

# ICES WKHRPB Report 2007

ICES Baltic Committee  
ICES CM 2007/BCC:03  
REF. BCC

## Report of the ICES/BSRP Workshop on Recruitment Processes of Baltic Sea herring stocks (WKHRPB)

27 February – 2 March 2007

Hamburg, Germany



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## **International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer**

H. C. Andersens Boulevard 44–46  
DK-1553 Copenhagen V  
Denmark  
Telephone (+45) 33 38 67 00  
Telefax (+45) 33 93 42 15  
[www.ices.dk](http://www.ices.dk)  
[info@ices.dk](mailto:info@ices.dk)

Recommended format for purposes of citation:

ICES. 2007. Report of the ICES/BSRP Workshop on Recruitment Processes of Baltic Sea herring stocks (WKHRPB), 27 February - 2 March 2007, Hamburg, Germany. ICES CM 2007/BCC:03. 75 pp. <https://doi.org/10.17895/ices.pub.9123>

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## Executive summary

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The ICES/BSRP workshop on Recruitment Processes of Baltic herring stocks (WKHRPB) was attended by 11 scientists from 6 countries bordering the Baltic Sea, as well as one invited expert from a third country (Italy). The main task of the workshop was to analyze recruitment-environment relationships for the different Baltic Sea herring stocks, i.e. the Western Baltic (ICES D IIIa & SD 22-24), the Main Basin (SD 25-29&32 excl. Gulf of Riga), the Gulf of Riga, the Bothnian Sea (SD 30) as well as the Bothnian Bay (SD 31). For comparison, analyses were conducted for the Baltic sprat stock (SD 22-32) as well.

A number of biological as well as hydro-climatic variables were tested for their effect on recruitment using two different approaches. The first approach uses the logarithm of the ratio between the annual numbers of recruits (R) and spawning stock biomass (SSB) as a response for regression analyses. In the alternative procedure, first the effect of SSB on R was tested. If a significant effect of SSB on R could be demonstrated, recruitment anomalies (Ra) were used as a response, otherwise climate variables and other biotic factors were directly correlated to recruitment (R) itself. The relationship between recruitment and abiotic-biotic factors was analysed with Generalized Additive Models (GAMs), using the *mgcv* library of R. First, all the hypothesized predictors (selected a priori on the basis of known ecological, biological and physiological mechanisms) were included in the model and a backward stepwise regression based on the GCV information criteria was applied to find the best possible set of predictors. Stepwise selected predictors in the best model were then screened using the ecological criterion, implying that the sign of the relationship of a variable with recruitment is acceptable.

For all stocks except from the Gulf of Riga (GOR), spawning biomass was found to significantly affect recruitment. Parental effects of the stock structure (indexed by the biomass of ages 5+) on Ra and R were found for Western Baltic (WB) and GOR herring, respectively. An effect of adult condition (indexed as weight-at-ages 3+) on Ra was only found for the Main Basin (MB) herring. In most of the analyses (except WB using Rs and Bothnian Bay (BB) using Rs) hydroclimatic variables were important predictors in the environment-recruitment models. The Baltic Sea Index (BSI) was found to be a useful predictor except for GOR and BB. For all stocks temperature was a significant predictor of recruitment and if complete zooplankton data were available, i.e. MB, GOR and sprat, the food supply was a significant predictor, suggesting that a part of changes in climate and hydrography affect herring and sprat recruitment indirectly. Predation mortality by cod was included in the analyses for MB and sprat. While the analyses for herring yielded biologically difficult to explain results (recruitment increased with predation mortality) and the derived models were thus discarded (although listed in Annexes 4 and 5), cod predation on sprat was a significant predictor.

Exercises to include the identified important environmental variables in S/R-relationships for the use in stock predictions, could not be performed due to time constraints. Thus a follow-up workshop on Developing and Testing Environmentally-Sensitive Stock-recruitment Relationships of Baltic Herring and Sprat stocks [WKSSRB] was suggested

The group further reviewed existing knowledge on herring recruitment processes in the Baltic Sea. The review served together with the results of the statistical analyses as the basis for suggestions for future research on Baltic Sea herring recruitment processes. Important research fields identified are (i) changes in reproductive potential, (ii) spawning ground usage, as well as (iii) growth and survival of early life-history stages.

## 1 Opening of the meeting and adoption of agenda

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An ICES/BSRP Workshop on Recruitment Processes of Baltic Sea herring stocks [WKHRPB] (C. Möllmann\*, Germany, and M. Cardinale\*, Sweden) has met in Hamburg, Germany, from 27 February to 2 March 2007 to:

- a) review and report on existing knowledge on recruitment processes of the different Baltic Sea stocks;
- b) review existing and compile new time-series on recruitment as well as biotic and hydroclimatic variables;
- c) investigate direct and indirect effects of climate (e.g. changes in salinity/temperature, zooplankton abundance and composition, competition) on recruitment;
- d) evaluate the feasibility of including environmental variables into stock-recruitment relationships;
- e) suggest scientific studies to investigate the processes behind climate-related trends in recruitment.

The Co-Chairs Christian Möllmann and Max Cardinale welcomed the participants (Annex 1) and introduced the agenda (Annex 2) for the workshop. The following 4 major objectives for the meeting were identified:

- 1) Conduct a review on recruitment processes of the different Baltic Sea herring stocks;
- 2) evaluation of the effect of the abiotic and biotic environment of herring recruitment;
- 3) Construction of environmentally-sensitive stock-recruitment relationships;
- 4) Outline of a scientific project addressing Baltic Sea herring recruitment.

The agenda proposed by the co-chairs (Annex 2) was discussed and accepted by the participants. The first day of the workshop was devoted to presentations on different topics of herring recruitment. The planned statistical analyses on recruitment-environment relationships was the major task of the next two days. In parallel groups performing a review and outlying a potential research programme were formed. The last day was entirely devoted to the reporting work.

## 2 Introduction

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Herring is an essential component of the Baltic ecosystem, being a food item for cod and exerting predation pressure on zooplankton populations. The different populations are of considerable commercial value for the countries bordering the Baltic. While growth of herring has been intensively studied, studies on recruitment processes of Baltic fish stocks have in recent decades been exclusively directed to cod and sprat. However, recruitment trends drive a large proportion of the dynamics of the different stocks, which are partly of opposite direction. Indications exist that these trends in recruitment are due to direct (temperature, salinity) and indirect effects (food availability, competition with sprat stocks) of climate. The Baltic, as many other ecosystems, underwent shifts between different regimes affecting most likely also the herring stocks. Reliably predicting recruitment is essential for proper stock management and environmentally-sensitive stock recruitment relationships are essential for implementing precautionary and ecosystem approaches.

The workshop intended thus use the extensive amount of biotic and abiotic time-series as well as expertise to i) statistically investigate recruitment – environment relationships, ii) model environmentally sensitive stock-recruitment relationships, and iii) suggest future scientific studies to investigate the processes behind the relationships.

### 3 Presentations given by participants

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The first part of the presentations given at the first day of the meeting comprised (i) reviews on the knowledge on recruitment processes of Baltic herring stocks, (ii) a report on ongoing studies on larval feeding, growth and survival in the Vistula Lagoon, and (iii) a report on ongoing activities investigating recruitment-environment relationships within the BSRP. The second part of the presentation session comprises overviews on the data availability for the workshop and the methodology to be applied. Finally one presentation reported on an ongoing study related to recent recruitment failure of North Sea herring.

A review on the knowledge on recruitment processes has been given by Tiit Raid. The review is based on work conducted within SGBFFI and will be continued during this meeting. The review will report on knowledge on biotic and abiotic factors influencing spawning success and survival of every life-stage of herring. The final goal will be to identify the key factors influencing recruitment of the different Baltic herring stocks.

Ania Grzyb reported on her PhD-work related to growth and survival of herring larvae in the Vistula Lagoon. A strong difference in herring larvae abundance was observed between 2004, when densities exceeded 300 ind/m<sup>3</sup>, and 2005 with abundances one order of magnitude lower. No significant differences in temperatures were observed. Hence the high survival of herring larvae could be explained by a match of larval hatching with peak abundance of copepod nauplii, which compared to 2005 ca. tenfold higher. The high abundance of early larvae in 2004 resulted in slower growth and condition due to food limitation. In contrary in 2005 low larval abundance resulted in food-unlimited fast growth and good condition. The results point towards the importance of feeding conditions in the nursery areas for herring recruitment success.

Piotr Margonski provided the state of the BSRP work on finding zooplankton indicators of productivity. The relationship between herring recruitment and environmental factors has been investigated in the Gulf of Riga and the Baltic Proper. For the Gulf of Riga correlations with temperature and salinity were tested. As many abiotic factors were auto-correlated (e.g. surface and deep-water layer temperature in May, surface and deep-water layer salinity in May, and air temperature in February and surface water temperature in May), only one of these was used in the analyses. Spearman Rank Order Correlations showed that herring recruitment is positively correlated with temperature and negatively with salinity. Herring mean weight-at-age 1 is correlated positively with salinity only and no significant correlation for mean weight-at-age 0 was detected. As a further exercise a multiple regression model was constructed with all the zooplankton data which were significantly correlated with herring recruitment. However, this model is not be regarded as final because some of identified relations were notbiologically explainable (e.g. negative relationship of recruitment with *E. affinis* and *Evadne nordmanni* in August). The final version will include only those predictor variables with reliable biological meaning. The Winter Baltic Climate Index (WIBIX) was also tested against herring recruitment 30% of the variance. For the Baltic Proper significant and positive correlations between herring recruitment were found with summer salinity in the surface waters and total summer zooplankton biomass. Other relationships (e.g. with *Pseudocalanus acuspes* and sprat SSB) need further investigations.

Jari Raitaiemi reviewed studies on the reproductive ecology of herring in the northern Baltic areas. Several density-dependent effects and effects of the environment have been detected to influence reproductive success in these areas. These results will be incorporated into the review on Baltic herring recruitment processes.

The next two presentations by the co-chairs summarized shortly the data available from the ICES single-species and multispecies assessments. SSB and recruitment data are available for a range of Baltic herrings stocks from the Western Baltic until the Bothnian Bay (see below).

Michele Casini reported biotic and abiotic data available for the investigation of environment – recruitment relationships for the different herring stocks. These have been collected beforehand and will be supplemented by data from individual participants.

The strategy for the investigation and modelling of environment – recruitment relationships was outlined by Max Cardinale which is based on recent work conducted by Cardinale and Hjelm (2006) and Stige et al. (2006). Details on the methodology can be found in Chapter 6. Valerio Bartolino reported on the possibilities of recruitment modelling in R, which will be used during the workshop. He gave a general introduction to the software, its possibilities and advantages especially for the purposes of the workshop.

Finally, Joachim Gröger presented a statistical study on evaluating the reasons behind the recent recruitment failure in North Sea herring. The result show a combination of density-dependent and climate-effects (represented by the NAO) on this herring stock. A number of hypotheses for the underlying processes (e.g. variable drift patterns, food availability for early larvae, cannibalism) have been presented and are planned to be investigated in a scientific project.

#### **4 Review on recruitment processes of the different Baltic Sea herring stocks**

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The herring stocks in the Baltic Sea area are assessed by the following assessment units:

- Western Baltic Spring Spawners (WBSS) (Division IIIa and Sub-divisions 22-24)
- Central Baltic (Sub-divisions 25-27, 28.2, 29 & 32)
- Gulf of Riga (SD 28.1)
- Bothnian Sea (Sub- division 30)
- Bothnian Bay (Sub- division 31)

The Herring Assessment Working Group for the Area South of 62 °N (HAWG) assesses the Western Baltic herring, while the rest of the Baltic herring stocks are assessed by the Baltic Fisheries Assessment Working Group (WGBFAS).

Besides to the spring spawning herring, the stocks of autumn spawners occur in the Baltic. Since the early 1970s, the spring spawners have been dominating in all Baltic areas, while the abundance of autumn spawners strongly decreased in the 1980-1990s (Rechlin, 1991, Parmanne et al., 1994). However, there are indications that share of autumn spawners has increased again in the most recent period. It is unclear, whether those autumn spawners belong to the autumn spawning herring populations or are delayed spring spawners. In the Gulf of Riga the proportion of autumn spawners in trawl catches is around 1% and the separation is based on the differences of otolith structure.

Both Central Baltic herring and the Western Baltic herring comprise a number of local stocks (ICES, 2001), but are regarded as open sea stocks. All other Baltic herring stocks belong to the gulf herrings.

The majority of gulf herrings spend all year in the big gulfs, while open sea stocks perform regular annual migrations to and from spawning grounds located along the coasts of the Baltic Proper as well as partly in gulfs.

The available information on reproduction and recruitment formation processes of different herring stock is unequal. Data are particularly scarce with respect to Bothnian Bay herring.



