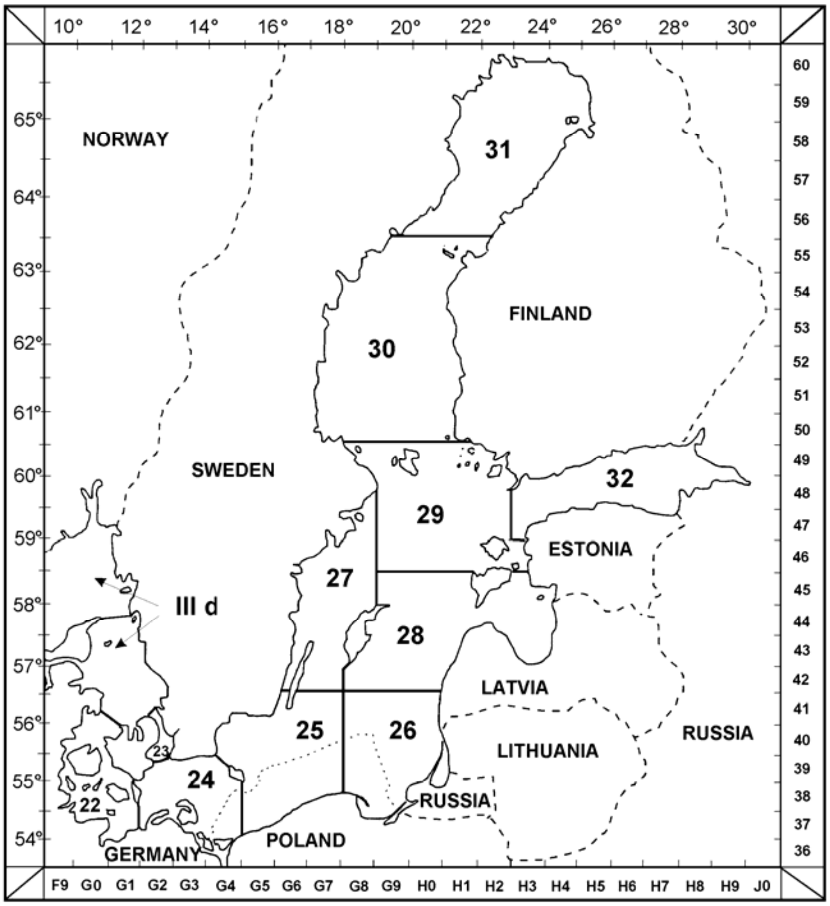
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Figure 1

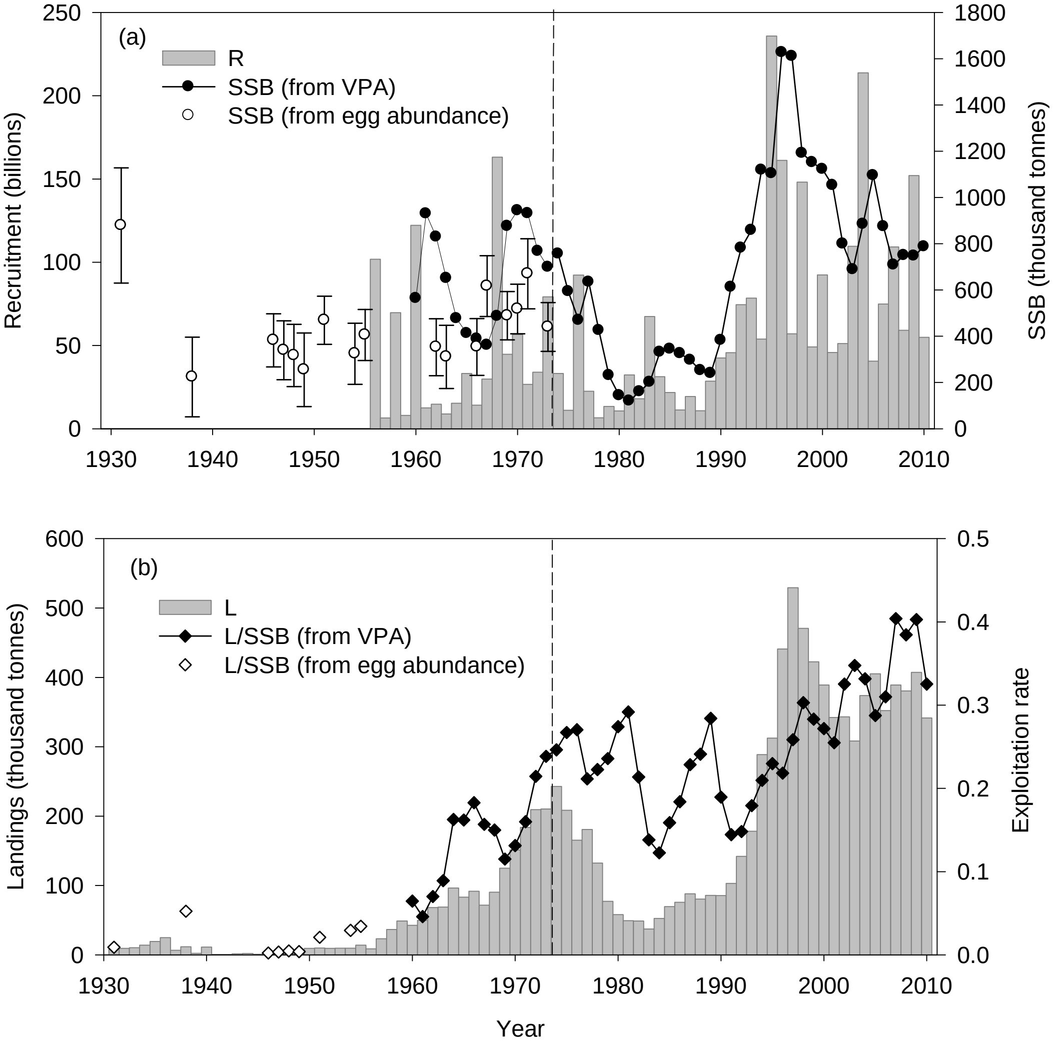
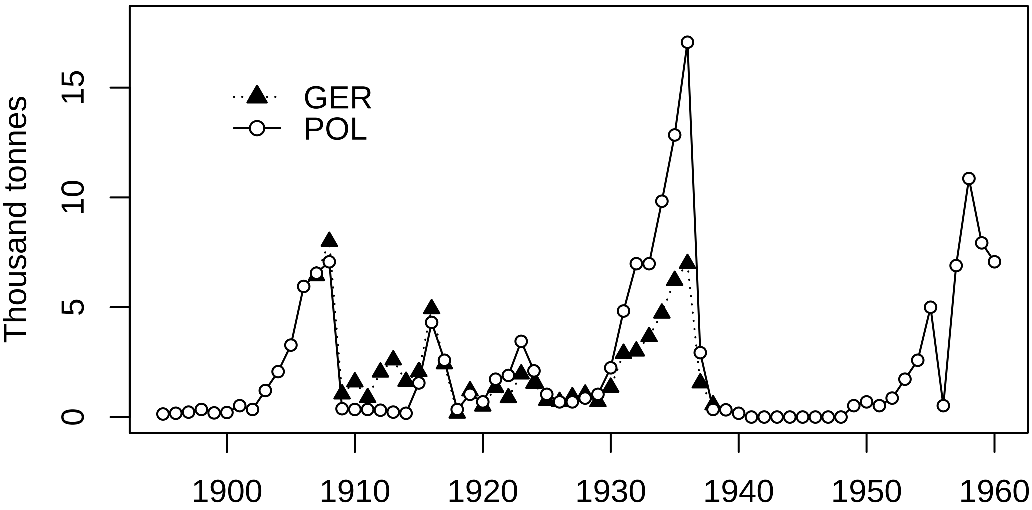
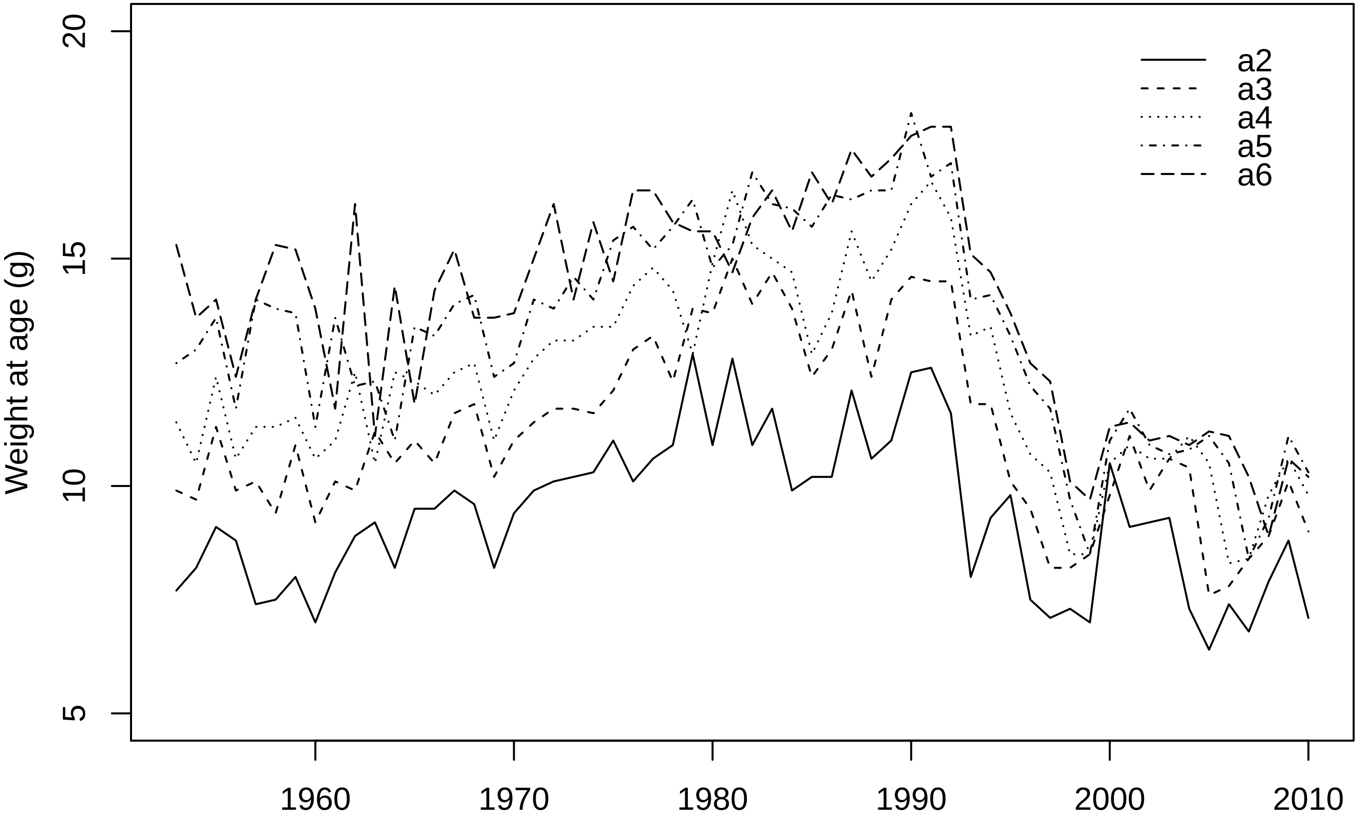