## 4.1 Western Baltic Spring Spawners (WBSS)

### Distribution

WBSS are distributed in the Kattegat/Skagerrak [Div. IIIa], and the Western Baltic [Sub-Div. 22-24] areas, spawning takes place in spring on spawning sites around the Danish Islands and along the German coast, mainly in Greifswalder Bodden/Rügen area (Parmane et al. 1994).

### Migration pattern

The North Sea autumn spawners enter Division IIIa (Skagerrak and Kattegat) as larvae (Anon. 1977/H:3, Bartsch et al 1989, Johannesen and Moksness 1991) and migrate back to the North Sea with an age of 2-3 years (Anon. 1991/Assess 15 and Johansen 1927). After spawning during their feeding migration at the age of 2 years (Aro 1989, Biester 1979 and Weber 1975), the Western Baltic spring spawners enter Division IIIa through the Sound and Belt Sea and spread out into the Western part of the Skagerrak and the Eastern North Sea. Towards the end of summer the herring aggregate in the Eastern Skagerrak and Kattegat before they migrate to the main wintering areas in the southern part of the Kattegat, the Sound and the Western Baltic (Anon. 1991/Assess 15).

### Spawning

The main spawning area is the waters around the Rügen Island (Greifswalder Bodden). Depending on the ice coverage the spawning season lasts from around March to May. At the beginning of the spawning season the arriving herring swarms are characterised by older and bigger fish (Klinkhardt, 1996).

The following parameters are characterising the spawning herring in the waters around Rügen island:

- Water depth for spawning 1-6 m (Klinkhardt 1996)
- Minimum salinity for spawning 4 promille (Klinkhardt 1996)
- Minimum temperature for spawning 4 °C (Klinkhardt 1996)
- Fecundity 10,000 - 100,000 eggs (Below 1979)
- Time before hatching about 7 days (Klinkhardt 1986)
- Length when hatching 5.5 - 7.3 mm (Klinkhardt 1986)
- Manifestation of first day
- ring on otoliths 4.5 days (Klinkhardt 1996)
- Time to spend yolk-sack 6.5 days (8 °C) (Klinkhardt 1996)
- Growth of Larvae 0.3 mm/day (Biester 1979)
- Rügen Herring Larvae Survey (RHLS)

The Rügen herring larvae survey (RHLS) is at present the only herring larvae survey in the Western Baltic. The survey is conducted by the German Institute for Baltic Sea Fisheries, Rostock, and its predecessor since 1977 in the Greifswalder Bodden and Stralsund. These waters between Rügen island and the mainland are known to be the major spawning site of the Western Baltic spring spawning herring stock (WBSS). Sampling takes place with a Bongo-net on 35 fixed stations and is weekly repeated during most of the spawning season. Additional hydrographic parameters are recorded.

During the last decade, the RHLS aimed at delivering a fishery independent recruitment estimate for the WBSS assessment conducted by the ICES Herring Assessment working group (HAWG). The resulting N30 index (extrapolated abundance of larvae at 30 mm length) has shown to reliably predict very strong year classes, however it failed to predict year classes of intermediate strength.

## 4.2 Central Baltic (SD 25-29 & 32 excl. Gulf of Riga)

### Distribution

Central Baltic Spring Spawning herring is distributed in Sub-Divisions 25-29 (excluding Gulf of Riga/SD 28.1) and 32.

### Migration pattern

Tag recaptures indicated that feeding migration during autumn and winter is confined to the Bornholm basin (Sub-division 25). However, occasional recaptures has also been reported from Sub-division 24 and north of the island Öland, i.e. in the Sub-division 27 (Otterlind 1978).

The spawning ground of the coastal herring (**Sub-division 25 and 26**) are situated near the coasts from Poland till Lithuania including the Gulf of Gdansk and the Vistula Lagoon. After spawning coastal spring spawning herring take the feeding migrations to the open waters of the southern Baltic where they mix with open sea and autumn populations. Part of them migrate to the Danish straits and North Sea. The most of these migrating part of herrings are naturally marked with nematode *Anisakis simplex*, which they infested there. After feeding period they migrate back to the traditional spawning grounds closing their biological cycle.

Results from tagging along the Swedish coast (**Sub-division 27**) in the 1960s revealed a distinct southbound migration towards the Bornholm basin where the Swedish spring spawning herring mix with other stocks (Otterlind 1978, Aro 1989).

Large part of the open sea herring (**Sub-division 28**) performs spawning migrations to the spawning grounds along the Lithuanian and Latvian coasts in March-April. A part of the open sea herring spawns in the Gulf of Riga. After spawning the herring returns to the open sea. The Gulf herring is wintering and spawning in the Gulf of Riga. After spawning some part of this herring migrates to the nearest parts of the open sea area for feeding.

The adult stock component in the Archipelago Sea (**Sub-division 29**) mainly migrates after spawning to the south into the Baltic sea proper and also to the north into the Bothnian Sea. Herring returns again for spawning in the next year. Part of young herring stay in the Archipelago Sea also in autumn and winter.

A part of adult stock in the Gulf of Finland (**Sub-division 32**) migrates after spawning to the Baltic Sea proper, and returns in winter for spawning in the next spring. Young herring mainly stays in the Gulf during the whole year.

### Spawning

Spring spawning at the Swedish coast (**Sub-division 25**) is concentrated to the northern archipelago of the Hanö Bight in April - May. Scuba diving studies indicate that spawning is confined to temperatures between 5.5 to 15 °C and occurs in very shallow waters from 0.5 to 5.5 m (Elmer 1982). Eggs are deposited mostly on *Zostera marina* but also on other phanerogams and benthic algae (e.g. *Fucus vesiculosus*). Samples from the fishery in recent years indicate a progressively lower length at first maturity and often malformed gonad development.

Further spawning grounds of spring spawning herring are accommodated along the whole Polish coast from the Pomerania Bay on the west to the Gulf of Gdansk (**Sub-division 25 and 26**), including the Vistula Lagoon. It is considered that these spawning grounds are used merely by so called Southern coast herring (ICES 2003). Three assessments of three separate Central Baltic stock units revealed that Southern coast herring is the most distinctive of them according to relative year-class strength (ICES 2003) The spawning period continues from

March (sometimes from the end of February depending on water temperature) mostly till the first half of May. In the western part of Polish coast it starts about two weeks earlier. The spawning fishes are caught mainly over 6 to 12 m of bottom depth. The roe is laid on the vegetation, sand, gravel, stones, and also on underwater artificial buildings and barriers. The maturation is reached in the second year of life (about 90 % of year class total number) with total fish length about 14 – 16 cm. The growth rate of these herrings decreases eastward.

Spring herring of the open part of the **Sub-division 28** spawns at the coasts of Saaremaa and other islands west of Estonia, at the Latvian open sea coasts and in the Gulf of Riga. Spawning period lasts from April to June. At the Latvian coast of the Baltic Sea *Furcellaria lumbricallis* was considered to be the most important spawning substrate. In 1980s after two accidents of oil tank ships the abundance of *F. lumbricallis* drastically decreased. In some locations previously known spawning grounds were totally lost. The renascence of the spawning grounds was very slow and only in the end of 1990s the situation on them was estimated as satisfactory. The spawning intensity at the Latvian coast of the Baltic Sea is much lower than in the Gulf of Riga. The catches of herring by trap-nets are 20-30 times lower than at the Latvian coast of the Gulf of Riga. After spawning the stock feeds in the open Baltic, probably mainly in the areas of high biological productivity west of the Irbe Sound and Saaremaa isle. Supposedly the stock performs only rather short migrations.

A certain component of the herring stock of **Sub-division 28** is distributed in the near-coast areas of the Gotland Island, west of the Gotland Deep. The data on this component are very insufficient.

In the **Sub-division 29** spawning occur during May and June mainly. The preferred temperatures range from 4 to 15 °C (e.g. Rannak, 1971, Aneer 1989). Eggs are deposited on algae (typically *Chorda filum*, *Pilayella littoralis*, *Ceramium* sp. and *Furcellaria* sp.; Rannak, 1954, 1959, 1971, Rajasilta et al., 1989), on available phanerogams, on blue mussels and even on sand and gravel from the water surface down to 20 m depths (Aneer 1989). Egg mortality has been estimated higher in the presence of filamentous algae (Aneer 1989). Egg density is generally low averaging 10,000 eggs per m<sup>2</sup> or 200 g/m<sup>2</sup>. Spawning beds are restricted to shallow waters along the shores but could cover long distances (km). Only 10 % of the estimated suitable shallow waters were occupied. (Aneer 1989, Raid, 1987).

Nearly all herring in the **Gulf of Finland (Sub-division 32)** are spring spawners. The spawning period is long. In early spring the spawning starts in the end of April, but usually in the first half of May. The main spawning months are May and June. The common length of herring is 15 – 18 cm. Fast-growing and old herring spawn first, slow growing and young herring later. Spawning takes place in shallow water along the whole coast. Usual spawning depth is 1 – 5 m. Spawning places are often in sounds or in underwater slopes with hard bottom covered by vegetation. Spawning begins in early spring in shallow water, even in the depth of 20 cm, and moves gradually deeper when water gets warmer. In summer spawning may take place even in the depth of 20 m. At the beginning of spawning period the temperature of the water is about 5 °C and at the end 15 °C (Parmanne et al. 1997).

A part of adult stock in the Gulf of Finland migrates after spawning to the Baltic Sea proper, and returns in winter for spawning in the next spring. Young herring mainly stays in the Gulf during the whole year (Parmanne, 1990).

The **Vistula Lagoon** is one of the main spawning grounds of Baltic herring in the southeastern Baltic Sea. Krasovskaya (2002) summed up changes in herring spawning in the Vistula Lagoon during the 1950-2000 period. Coastal spring spawners constitute from 94 to 98% of the total herring catches in the lagoon. Autumn herring spawning are also observed but always in low abundances. Herring enter lagoon only to spawn and leave immediately after. The presence of herring schools in the lagoon varied from 34 to 104 days throughout the 1950-

2000 period and spawning extended from February 12 to June 25 in different years (March 24-May 27, on average).

The principal factor which has a prevailing effect on spawning timing is the time of ice breakup and clearing from the lagoon, which is related to the severity of the preceding winter. Average water temperature within the spawning period ranged from 7.7 to 14.1°C and it may rise quickly from about 1°C the beginning to more than 19°C during the last spawning waves. The distinct shift of herring spawning in the lagoon towards an earlier time and at lower temperatures was observed in spite of the positive trend of mean water temperature in spring (Krasovskaya 2002).

### 4.3 Gulf of Riga

#### Distribution

Gulf of Riga herring is a separate population of Baltic herring (*Clupea harengus membras*) that is met in the Gulf of Riga (Sub-division 28.1 - the eastern part of ICES Sub-division 28).

#### Migration pattern

The stock does not perform migrations into the Baltic Proper; only minor part of the older herring leaves the gulf after spawning season in summer –autumn period but afterwards returns to the gulf. There is evidence, that the migrating fishes mainly stay close to the Irben Strait region in Sub-division 28 and do not perform longer trips. The extent of this migration depends on the stock size and the feeding conditions in the Gulf of Riga. In 1970s and 1980s when the stock was on a low level the amount of migrating fishes was considered negligible. In the beginning of 1990s when the stock size increased also the number of migrating fishes increased and the catches of Gulf of Riga herring outside the Gulf of Riga in Sub-division 28 were taken into account in the assessments.

#### Spawning

The Latvian coast of the Gulf of Riga is characterised by 10 spawning grounds with areas ranging from 0.1 – 2.35 km<sup>2</sup>. In Estonian part of the Gulf of Riga the most important herring spawning grounds are located in the Pärnu Bay area and on southern coast of Saaremaa isle. The spawning grounds are situated on stony grounds on which seaweeds are growing. The eggs are usually found on algae, but sometimes also on stones, sand and gravel.

Spawning takes place at a broad range of water temperature from 3.5 – 19 °C. In late spring the spawning begins at 3.5 – 4 °C. In normal terms the water temperature for spawning is reaching about 6 °C. On the average the spawning period is two months long – from the end of April till the beginning of July. The highest spawning intensity is observed in the end of May – beginning of June, by water temperatures around 9.5 – 16.9 °C (Lisivnenko, 1957, Rannak, 1971, Raid, 1987, Kornilovs 1994). It was stated that after severe winters the spawning starts later and the spawning period is shorter. After mild winters the spawning period is longer and the spawning activity is distributed more evenly.

Open sea herring, spawning also in the Gulf of Riga, starts to spawn at lower temperatures than the gulf herring. As temperature increases the gulf herring gradually joins the spawning. The spawning is finished by the youngest age groups of the gulf herring. During the spawning period the size and age of the herring diminish. The spawning in the Gulf of Riga is further characterised by following conditions/parameters (Kornilovs 1994):

- Salinity of water 1.76– 6.49 PSU
- water depth range of 0.5 – 7.5 m,
- grounds with stony bottom covered by seaweeds (red, brown and green algae),

- usually the density of eggs are 10,000 – 300,000 per m<sup>2</sup>,
- 1.0– 2.5 millions eggs per 1 m<sup>2</sup> forming 1 – 1.5 cm thick carpets.

The first investigations of the spawning grounds were performed in 1950s by Lisivnenko (1957). They revealed that the spawning grounds were situated till the depth of 14 m, the mortality of eggs was very low - till 5%, the fertilisation rate high. In 1980s the investigations were repeated along the Latvian coast (Kornilovs 1994). It was stated that the spawning grounds are permanent since they were found in the same places as in 1950s. One spawning ground could be used till 3 times during the spawning season. The utilization of certain spawning grounds mainly depends on hydro-meteorological conditions governing the distribution of spawning shoals. The area of the spawning grounds has considerably decreased in comparison with 1950s. The spawning was found till the depth of 7 m, mainly till the depth of 5 m due to disappearance of vegetation on bigger depth. The mortality during egg stage has considerably increased especially in the southern part of the Gulf of Riga. In some cases 100% mortality of eggs was recorded especially in the cases when the eggs were not laid on vegetation. It was considered that the increase in egg mortality was caused by pollution since the highest mortality rates were observed in the most polluted areas. It is believed that the conditions on the spawning grounds have improved since 1990s due to much better treatment of waste- waters in comparison with the previous period.

The larval survey was performed since 1970s till the beginning of 2000 during July by Latvian Fish Resources Agency. The larvae were caught by Isaac-Kidd trawl. However, no significant relationship between year-class strength and the abundance of larvae was found. It is considered that the majority of larvae stayed in the coastal area where the sampling is difficult. Its distribution in higher numbers in off-shore area is mainly caused by hydro-meteorological factors.

L. Rannak (1971) was the first who observed that after mild winters rich year-classes of Gulf of Riga herring appear. Afterwards it was approved also in 1980-1990s (Kornilovs 1995). The reason for this relationship was connected to better survival of larvae when feeding conditions after mild winters were much better due to higher abundance of zooplankton. After mild winters the water temperature in spring was higher that determined the earlier start and the longer duration of the spawning period. The relationships between abundance of 1 year old herring from VPA and the mean water temperature in April and the abundance of two Copepoda species (*Acartia* spp., *Eurytemora affinis*) in May are used for the prediction of recruitment of the Gulf of Riga herring using RCT3 in the Baltic Fisheries Assessment Working Group. Since 1989 a period of mild winters has entered that was accompanied by a row of rich year-classes of Gulf of Riga herring and considerable increase of the stock size.

#### 4.4 Bothnian Sea (Sub-division 30)

##### Distribution

Bothnian Sea herring is distributed in Sub-Division 30.

##### Migration pattern

Migrations to the south or north are scanty.

##### Spawning

Two spring spawning coastal herring populations are inhabiting the Bothnian Sea: one along the west and one along the east coast (Aro 1989). Both populations are spawning in May-July. The feeding migration starts soon after spawning. The main feeding/wintering areas are the slopes/open sea of the Bothnian Sea. The autumn spawning stock is very sparse.

In the data of the relationship of spawning stock biomass and recruited 1-year-olds, two different periods can be identified (ICES 2006): the period of lower recruitment in 1974–1987 and the period of higher recruitment in 1988–2005. If these periods are examined separately, no correlations can be found between SSB and the number of recruits. In the Bothnian Sea, the most spectacular difference between these two periods is in the abundance of cod that was very abundant in the latter half of the 1970s and the first half of the 1980s and has been practically missing since the beginning of the 1990s. In the period of 1988–2005, the number of potential predators on herring has probably been essentially smaller than in the earlier period.

There is some indication that during the present period of relatively high herring density in the Bothnian Sea, the condition of herring females at spawning time has been affected by food competition with young herring age groups in the feeding areas. Furthermore, female condition at spawning can be an essential factor concerning the reproductive success. According to Rajasilta & Laine (2003), there was a negative correlation between the average fat content of spawning herring females in the Archipelago Sea near Turku and the abundance of young (1–2-year-old) herring in the Bothnian Sea in 1988–1998 ( $r=-0.748$ ;  $p<0.01$ ). In addition, there was a positive correlation between the fat content of herring females at spawning and the number of 1-year-old herring in the Bothnian Sea in the next year ( $r=0.576$ ;  $p<0.05$ ). In experimental conditions, Laine & Rajasilta (1999) have shown that herring females that have high fat content produce eggs, which have higher hatching rates than those having low fat content do.

These results also support the findings that a large proportion of the herring that spawn in the Archipelago Sea (Sub-Division 29) spend most of their lives in the Bothnian Sea.

In a time series from 1988–1997, Laine et al. (2003) found correlations that not only support the importance of female condition in the reproductive success, but also stress the importance of environmental factors during the larval stage. Ovarian fat content correlated negatively with egg mortality in spawning beds and positively with the density of small ( $< 10$  mm) larvae in May. The density of larger larvae ( $> 15$  mm) correlated positively with 2-year-old fish in early season trap net samples two years later. No relationship was found between ovary fat content and the density of large larvae ( $>15$  mm) in the early spawning season, however, there was a connection between the densities of yolk-sac larvae and larger larvae (whole season averages) when summer water temperature was partialled out from the correlation.

#### **4.5 Bothnian Bay (Sub-division 31)**

##### **Distribution**

Bothnian Bay herring is distributed in Sub-Division 31.

##### **Migration pattern**

Herring is stationary in this area. Some migrations to the south (Bothnian Sea) may occur.

##### **Spawning**

Spawning starts in late May and is over by late July. The feeding migration occurs mainly inside the Bothnian Bay (Aro 1989).

It is typical for the Bothnian Bay herring that good year classes appear irregularly and less often as in more southern areas in the Bothnian Sea. Winter is more severe and summer colder and shorter than in other Baltic areas. Zooplankton is less abundant than in more southern areas. Salinity is the lowest in the Baltic Sea, from almost fresh water to 4 ‰. Strong year classes have often appeared in warm summers, such as 1988, 1994, and 2002.

#### 4.6 Factors Effecting the Recruitment Processes of Herring in the Baltic

Very few studies exist investigating factors influencing herring recruitment. Birjukov and Shapiro (1971) in the Vistula Bay (south-east Baltic) found that the strength of a certain year-class closely related to the abundance of larvae ( $r = 0.91$ ) that was, in turn, related to the abundance of laid eggs ( $r = 0.95$ ). The number of eggs spawned and the abundance of larvae depended not only on the number of spawners, but also on their fecundity. In particular, 3-year old females had eggs of the best quality, i.e. giving higher (and less variable) survival. Age 2 females (first time spawners), in contrast, showed lower (higher variable) survival. Therefore, the size of a certain year-class was influenced by the age composition of the spawning population (Birjukov and Shapiro, 1971). According to this study, in the Vistula Bay herring year-class abundance is determined before spawning and the period between egg deposition and year-class formation plays only a minor role.

The above findings contrast with Raid (1985) who found that year-class strength was inversely correlated to larval mortality in the Gulf of Finland. This hypothesis is supported by Rannak (1971) who found that north-eastern Baltic herring year-class was mainly determined at the transition between the yolk-sac resorption and the development of the primary finfold (length under 10mm) of the larvae. Parmanne and Sjöblom (1982) found also high correlations between abundance of larvae  $\geq 10$  mm collected along the Finnish coast and year-class abundance between 1974-1979 in Subdivisions 29N, 30-32 ( $r = 0.77$ ). Parmanne and Sjöblom (1988) found significant correlations between the density of copepods nauplii collected along the Finnish coast in June and 0-group herring in the Subdivisions 29N, 30-32 between 1974-1982 ( $r$  between 0.65-0.87), whereas all the other zooplankton groups (copepods juveniles and adults, cladocerans, rotatoria) did not correlate with 0-group herring abundance. In June a large part of the larval population has passed to external feeding in these areas and a high density of food would likely allow them to grow big enough to survive the winter (Parmanne and Sjöblom, 1988). Briemann (1989) too showed that 0-group herring abundance could be predicted by the larval abundance in Subdivisions 22 and 24 ( $r = 0.81$ ) and that larval abundance was correlated to the abundance of calanoid copepods in June. In the Eastern Baltic, on the other hand, 0-group abundance was related to the biomass of crustacean plankton between in August and to 0-group herring in the adjacent Gulf of Riga (Evtukhova et al., 1989). Evtukhova et al. (1989) additionally found that herring 0-group abundance was linked to the water temperature in spring and summer and to sun radiation in the same year in the Gulf of Riga, whereas the biomass of cod seemed not to affect 0-group abundance. In this study, a model including water temperature in spring and summer, sun radiation and cod spawning biomass could explain the 0-group abundance ( $r = 0.99$ ). Cod spawning biomass, however explained only a minor part of the variance (Evtukhova et al., 1989). Ojaveer et al. (1985) stated that in the eastern Gulf of Finland herring year-class depends on the intensity of water mixing that releases nutrients to the surface promoting primary and secondary production.

According to the above studies, both biotic and abiotic conditions have the greatest impact on year-class strength during of the larval phase of herring development (Rannak, 1971; Raid, 1985), and temperature and feeding conditions could be the main factors mediating this process (Rannak, 1971; Parmanne and Sjöblom, 1988). In warm springs following mild winters rich year-classes develop, whereas in cold and late springs poor year-classes appear mainly due to a delay of the spawning period and low zooplankton production. However, as stated below, too high temperature can cause high mortality in embryonic and larval stages increasing the percentage of abnormality in these early stages of development (Rannak, 1971). This occurs mostly at the end of the spawning season when higher temperatures are encountered (Rannak, 1971). However, many of these studies did not take in account the effects of spawning stock biomass. A more recent study on herring included YOY density, a climate index (NAO's winter index) and spawning stock biomass and these factors explained

93 % of the variance in the number of age 2 herring during 1985-2000 (Axenrot & Hansson, 2003) in Subdivision 27. Despite the diverse approaches and sampling procedure used, these studies indicate that the main factors determining herring recruitment are most likely area-specific.

Herring commonly spawn on the vegetation growing on hard bottoms, although bare stones, gravel, sand and blue mussels can also be used as substrate for eggs (Oulasvirta et al., 1985; Aneer and Nellbring, 1982; Rajasilta et al., 1989; Kääriä et al., 1997; Parmanne et al., 1997). Eggs are usually not deposited on soft bottoms. In natural conditions almost all the deposited eggs are fertilised (Rannak, 1971; Raid, 1991), although Ojaveer (1981) observed that around 6% of spawned eggs remained unfertilised in the Gulf of Riga. The largest amount of eggs is usually observed during the first part of the spawning period (Oulasvirta et al., 1985). The mortality rate of spring spawning Baltic herring eggs is generally considered to be on average low (less than 15%) (Rannak, 1971; Rajasilta et al., 1989) even though highly variable, both seasonally and annually (Rannak, 1971; Parmanne and Sjöblom, 1982; Oulasvirta et al., 1985; Rajasilta et al., 1993). An important factor regulating egg survival seems to be constituted by water temperature. It has been observed in many areas of the northern Baltic Proper and of the Gulf of Finland that herring start to spawn in very shallow areas and increase the spawning depth later in the season (Rannak, 1971; Aneer and Nellbring, 1982; Oulasvirta et al., 1985; Rajasilta et al., 1989, 1993; Parmanne et al., 1997). However, the temperature where eggs occur increase from the beginning to the end of the spawning due to the warming of the water column during spring and summer (Rannak, 1971). Field as well as experimental studies have shown that egg mortality are higher at the end of the spawning season due to higher water temperature that can cause abnormalities to the embryos and larvae in the Gulf of Finland and Gulf of Riga (Rannak, 1971; Ojaveer, 1981b; Oulasvirta et al., 1985, 1993; Raid, 1991). For example, in the Archipelago Sea during 1987-1989, egg mortality was around 3.5% in May and around 24% in June-July, and correlated positively with water temperature and depth (Rajasilta et al., 1993). In the northern and eastern Baltic Proper, above the optimal temperatures of 16-17°C seem to cause high mortality of embryos (Rannak, 1971; Ojaveer, 1981b, 1985; Rajasilta et al., 1989). High water temperatures (above 15 °C) can also inhibit herring spawning in the western part of the Gulf of Finland (Oulasvirta et al., 1985; Parmanne et al., 1997 and references therein) and increase the risk of bacterial and fungal infections (Rajasilta et al., 1993). In contrast, high temperature shortens the incubation period and, hence, decreases the predation risk at this stage (Rajasilta et al., 1993). Temperature as low as 3 °C may as well be harmful for herring eggs Ojaveer (1981b). High mortality in summer can also be explainable by the life cycle of filamentous algae (e.g. *Pilayella* spp. and *Ectocarpus* spp.) which during this period torn loose and form drifting mats transported by currents. Within these algal mats the oxygen level is often reduced likely creating adverse conditions for eggs to survive (Aneer, 1985; Aneer and Nellbring, 1982; Rajasilta et al., 1993). Moreover, it has been demonstrated in laboratory that when decomposing, filamentous brown algae (e.g. *Pilayella* spp. and *Ectocarpus* spp.), two of the dominant spawning substrate during summer in the northeast Baltic Proper, release toxic exudate that are deleterious for egg survival (Aneer, 1987). Egg mortality is lower if the eggs are deposited on coarse vegetation (Aneer, 1985; Rajasilta et al., 1993). Moreover, the likely lower water circulation at increasing depths where the eggs are deposited during the end of the spawning season could be a further reason of high mortalities of late spawned eggs (Oulasvirta et al., 1985, Rajasilta et al., 1989). Salinity also influences egg fertilisation and embryos development. Ojaveer (1981b) showed experimentally that in the Gulf of Riga the optimum salinity for egg survival was in the range 5-20 psu. It seems also that the substrate type affects the egg survival. Bed preferences for spawning need to be better addressed. For example Rajasilta et al. (1989, 1993) found a higher egg mortality if attached to red algae (e.g. *Furcellaria*, *Phyllophora*) than on *Cladophora*, *Potamogeton*.