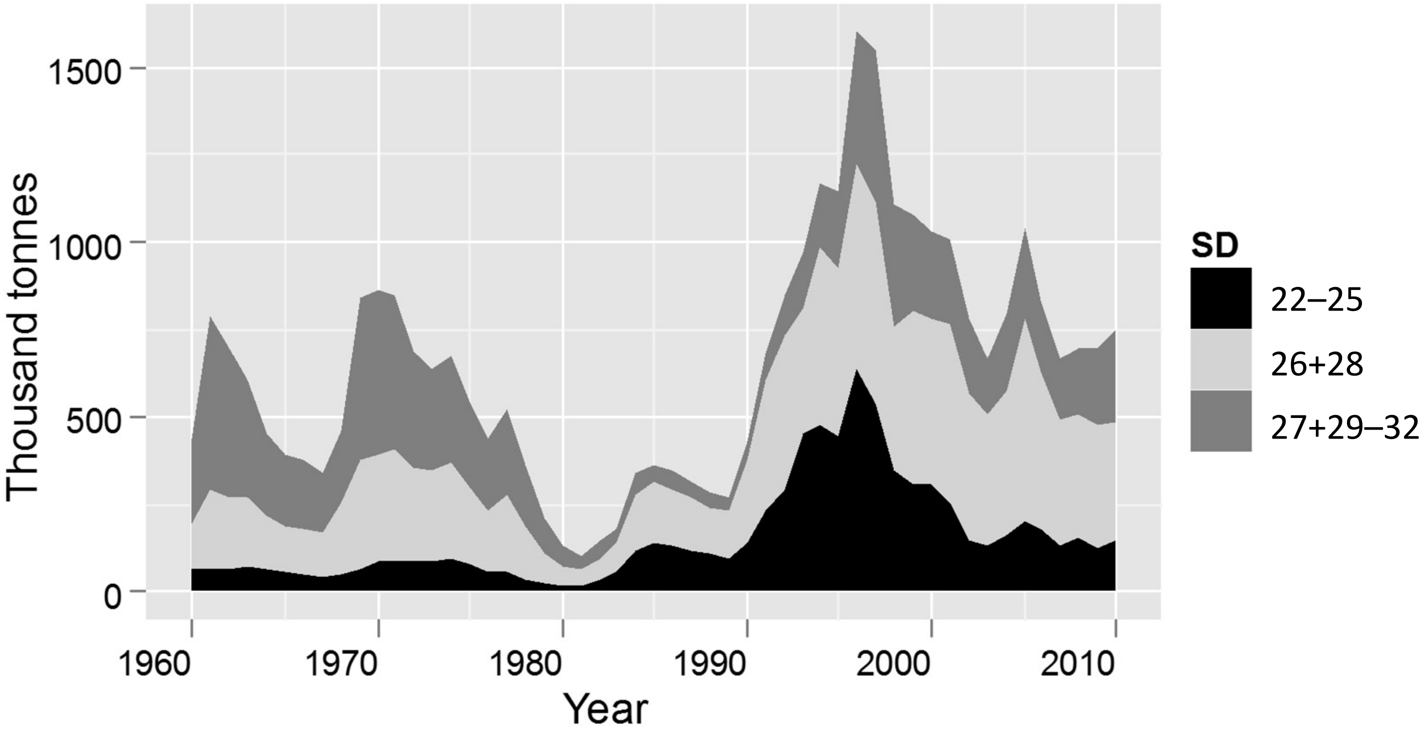

(a)
R
SSB (from VPA)
SSB (from egg abundance)
Recruitment (billions)
SSB (thousand tonnes)
0
50
100
150
200
250
0
200
400
600
800
1000
1200
1400
1600
1800
1930
1940
1950
1960
1970
1980
1990
2000
2010
(b)
L
L/SSB (from VPA)
L/SSB (from egg abundance)
Landings (thousand tonnes)
Exploitation rate
0
100
200
300
400
500
600
0.0
0.1
0.2
0.3
0.4
0.5
Year

Figure 2



GER
POL
Thousand tonnes
0
5
10
15
1900
1910
1920
1930
1940
1950
1960


Weight at age (g)
5
10
15
20
1960
1970
1980
1990
2000
2010
a2
a3
a4
a5
a6


1500
1000
500
0
Thousand tonnes
1960
1970
1980
1990
2000
2010
Year
SD
22–25
26+28
27+29–32