High temperatures can affect herring larval-juveniles survival either directly, acting on the metabolism, or indirectly, changing the food availability (Hakala et al., 2003). It seems that larval growth rates are higher and mortality lower in more sheltered areas (Peltonen, 1990; Hakala et al., 2003), probably because of higher water temperatures (Hakala et al., 2003). This could show that retention mechanisms are very important in larval survival. High temperatures can, however, increase the rate of toxic exudates excretion from algae (Rajasilta et al., 1993). On the contrary, high temperature shortens the incubation period and, hence, decreases the predation risk at this stage (Rajasilta et al., 1993).

Gonad maturation in Baltic herring occurs mostly during winter before spawning using the energy accumulated during the growth period, coinciding with the main feeding season (Laine et al., 1998; Rajasilta et al., 2001). From the studies performed by Rajasilta (1992) and Rajasilta et al. (2001) in the Archipelago Sea, it seems also that ovarian weight of the herring early spawners is determined by the energy reserves accumulated during the previous feeding period before overwintering, whereas the later spawners allocate directly the energy taken from the food (see also Anokhina, 1971). Herring with higher condition and fat content reproduce also earlier (Rajasilta, 1992).

Size and condition of females are also important in egg development and hatching of Baltic herring. From field and experimental studies performed in the Archipelago Sea, Rajasilta (1992) and Laine and Rajasilta (1999) found that fish larger with a better condition and with higher fat content had larger gonads before spawning and produced eggs with better survival and hatching success. Neither ovary fat content nor egg size was however correlated to egg survival or hatching success (Laine and Rajasilta, 1999). In the Archipelago Sea, a decrease of the ovarian weight during and an increase at the end of the spawning period has been observed which was independent of fish length (Rajasilta et al., 2001). This could indicate that the females with larger gonads (that likely stored more energy during the feeding period) spawn earlier. In summer, which corresponds to the onset of zooplankton production in this area, herring can allocate the energy taken from food directly to the gonads and the ovarian weight increases again (Rajasilta et al., 2001). Therefore, environmental cues, acting on plankton production, may play a crucial role in herring fecundity and egg release. Ovarian weight corresponds well to egg number and, thus, to fecundity in this area and, thus, at the end of the spawning season, herring fecundity could be as high as at the beginning, or even higher (Rajasilta et al., 2001). Although a decrease in egg size during spawning has been sometimes observed (Rajasilta et al., 1993), it seems that herring egg size is rather stable (Laine et al., 1998). Therefore, herring can regulate its reproduction in face of environmental changes (i.e. feeding) by regulating the egg number rather than egg size (Anokhina, 1971; Laine et al., 1998). This is in contrast to other areas, e.g. the White Sea (Anokhina, 1971).

Laine et al. (1998) and Laine and Rajasilta (1999) found that herring reproductive success (GSI and fecundity) was better after cool overwintering seasons, possibly because of the lower metabolic rate and energy demands for maintenance (Laine and Rajasilta, 1999). Another explanation could be that also the organisms herring feed upon in winter (mostly zoobenthos) consume their energy reserves during the winter period (Laine and Rajasilta, 1999). It seems, therefore, that cool pre-spawning period and warm spawning period constitute the most suitable conditions for herring reproduction, at least in the Archipelago Sea.

Baltic herring have different age-specific spawning waves, with older individuals spawning earlier than the younger ones. This phenomenon has been observed in the Bothnian Bay and Bothnian Sea (Parmanne, 1993), Vistula Bay (Krasovskaya, 2002), Archipelago Sea (Rajasilta et al., 2001) and Rügen area (Jørgensen et al., 2005) and seems to be the rule in both Atlantic and Pacific herring as well (see Rajasilta, 1992). Probably older individuals mature earlier than younger ones because large fish seem to be more efficient in collecting energy and have lower metabolic costs during overwintering than the smaller ones (see Rajasilta et al., 2001). Interannual differences in this pattern occur (Rajasilta et al., 1992; Jørgensen et al., 2005).

depending possibly on the feeding conditions before spawning. Krasovskaya (2002) found that since the 1950s spawning starts earlier in the Vistula Bay, likely due to milder winter and earlier ice break-up and clearing of ice from the bay. In these situations, herring have more spawning waves and the spawning period is protracted over a wider range of temperature (Krasovskaya, 2002). Salinity also affects the timing of herring reproduction with high salinity anticipating and prolonging herring spawning period (Krasovskaya, 2002), even though the mechanisms are unknown. A longer spawning period could ensure that at least a part of the offspring would meet the optimal condition for growth and survival and would reduce intra-cohort competition. Moreover, a protracted spawning period could reduce the risk of eggs being deposited in multiple layers, thus reducing the risk of oxygen deficiency (Oulasvirta et al., 1985). Ojaveer (1981a) found also that multiple layers might cause a lower fertilisation in the lowest eggs. Genetic separation has been found between successive spawning waves in the Rügen population (Jørgensen et al., 2005). Considering the high mortality of herring eggs in summer (see above) and that larger larvae, usually hatching from larger eggs, could have a higher viability than larvae hatching from small eggs, the early spawned eggs could be thought to be the most important for recruitment. However, other factors may have an impact on egg survival. For example, the differences in predation on eggs by coastal fish and seabirds during herring spawning have not been addressed. These could help in understanding whether egg mortality is higher at the beginning or end of the spawning season.

Pollution is a further factor potentially affecting herring reproductive behaviour. For example, in the Gulf of Finland spawning schools avoid polluted areas and areas of sand extraction (Ojaveer et al., 1985; Oulasvirta and Lehtonen, 1988; Lappalainen and Pesonen, 2000). In the same area eutrophication and sedimentation likely resulted in a shift from hard to soft, muddy bottoms that are unsuitable for herring spawning (Parmanne et al., 1997). Eggs deposited directly on soft bottom tend to be in denser patches than on the algae and, thus, undergo higher mortality likely due to worse aeration conditions and ineffective removal of metabolic wastes (Raid, 1991). Other human activities could be, on the other hand, favourable. For example, the warm cooling water discharge of nuclear power plants made herring to spawn earlier than normal and had beneficial effects on the stock (Karås, 1989). The effects of pollution on herring early life-stages have also been observed by both in-situ and laboratory analysis. Reproduction efficiency decrease in areas of oil spills (Lindén, 1974; Aneer and Nellbring, 1982; Urho, 1991) due to the maturation of females with smaller ovaries (Urho, 1991), higher percentage of abnormal embryos and a decrease in successful hatching (Lindén, 1974). Ojaveer et al. (1980) showed experimentally that fertilization, total hatch, normal embryos at hatching and average length of newly hatched larvae of Gulf of Riga herring, all decreased in the presence of even very small amounts of metals, such as Cu, Cd and Zn, in the water. These metals accumulate along the food chain and could reach high density in seals and birds (Jansson and Dahlberg, 1999). In the southern Baltic herring hatching success was affected by the presence of chlorinated hydrocarbons in the parents fish (Hansen et al., 1985).

There are important indications that, due to eutrophication, the composition of bottom vegetation has changed during the last decades and the amount of filamentous algae has increased and that of macrovegetation has diminished in several coastal areas around the Baltic (Rönnberg and Bonsdorff, 2004). Considering the adverse effects filamentous algae can have on herring eggs (see above), this shift might be disadvantageous for herring. However, there are not clear-cut studies indicating whether this shift has had negative effects on herring early-life stages. Raid (1991) showed that in the northeastern Baltic proper it seems that egg mortality has increased from the 1940s (and particularly between 1970s-1990s). This could be due to the partial extinction of bottom vegetation, increase of filamentous algae or increase in water temperature above the optimum level for Baltic herring development (Raid, 1991).

The fact that the strength, if any, of the stock-recruitment relationship is different among the different assessed areas of the Baltic shows that regional studies have to be carried out in order

to understand the different components that influence the recruitment of herring in the Baltic. This was, for example, done by Axenrot and Hansson (2003) for Subdivision 27. Some factors acting on herring recruitment have been fairly deeply investigated, as temperature, food availability and spawning biomass. Some other factors, as for example the effects of predation on eggs, spawning behaviour and spawning bed selection have not been sufficiently studied, and could help understanding the processes driving herring recruitment in different areas of the Baltic. For example, the dependence of herring spawning on particular grounds and types of bottom vegetation shows that it is urgent to monitor spawning areas and protect them against human impact. Degradation of preferred spawning substrates could limit the reproduction volume and success of herring. All the same, retention mechanisms have not been investigated so far.

There are differences in fecundity among the several herring stocks of the Baltic. For example, fecundity is lower in the central than in the western Baltic (Kändler and Dutt, 1957). In the northern parts of the Baltic, on the contrary, there seems to be an opposite south-north gradient with fecundity increasing from the northern Baltic proper to the Bothnian Bay (Parmanne and Kuittinen, 1991). This has been tentatively been explained by a lower salinity and as compensation mechanism for the higher larval mortality in the northern parts of the Baltic (Parmanne and Kuittinen, 1991). To our knowledge there are no studies on the fecundity of different herring sub-populations in the central Baltic. If the sub-populations with higher fecundity would be reduced due for example to fishing or spawning ground deterioration, the effects on the stock of the central Baltic could be deleterious. Therefore, we stress the importance of investigating the fecundity of herring from different sub-populations in the Central Baltic.

## 5 Overview on data for statistical analyses

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This section summarizes the SSB and recruitment data, as well as biotic and abiotic predictor variables collected by WKHRPB for the statistical analyses. 6 stocks were considered, i.e. herring in the western Baltic (D IIIa & SD 22-24), main basin herring (SD 25-29+32 excl. Gulf of Riga), Gulf of Riga herring, Bothnian Sea (SD 30) and Bothnia Bay herring (SD 31), as well as Baltic sprat (SD 22-32) for comparison (Fig. 5.1). All data are presented on a single stock basis. Data sources for the time-series used in the statistical analyses are given in Annex 3.

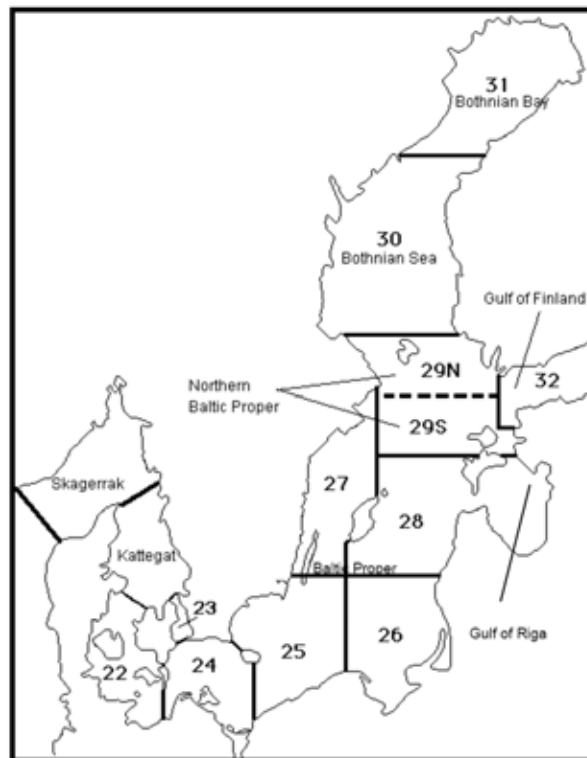


Fig. 5.1. Map of the Baltic Sea with ICES Sub-divisions indicated by numbers.

### 5.1 Western Baltic herring (D IIIa & SD22-24)

Stock and recruitment data for Western Baltic herring were available from 1991 onwards (Fig. 5.2). SSB declined since the early 1990s, while recruitment fluctuated and was low since the beginning of the present century. Decreasing biomasses are accompanied by stable individual weights. Hydro-climatic variables (Baltic Sea Index, temperature, salinity) fluctuated moderately with no apparent trend.

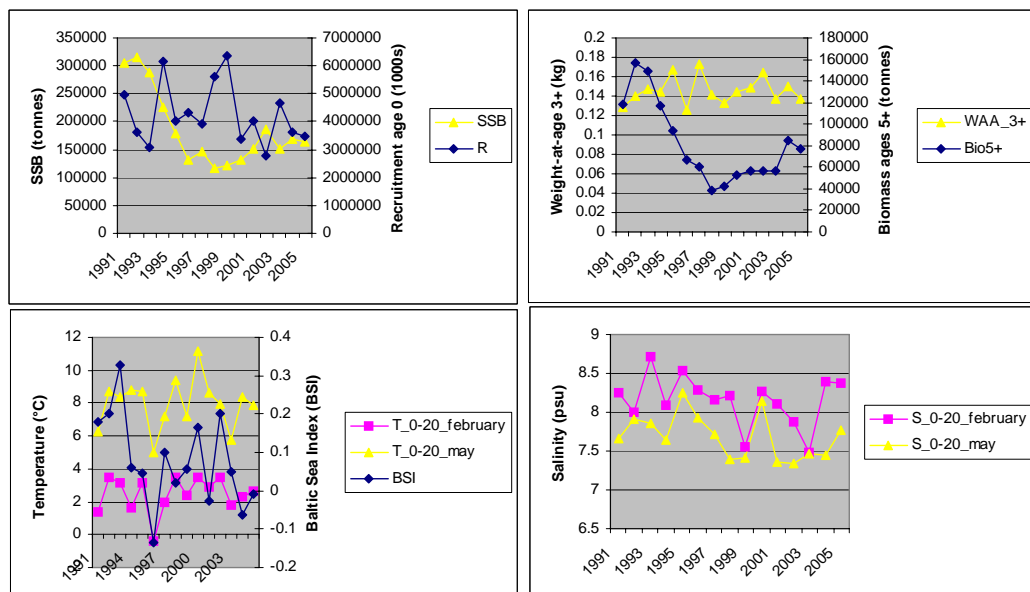
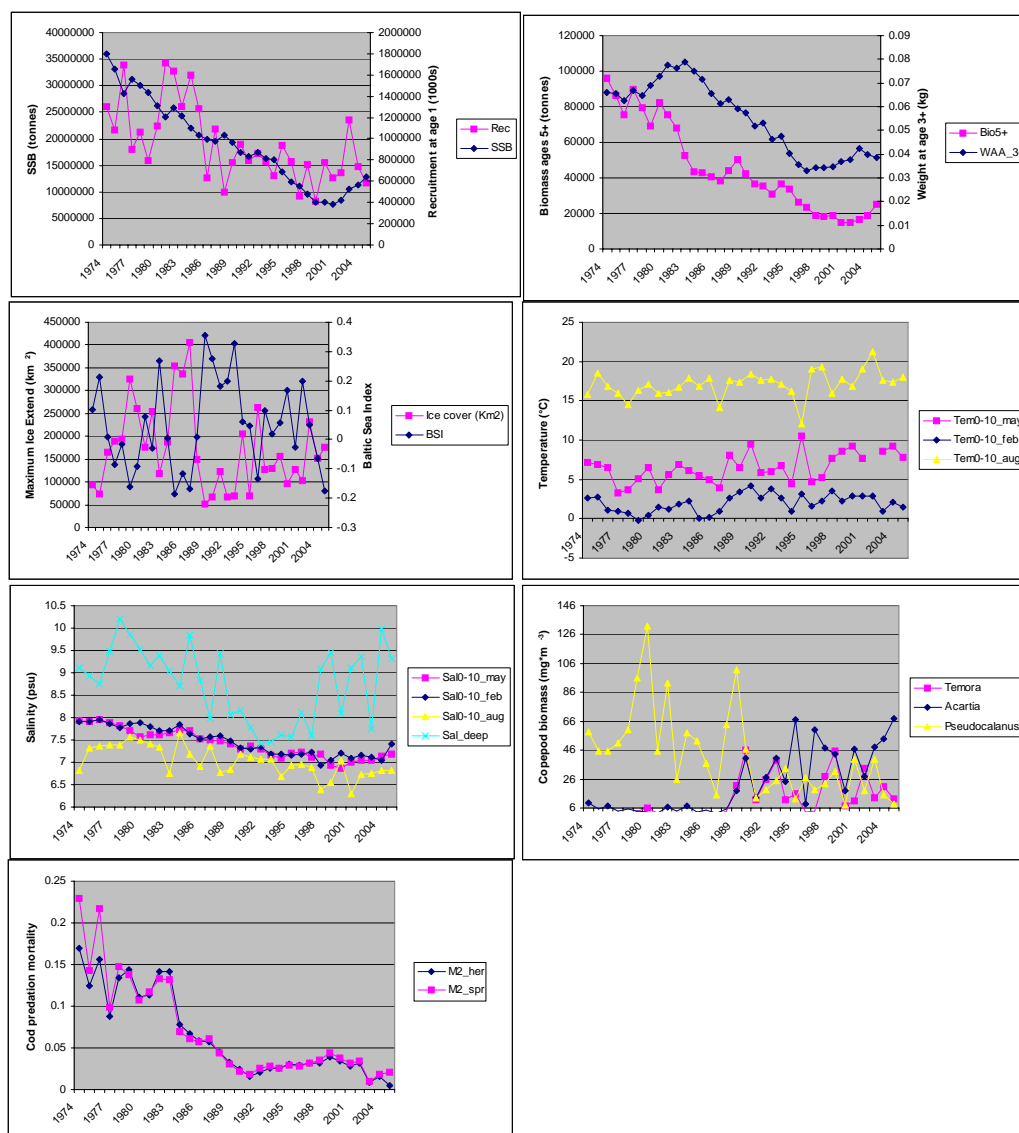


Fig. 5.2. Biotic and abiotic time-series available for the Western Baltic (SD22-24) analyses.

## 5.2 Main basin herring (SD25-29&32 excl. Gulf of Riga)

Spawning Stock Biomass (SSB) and recruitment displayed decreasing trends since the mid 1970s, with a slight increase during the past few years (Fig. 5.3). The same is true for the weight-at-age 3 and the biomass of ages 5+. The Baltic Sea Index increased sharply in the late 1980s is negatively correlated to the Maximum Ice Extend. Sea-surface temperature (SST) increased during the past three decades, both in spring and summer (August). Surface salinity, on the other hand, decreased constantly during the same period, levelling off or slightly increasing from 2000 and onwards. Deepwater salinity showed a clear response to the occurrence of inflow events Spring biomass of the copepods *Acartia* spp. and *Temora longicornis* increased strongly after the end of 1980s, whereas the biomass of the copepod *Pseudocalanus acuspes* declined. Predation mortality by cod was decreasing since the early 1990s.



**Fig. 5.3.** Biotic and abiotic time-series available for the Main Basin herring (SD25-29+32 excl. GOR) analyses; copepod biomass is from May.

## 5.3 Gulf of Riga herring

SSB and recruitment of herring in the Gulf of Riga increased sharply throughout the 1990s, and consequently the biomass of ages 5+ as well (Fig. 5.4). In contrast weight-at-age 3+

dropped sharply in parallel. Hydroclimatic conditions are characterized by the sharp increase of the BSI during the late 1980s, causing a temperature increase as well.

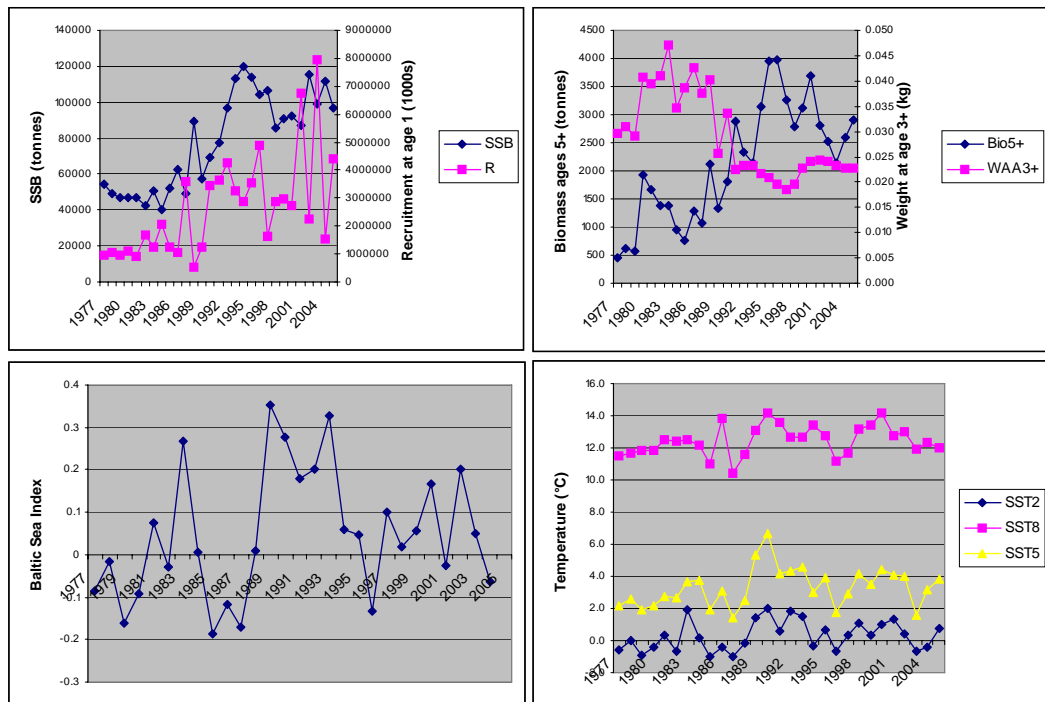


Fig. 5.4. Biotic and abiotic time-series available for the Gulf of Riga analyses.

#### 5.4 Bothnian Sea herring (SD30)

The herring stock in the Bothnian Sea is characterized by drastically increasing SSB and biomass of ages 5+ in the early 1990 (Fig. 5.5). Recruitment was on a higher levels since the 1990s as well with an outstanding peak in 2002. In parallel individual weights were decreasing. Abiotic and biotic conditions in the Bothnian Sea changed considerably during the last 2 decades. The Baltic Sea Index (BSI) increased in the late 1980s and is negative correlated to the Maximum Ice Extend. Temperatures in June increased since the late 1980s as well, while summer temperatures were more constant. Salinity decreased throughout the whole time-series. Copepod biomass fluctuated strongly, with no clear trend.

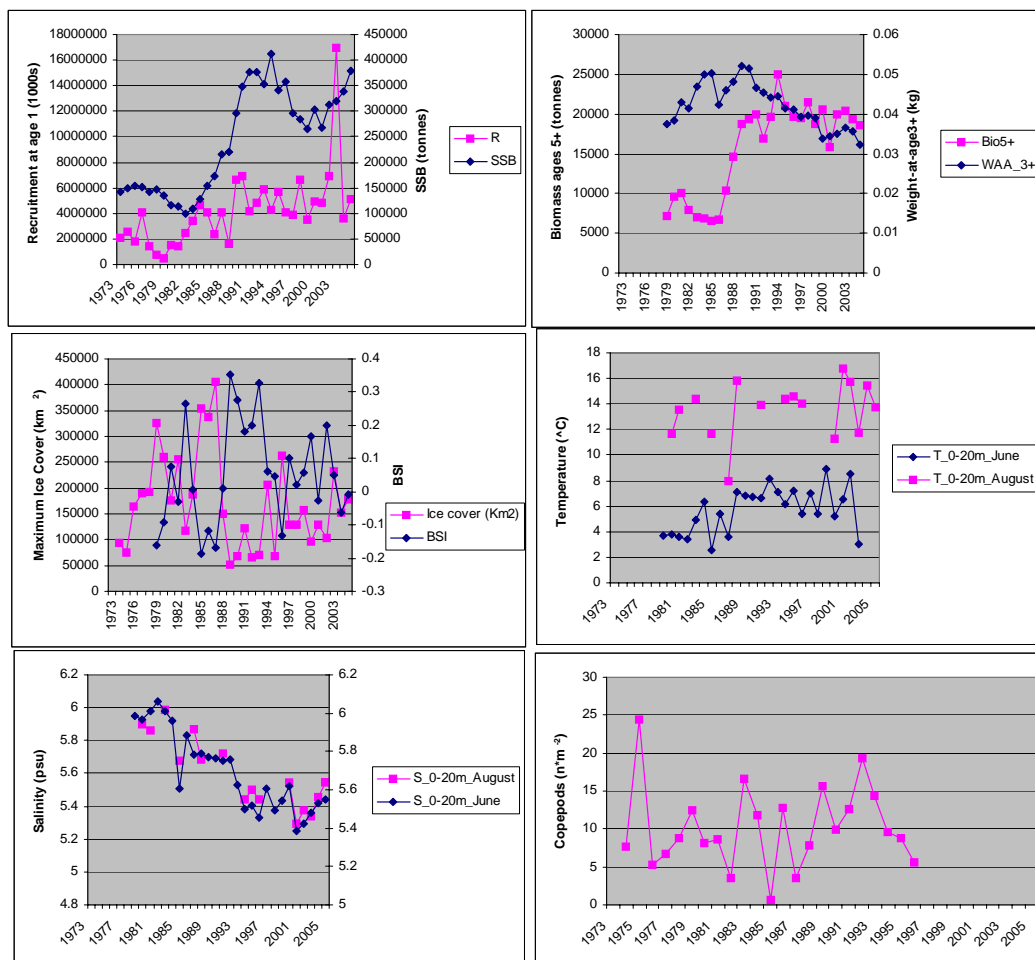


Fig. 5.5. Biotic and abiotic time-series available for the Bothnian Sea (SD30) analyses.

## 5.5 Bothnian Bay herring (SD31)

The herring stock in the Bothnian Bay is characterized by decreasing biomasses in the early 1990s, accompanied by decreasing individual weights (Fig. 5.6). Recruitment was very variable with a tendency to decrease in the 1990s and slight increasing recently. Abiotic and biotic conditions in the Bothnian Bay changed considerably during the last 2 decades (Fig. 5.6). The Baltic Sea Index (BSI) increased during the late 1980s and is negatively correlated to the Maximum Ice Extend. Spring temperatures increased since the late 1980s as well, while summer temperatures were more constant. Salinity decreased throughout the whole time-series. Copepod biomass fluctuated strongly, with a slight negative trend until mid 1990s.

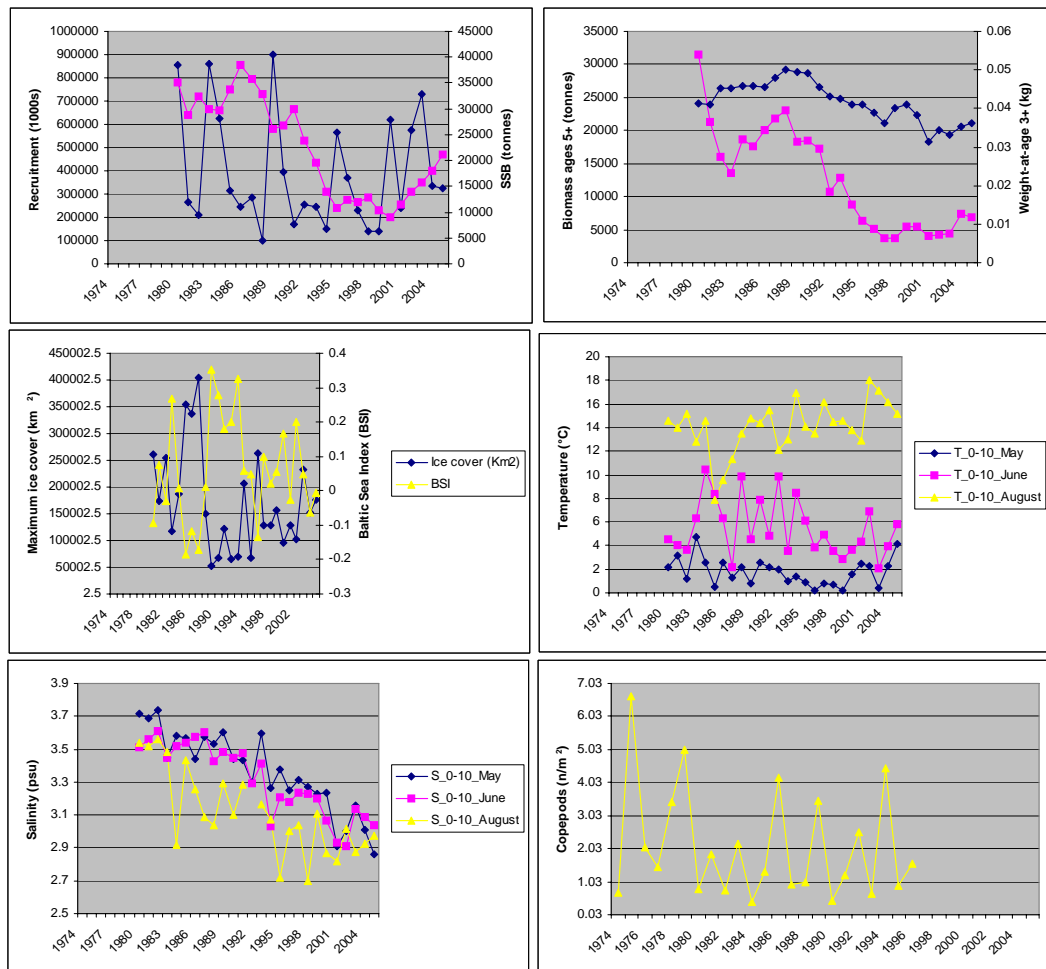


Fig. 5.6. Biotic and abiotic time-series available for the Bothnian Bay (SD31) analyses.

## 5.6 Baltic sprat (SD 22-32)

For the analyses of the sprat stock the same biotic and abiotic variables as for the Main basin herring stock have been used (Fi. 5.3).

# 6 Statistical analyses of recruitment-environment relationships

## 6.1 Statistical methods applied

Two rather similar approaches on analysing the effect of environmental conditions have been used, i.e. (i) the approach recently published in Stige et al. 2006, and (ii) the approach by Cardinale and Hjelm (2006).

(i) As described in Stige et al. (2006), the logarithm of the ratio between the annual numbers of recruits (R) and spawning stock biomass (SSB) was used as response. According to the models by Ricker (Ricker 1954) and Beverton and Holt (1995), this ratio is a linear function of SSB:

$$(1) \ln(R/SSB) = a + b \text{ SSB}.$$

The other effects can be modelled as predictors in (1).

(ii) Alternatively the procedure suggested by Cardinale and Hjelm (2006) was followed. The first step here is to test for and disentangle the SSB effect on R. In one of his last lectures at Woods Hole, Beverton (2002) suggested an approach for exploring this relationship. Because



of the biological mechanisms behind the classical SSB–R relationships, recruitment success ( $R_s$ ) should improve as SSB decreases (Fig. 1 in Cardinale and Hjelm 2006). However, if recruitment is mediated both by physical environmental events and other biotic factors, this negative relationship may not be as obvious. For example, when the stock is declining, a negative effect of the climate on  $R$  will result in a decrease in  $R_s$ ; this is reversed in the case of a positive effect of climate on  $R$ . Therefore, the variability in the relationship between  $R_s$  and SSB can be considered as a proxy for recruitment anomalies ( $R_a$ ) and is assumed to be partially determined by the stochasticity in the physical environment (Beverton 2002) as well as other biotic factors. Nevertheless, this approach is only valid when a significant effect of SSB on  $R_s$  can be demonstrated. Only in such cases can  $R_s$  and therefore  $R_a$  be used in climate–recruitment analysis. On the other hand, and as a second step, when SSB has no significant effect on  $R_s$ , climate variables and other biotic factors can be directly correlated to recruitment itself. Importantly, if SSB has no effect on  $R$ , using  $R_s$  instead of  $R$  can actually mask any recruitment–climate relationship. The rationale behind this assumption is mathematically formalized in the classical Ricker (1954) or Beverton and Holt (1995) recruitment functions, and these functions are in turn based on sound ecological mechanisms (e.g. cannibalism and predation). The point here is that the number of recruits in a fish species is generally related to egg number or SSB, a proxy of egg production (Myers and Barrowman 1996).

The relationship between recruitment and abiotic-biotic factors was analysed with Generalized Additive Models (GMAs), using the *mgcv* library of R (Wood 2001). The optimal roughness of the smooth terms was estimated by minimizing the generalized cross validation (GCV, Wood 2001, 2004). The GCV of a model is a proxy for the model's out-of-sample predictive mean squared error. Therefore, a model with lower GCV has more explanatory power, and hence is preferred, compared to a model with higher GCV.

First, all the hypothesized predictors (selected a priori on the basis of known ecological, biological and physiological mechanisms, see Annex 5) were included in the model and a backward stepwise regression based on GCV information criteria was applied to find the best possible set of predictors. Stepwise selected predictors in the best model were then screened using the ecological criterion (see Cardinale and Svedang, 2004; Casini et al., 2006 for a use of the ecological criteria in model selection). The ecological criterion implies that the sign of the relationship of certain variables cannot be accepted although they are statistically significant because of a lacking ecological basis (Dippner and Ottersen 2001). For example, there is no ecological basis for zooplankton species to negatively affect fish condition (i.e. more zooplankton, lower condition) and therefore such a relationship was discarded a-priori. If some of the relationships found in the best model selected by GCV were not fulfilling the ecological criterion, the variable was excluded and the backward selection was continued.

Thus, the final model per stock was selected based on the following criteria assuming that those were fulfilled at the same time: Parsimonious principle (the largest amount of deviance explained with the minimum number of predictors) and ecological criterion (meaningful ecological relationships).

## 6.2 Results and Discussion

All models investigated during the statistical analyses are given in Annexes 4 and 5. Diagnostic plots of the finally selected models can be found in Annex 6. The finally selected models are shown in Table 6.1. For all stocks except for the Gulf of Riga (GOR), spawning biomass was found to significantly affect recruitment. Hence, recruitment anomalies  $R_a$  (acc. to Cardinale & Hjelm 2006) were used instead of the plain recruitment in numbers for these stocks. Also from using recruitment success  $R_s$  (according to Stige et al. 2006) SSB is the most frequent factor explaining recruitment variability since it is selected in all models except

for the GOR. For the Western Baltic (WB) and the Bothnian Bay (BB), SSB is in fact the only explanatory variable.

Parental effects of the stock structure (indexed by the biomass of ages 5+) on Ra and R were found for WB and GOR herring, respectively. An effect of adult condition (indexed as weight-at-ages 3+) on Ra was only found for the Main Basin (MB) herring.

In most of the analyses (except WB using Rs and BB using Rs) hydroclimatic variables were the important predictors in the environment-recruitment models. The BSI was found to be a useful predictor except for GOR and BB. For all stocks (except Baltic sprat) temperature was a significant predictor of recruitment.

For all stocks where complete zooplankton data were available, i.e. MB, GOR and sprat, the food supply was a significant predictor, suggesting that a part of changes in climate and hydrography affect herring and sprat recruitment indirectly. Predation mortality by cod was included in the analyses for MB and sprat. While the analyses for herring yielded biologically difficult to justify results (recruitment increased with predation mortality) and the derived models were thus discarded (although listed in Annexes 4 and 5), cod predation on sprat was a significant predictor.

**Table 6.1. Finally selected environment-recruitment relationships for the different Baltic herring and the Baltic sprat stock; WB – Western Baltic Herring (DIIIa & SD22-24), MB – Main Basin herring (SD26-29&32excl. GOR), GOR – Gulf of Riga, BS – Bothnian Sea (SD30), BB – Bothnian Bay); R – recruitment, Ra – recruitment anomaly, Rs – recruitment success; for codes of the variables see Annex 3.**

STOCK	RESPONSE	MODEL	GCV	EXPL. DEV.
WB	Ra	BIOM5pl, SST2, BSI	0.063554	62.4
WB	Rs	SSB	0.059221	93.0
MB	Ra	WAA3pl, TEM, BSI, SST8	0.053562	76.5
MB	Rs	SSB, WAA3pl, PSE, BSI, SST8	0.052302	83.6
GOR	R	BIOM5pl, EUR, SST5	0.15635	73.9
GOR	Rs	SST5	0.11269	62.9
BS	Ra	BSI, SST6	0.1344	62.3
BS	Rs	SSB, SST6	0.12167	87.0
BB	Ra	SST6	0.3875	6.1
BB	Rs	SSB	0.41263	40.2
Sprat	Ra	BSI, PSE	0.30179	74.6
Sprat	Rs	SSB, BSI, PSE, PM	0.35592	69.5

#### Environmental effects on Baltic herring (and sprat) stocks

Temperature changes induced by climate variability seemed to be the major factor influencing recruitment of all Baltic herring stocks beside the size of the parental stocks. Significant effects of temperature just before (WB) and during spawning time (GOR, BS, BB) indicate a direct effect on the survival of early life-stages, i.e. eggs and larvae. On the other hand, temperature can influence larval survival through enhanced food production. This indicated by the significant effect of the copepod *Eurytemora affinis* on the recruitment of GOR herring (Kornilovs et al. 1992). Unfortunately no sufficiently long zooplankton time-series were available for the other stocks (except MB) to verify this mechanism.

The effect of summer temperature on MB herring indicates a coupling to feeding conditions, which is supported by the significant effects of the copepods *Temora longicornis* and *Pseudocalanus acuspes* on herring recruitment. The effect of summer temperature and

zooplankton works obviously via the growth and condition of MB herring which declined drastically in recent decades (Cardinale and Arrhenius 2000, Casini et al. 2006, Möllmann et al. 2005). This hypothesis is supported by the significant effect of the mean weight of the MB herring. A potential effect of spring temperatures on early life stage survival is indicated by the significant effect of the BSI.

The proportion of older individuals in the stock, i.e. a parental effect, has clearly importance for the recruitment of WB and GOR herring. Especially for the latter this has potentially stabilized the high recruitment level during the 1990s.

The effect of environmental variables on sprat recruitment was analysed for comparison with the herring stocks. The analyses confirmed beside the importance of the size of the spawning stock an effect of the atmospheric forcing as indicated by the BSI (Baumann et al. 2006). Presently not considered variables in stock-recruitment relationships of sprat were the biomass of *Pseudocalanus acuspes* and predation mortality by cod on 0-group sprat. The former can influence sprat recruitment via availability of nauplii (Dickmann et al. in press) or growth and condition of adults (Möllmann et al. 2005). More detailed analyses are necessary to confirm the processes behind these relationships.

## 7 Environmentally-sensitive stock-recruitment relationships

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The above described statistical analyses of environment-recruitment relationships show that beside SSB hydroclimatic variables are additionally important predictors of recruitment. Also the proven effect of the food supply, i.e. zooplankton, is an effect of changes in hydrography. Hence, it will be a valuable exercise to include these in S/R-relationships for the use in stock predictions. Due to time constraints this exercise could not be performed during the workshop. WKHRPB thus suggests a follow-up workshop on **Developing and Testing Environmentally-Sensitive Stock-recruitment Relationships of Baltic Herring and Sprat stocks [WKSSRB]** (see Annex 7). A key task of this workshop would also be to test the performance of these environmentally-sensitive stock-recruitment relationships in stock forecasts as has been done for sprat by MacKenzie & Köster (2004).

## 8 Scientific studies to investigate the processes behind climate-related trends in recruitment.

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The analyses of climate-recruitment relationships indicated a strong dependence of Baltic herring recruitment on the prevailing thermal conditions induced by atmospheric forcing. These will mainly affect the survival of early life stages through direct (physiological) and indirect (food availability) processes. Further on variability in food, i.e. zooplankton production can cause changes in the condition of the adult stock which can affect the reproductive potential of the populations. Based on the review and the statistical analyses key areas for a future research project on Baltic herring recruitment have been identified and are outlined below

### Improving estimates of stock reproductive potential of herring

Historically, much effort has been put into research enhancing understanding of the large fluctuations in stock sizes of Northeast Atlantic herring stocks. Whereas the external, environmental drivers for variations in recruitment have received a lot of attention, the parental contribution to these variations, i.e., the stock reproductive potential (SRP), has only rarely been considered in this respect, although a number of studies recently e.g. showed the importance of variations in fecundity for herring (Oskarsson et al. 2002; Kurita et al. 2003). For all Baltic herring stocks recent studies on fecundity are lacking, although some groundwork has been done mainly for the eastern stocks between the 1950's and 1980's. A first attempt to collect the available information in a systematic manner has been undertaken

by the NAFO WG on reproductive potential and in the frame of the ICES SGGROMAT. Information was collected in a meta-database and made publicly available as printable tabled information (see appendices). For Baltic cod and sprat stocks, an update is presently being done in the frame of the EU-project “UNCOVER”, whereas this is lacking for Baltic herring stocks. In order to establish reliable time series (and models) of herring SRP it is essential to have the most comprehensive data collection available to improve SSB as a measure of SRP. It is thus recommended to use the NAFO / SGGROMAT table approach to achieve a comprehensive collection of all available data on herring SRP, which may be used in the follow up initiatives of this workshop. ICES SGBFFI may be the platform to initiate an update of the existing datasets. An extension to other fish stocks should be envisaged to explore the possibilities to incorporate SRP into recruitment models with the goal to improve assessment methodology.

### **Identification of spawning areas**

Timing and location of spawning are potentially sensitive to climate and anthropogenic effects (e.g. eutrophication) and are hence crucial for investigating the recruitment process of Baltic herring. It is generally believed that herring spawn almost everywhere along the Baltic Sea coasts. However, only a relatively limited part of the potential spawning areas has been investigated yet. Moreover, in several, historically relatively well studied areas, the most recent data originate from 1970-1980s or even from earlier periods (e.g. the southern coast of the Gulf of Finland, northern part of the Gulf of Riga). With respect to recruitment processes studies, the knowledge of the extent and productivity of the spawning grounds would be of crucial importance. In order to estimate the human impact to the coastal zone, the information on location of spawning grounds is also essential.

Several possibilities to investigate the location of spawning grounds exists.

- In case of an existing fishery on spawning grounds, information from fishermen and the spatial distribution of the trap-net fishery, indicating the concentration of pre-spawning concentrations could be serve as essential source data;
- Larval surveys give information on the distribution of newly hatched larvae;
- Research vessel surveys on spawned eggs using various submerged gears (e.g. dredges);
- Scuba-diving for spawned eggs.

The last to options allow to cover relatively large areas during one survey, while the scuba-diving, although allowing probably the most comprehensive results on egg distribution and survival, is obviously most costly.

### **Studies on the growth and survival of early life-history stages**

Investigations on egg mortality are crucial for identifying the climate effect on Baltic herring recruitment. In the 1980 investigations were performed at the Latvian coast of the Gulf of Riga using of SCUBA divers, which can be a template for future studies. The investigation covered an area of the coastline of c. 20 km where several well-known and frequently used spawning grounds are situated. The investigations covered the spawning period from the beginning of May until the beginning of July. 14 transects perpendicular to the coastline were chosen on the most frequently used spawning sites and those were covered once a week. In the case of finding herring eggs the area of the spawning was estimated and several samples of vegetation with eggs were taken for the calculation of egg density per square metre. It was striven to take the samples during the embryological development and before the hatching of larvae when the most precise estimate of egg mortality could be obtained. Regular recording of water temperature and other environmental parameters (e.g. zooplankton) was conducted.

Among the most important factors influencing fish recruitment are usually changes in larval survival attributable to changing environmental conditions: food/predation or larval drift patterns altered by ocean circulation). Little is known on the effects of the environment on larval survival of Baltic herring. Hence, regular surveys and process studies in those areas which are regarded as important spawning grounds of Baltic herring e.g. Greifswalder Bodden/Rügen, Gulf of Gdansk/Vistula Lagoon, and Pärnu Bay are needed.

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**Annex 1: List of participants**

NAME	ADDRESS	EMAIL
Anna Grzyb	Sea Fisheries Institute Gdynia ul. Kollataja 1 PL-81-332 Gdynia Poland	aniagrzyb@mir.gdynia.pl]
Christian Möllmann (Co-chair)	University of Hamburg Institute of Hydrobiology and Fishery Science Olbersweg 24 D-22767 Hamburg Germany	christian.moellmann@uni-hamburg.de
Georgs Kornilovs	Latvian Fish Resources Agency 8 Daugavgrivas Str. LV-1048 Riga Latvia	georgs.kornilovs@latzra.lv
Jari Raitaniemi	Finnish Game and Fisheries Research Institute Turku Game and Fisheries Research Itäinen Pitkätatu 3 20520 Turku Finland	jari.raitanemi@rktl.fi
Joachim Gröger (part-time)	Federal Research Centre for Fisheries Institute for Sea Fisheries Palmaille 9 D-22767 Hamburg Germany	joachim.groeger@ish.bfa-fisch.de
Max Cardinale (Co-chair)	Swedish Board of Fisheries Institute of Marine Research, Lysekil P.O. Box 4 SE-453 21 Lysekil Sweden	massimiliano.cardinale@fiskeriverket.se
Michele Casini	Swedish Board of Fisheries Institute of Marine Research, Lysekil P.O. Box 4 SE-453 21 Lysekil Sweden	michele.casini@fiskeriverket.se
Norbert Rohlf (part-time)	Federal Research Centre for Fisheries Institute for Sea Fisheries Palmaille 9 D-22767 Hamburg Germany	norbert.rohlf@ish.bfa-fisch.de
Piotr Margonski	Sea Fisheries Institute in Gdynia ul. Kollataja 1 PL-81-332 Gdynia Poland	pmargon@mir.gdynia.pl

NAME	ADDRESS	EMAIL
Tiit Raid	Estonian Marine Institute, University of Tartu Mäealuse 10A, Tallinn EE-12618 Estonia	tiit.raid@ut.ee
Tomas Gröhsler	Federal Research Centre for Fisheries Institute for Baltic Sea Fisheries Alter Hafen Süd 2 D-18069 Rostock Germany	tomas.groehsler@ior.bfa-fisch.de
Valerio Bartolino	Dep. Animal and Human Biology, University of Rome La Sapienza. Viale dell'universita, 32 I-00185 Rome Italy	valerio.bartolino@uniroma1.it

## Annex 2: Agenda

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### Tuesday 27/02/07

1000 – 1045 Practical information, Introduction to the Workshop and Discussion of the Agenda (Christian Möllmann & Max Cardinale)

1045 – 1100 Coffee & Tea

1100 – 1300 Presentations:

- 1) Review of Baltic herring recruitment processes (Tiit Raid)
- 2) Herring/zooplankton relationships in the Vistula Lagoon (Ania Grzyb)
- 3) Report on the work of the Baltic Sea Regional Project on herring- environment relationships in the Gulf of Riga, the Gotland Basin and the Gulf of Finland (Piotr Margonski)
- 4) Herring reproduction in the Northern Baltic (Jari Raitaniemi)
- 5) Review of available single-species stock assessment data & trends of the Baltic Sea herring stocks (Max Cardinale)
- 6) Review of recent multispecies modelling activities – area-aggregated and disaggregated runs (Christian Möllmann)
- 7) Biotic and abiotic data available for the investigation of environment – recruitment relationships for the different herring stocks (Michele Casini)
- 8) Strategy for the investigation and modelling of environment – recruitment relationships (Max Cardinale)
- 9) Recruitment modelling in R (Valerio Bartolino)

1300 – 1415 Lunch

1415 – 1530 Presentations cont.:

1530 – 1600 Coffee & Tea

1600 – 1800 Discussion of group work and forming of sub-groups

#### *Potential sub-groups*

- 1) Reviewing knowledge on Baltic herring recruitment processes (incl. reproductive potential)
- 2) Description of available data for the report: Single- and multispecies assessments, biotic and abiotic time-series
- 3) Statistical analyses and recruitment modelling

1900 - Common Dinner with GLOBEC-GERMANY Synthesis Workshop  
“Zooplankton Dynamics” – Restaurant “Feuerstein”

### Wednesday 28/02/07

0930 – 1045 One more presentation: On the Detection of Internal and External Signals in the Stock-Recruitment Relationship of North Sea Herring and their Effects on the Methodologies used (Joachim Gröger)

afterwards: Work in subgroups

1045 – 1100 Coffee & Tea

1100 – 1300 Work in subgroups cont.

1300 – 1415	Lunch
1415 – 1530	Plenary: 1st summary of the state of the sub-groups
1530 – 1600	Coffee & Tea
1600 – 1800	Work in subgroups cont.

#### **Thursday 01/03/07**

0900 – 1045	Plenary: Review of the statistical analyses and the recruitment modelling
1045 – 1100	Coffee & Tea
1100 – 1300	Work in subgroups cont  new parallel group: “suggest scientific studies to investigate the processes behind climate-related trends in recruitment”
1300 – 1415	Lunch
1415 – 1530	Plenary: Summarizing results of subgroups; decision on structure and contents of the report
1530 – 1600	Coffee & Tea
1600 – 1800	report writing and (if needed) additional work in subgroups

#### **Friday 02/03/07**

0900 – 1045	Plenary: Wash-up
1045 – 1100	Coffee & Tea
1100- 1300	Report writing
1300	Closure of workshop

### Annex 3: Overview table on data series used in statistical analyses of environment-recruitment relationships

AREA	ABBREVIATION	VARIABLE	SOURCE
DIIIa & SD 22-24	SSB	Spawning biomass	ICES 2006a
SD 25-29+32excl.GOR	SSB	Spawning biomass	ICES 2006b
Gulf of Riga (GOR)	SSB	Spawning biomass	ICES 2006b
SD 30	SSB	Spawning biomass	ICES 2006b
SD 31	SSB	Spawning biomass	ICES 2006b
SD 22-32 (Sprat)	SSB	Spawning biomass	ICES 2006b
DIIIa & SD 22-24	R0	Recruitment age 0	ICES 2006a
SD 25-29+32excl.GOR	R1	Recruitment age 1	ICES 2006b
Gulf of Riga (GOR)	R1	Recruitment age 1	ICES 2006b
SD 30	R1	Recruitment age 1	ICES 2006b
SD 31	R1	Recruitment age 1	ICES 2006b
SD 22-32 (Sprat)	R1	Recruitment age 1	ICES 2006b
Whole Baltic Sea	BSI	Baltic Sea Index	Lehmann et al. 2002
DIIIa & SD 22-24	BIOM5pl	Biomass ages 5+	ICES 2006a
DIIIa & SD 22-24	WAA3pl	Weight-at-age 3+	ICES 2006a
DIIIa & SD 22-24	SAL2	Sea Surface Salinity February	SMHI
DIIIa & SD 22-24	SST2	Sea Surface Temperature February	SMHI
SD 25-29+32excl.GOR	BIOM5pl	Biomass ages 5+	ICES 2006b
SD 25-29+32excl.GOR	WAA3pl	Weight-at-age 3+	ICES 2006b
SD 25-29+32excl.GOR	ACA	<i>Acartia</i> spp. biomass	LatFRA
SD 25-29+32excl.GOR	TEM	<i>Temora longicornis</i> biomass	LatFRA
SD 25-29+32excl.GOR	SSS5	Sea Surface Salinity May	SMHI
SD 25-29+32excl.GOR	SALD	Deep Water Salinity May	SMHI
SD 25-29+32excl.GOR	SST5	Sea Surface Temperature May	LatFRA
SD 25-29+32excl.GOR	SST8	Sea Surface Temperature August	LatFRA
SD 25-29+32excl.GOR	PSE	<i>Pseudocalanus acuspes</i> biomass	LatFRA
SD 25-29+32excl.GOR	PM	Predation mortality age 0	ICES 2007
Gulf of Riga (GOR)	BIOM5pl	Biomass ages 5+	ICES 2006b
Gulf of Riga (GOR)	WAA2pl	Weight-at-age 2+	ICES 2006b
Gulf of Riga (GOR)	ACA	<i>Acartia</i> spp. biomass	LatFRA
Gulf of Riga (GOR)	EUR	<i>Eurytemora affinis</i> biomass	LatFRA
Gulf of Riga (GOR)	SST5	Sea Surface Temperature May	LatFRA
SD 30	BIOM5pl	Biomass ages 5+	ICES 2006b
SD 30	WAA3pl	Weight-at-age 3+	ICES 2006b
SD 30	SST6	Sea Surface Temperature June	FIMR

AREA	ABBREVIATION	VARIABLE	SOURCE
SD 31	BIOM5pl	Biomass ages 5+	ICES 2006b
SD 31	WAA3pl	Weight-at-age 3+	ICES 2006b
SD 31	SST6	Sea Surface Temperature June	FIMR

SMHI – Swedish Meteorological and Hydrological Institute; FIMR – Finnish Institute for Marine Research; LatFRA – Latvian Fish Resources Agency

## Annex 4: Output of statistical modelling of environment-recruitment relationships

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For codes of the variables see Annex 3.

### Western Baltic Herring

Formula:

$Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{SAL2}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.07533	0.04761	1.582	0.158

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.805	2	2.785	0.1293
s(WAA3pl)	1.000	1	2.624	0.1496
s(SAL2)	1.257	2	1.087	0.3882
s(BSI)	1.986	2	4.987	0.0454 *
s(SST2)	1.000	1	3.738	0.0947 .

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.503 Deviance explained = 75.3%

GCV score = 0.073361 Scale est. = 0.034003 n = 15

Formula:

$Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.07533	0.04957	1.52	0.165

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.642	2	1.872	0.2124
s(WAA3pl)	1.000	1	2.956	0.1219
s(BSI)	1.912	2	4.025	0.0592 .
s(SST2)	1.000	1	1.888	0.2048

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.461 Deviance explained = 67.5%

GCV score = 0.065461 Scale est. = 0.036858 n = 15

Formula:

$Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{SST2}, k = 3) + s(\text{BSI}, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.07533	0.05102	1.477	0.173

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.873	2	3.915	0.0588 .
s(SST2)	1.000	1	5.742	0.0395 *
s(BSI)	1.911	2	4.564	0.0419 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.429 Deviance explained = 62.4%  
GCV score = 0.063554 Scale est. = 0.039047 n = 15

Formula:

$Ra \sim s(SST2, k = 4) + s(BSI, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.07533	0.06286	1.198	0.256

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SST2)	1.000	1	2.863	0.119
s(BSI)	1.933	3	1.456	0.280

R-sq.(adj) = 0.133 Deviance explained = 31.5%  
GCV score = 0.080334 Scale est. = 0.059271 n = 15

Formula:

$Rs \sim s(SSB, k = 3) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(SAL2, k = 3) + s(BSI, k = 3) + s(SST2, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.16200	0.04733	66.81	3.15e-09 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	1.862	0.2255
s(BIOM5pl)	1.881	2	2.923	0.1364
s(WAA3pl)	1.000	1	1.629	0.2530
s(SAL2)	1.609	2	1.706	0.2650
s(BSI)	2.000	2	5.913	0.0425 *
s(SST2)	1.000	1	4.786	0.0753 .

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.837 Deviance explained = 93.6%  
GCV score = 0.09147 Scale est. = 0.033599 n = 15

Formula:

$Rs \sim s(SSB, k = 3) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST2, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.16200	0.05314	59.5	2.25e-11 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	4.508	0.0685 .
s(BIOM5pl)	1.558	2	1.243	0.3415
s(WAA3pl)	1.000	1	2.742	0.1386
s(BSI)	1.883	2	3.455	0.0860 .
s(SST2)	1.000	1	1.562	0.2486



---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.795 Deviance explained = 88.9%

GCV score = 0.084057 Scale est. = 0.042357 n = 15

Formula:

$$Rs \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST2, k = 3)$$

Parametric coefficients:

Estimate Std. Error t value Pr(&gt;|t|)

(Intercept) 3.16200 0.05385 58.72 8.98e-13 \*\*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

edf Est.rank F p-value

s(SSB) 1.335 2 9.781 0.00574 \*\*

s(WAA3pl) 1.000 1 3.211 0.10733

s(BSI) 1.819 2 2.652 0.12519

s(SST2) 1.000 1 0.693 0.42720

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.789 Deviance explained = 86.7%

GCV score = 0.073749 Scale est. = 0.043489 n = 15

Formula:

$$Rs \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3)$$

Parametric coefficients:

Estimate Std. Error t value Pr(&gt;|t|)

(Intercept) 3.16200 0.05306 59.59 5.55e-14 \*\*\*

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

edf Est.rank F p-value

s(SSB) 1.000 1 18.834 0.00150 \*\*

s(WAA3pl) 1.394 2 4.173 0.04849 \*

s(BSI) 1.708 2 2.106 0.17294

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.795 Deviance explained = 85.5%

GCV score = 0.064006 Scale est. = 0.042234 n = 15

Formula:

$$Rs \sim s(SSB, k = 4) + s(WAA3pl, k = 4)$$

Parametric coefficients:

Estimate Std. Error t value Pr(&gt;|t|)

(Intercept) 3.16200 0.05577 56.7 4.32e-15 \*\*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

edf Est.rank F p-value

s(SSB) 1.000 1 41.306 4.58e-05 \*\*\*

s(WAA3pl) 1.839 3 3.479 0.0534 .

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.774 Deviance explained = 82%  
GCV score = 0.062696 Scale est. = 0.046652 n = 15

---

Formula:  
Rs ~ s(SSB)

Parametric coefficients:  
Estimate Std. Error t value Pr(>|t|)  
(Intercept) 3.1620 0.0434 72.86 1.54e-11 \*\*\*

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:  
edf Est.rank F p-value  
s(SSB) 6.844 9 10.81 0.00221 \*\*

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.863 Deviance explained = 93%  
GCV score = 0.059221 Scale est. = 0.028251 n = 15  
>

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### Main Basin Herring

Formula:  
Ra ~ s(BIOM5pl, k = 4) + s(WAA3pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4)  
+ s(SST5, k = 3) + s(SST8, k = 3) + s(PSE, k = 4) + s(PM, k = 4) + s(SALD, k = 4)

Parametric coefficients:  
Estimate Std. Error t value Pr(>|t|)  
(Intercept) 0.01445 0.01798 0.804 0.439

Approximate significance of smooth terms:  
edf Est.rank F p-value  
s(BIOM5pl) 2.517 3 7.023 0.006597 \*\*  
s(WAA3pl) 1.000 1 10.687 0.007469 \*\*  
s(ACA) 2.198 3 3.925 0.039555 \*  
s(TEM) 2.969 3 21.720 6.28e-05 \*\*\*  
s(BSI) 2.117 3 5.756 0.012838 \*  
s(SST5) 1.670 2 3.422 0.069841 .  
s(SST8) 1.000 1 27.818 0.000262 \*\*\*  
s(PSE) 1.000 1 0.009 0.926386  
s(PM) 2.519 3 20.328 8.54e-05 \*\*\*  
s(SALD) 1.000 1 2.532 0.139831

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.89 Deviance explained = 95.8%  
GCV score = 0.02642 Scale est. = 0.0096962 n = 30

---

Formula:  
Ra ~ s(BIOM5pl, k = 4) + s(WAA3pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4)  
+ s(SST5, k = 3) + s(SST8, k = 3) + s(PM, k = 4) + s(SALD, k = 4)

Parametric coefficients:  
Estimate Std. Error t value Pr(>|t|)  
(Intercept) 0.01445 0.01731 0.835 0.42

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	2.493	3	9.865	0.001496 **
s(WAA3pl)	1.000	1	11.036	0.006140 **
s(ACA)	2.235	3	4.240	0.029501 *
s(TEM)	3.000	3	28.545	1.00e-05 ***
s(BSI)	2.106	3	7.778	0.003844 **
s(SST5)	1.652	2	3.997	0.046944 *
s(SST8)	1.000	1	32.054	0.000108 ***
s(PM)	2.596	3	23.351	2.80e-05 ***
s(SALD)	1.000	1	2.739	0.124017

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.898 Deviance explained = 95.8%  
GCV score = 0.022623 Scale est. = 0.0089878 n = 30

Formula:

$Ra \sim s(WAA3pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST5, k = 3) + s(SST8, k = 3) + s(PM, k = 4) + s(SALD, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01445	0.02249	0.642	0.53

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	1.897	3	3.723	0.034501 *
s(ACA)	1.000	1	2.179	0.160258
s(TEM)	2.989	3	15.253	7.33e-05 ***
s(BSI)	2.346	3	3.639	0.036935 *
s(SST5)	1.000	1	0.059	0.811990
s(SST8)	1.000	1	18.467	0.000611 ***
s(PM)	2.493	3	10.621	0.000505 ***
s(SALD)	1.000	1	0.510	0.485734

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.827 Deviance explained = 90.9%  
GCV score = 0.029812 Scale est. = 0.01518 n = 30

Formula:

$Ra \sim s(WAA3pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 3) + s(PM, k = 4) + s(SALD, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.03760	0.02391	1.572	0.136

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	2.668	3	4.057	0.026398 *
s(ACA)	1.000	1	0.120	0.733921
s(TEM)	3.000	3	12.532	0.000212 ***
s(BSI)	2.652	3	4.718	0.015997 *
s(SST8)	1.683	2	19.862	5.56e-05 ***
s(PM)	2.676	3	9.347	0.000938 ***
s(SALD)	1.000	1	0.002	0.962998

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.825 Deviance explained = 91.1%  
GCV score = 0.035868 Scale est. = 0.017726 n = 31

---

Formula:

$Ra \sim s(WAA3pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 3) + s(PM, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.03760	0.02313	1.625	0.123

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	2.714	3	4.317	0.020433 *
s(ACA)	1.000	1	0.149	0.704544
s(TEM)	3.000	3	13.754	0.000102 ***
s(BSI)	2.676	3	6.097	0.005619 **
s(SST8)	1.693	2	22.717	1.99e-05 ***
s(PM)	2.711	3	10.853	0.000374 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.837 Deviance explained = 91.2%  
GCV score = 0.031724 Scale est. = 0.016584 n = 31

---

Formula:

$Ra \sim s(WAA3pl, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 3) + s(PM, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.03760	0.02266	1.659	0.115

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	2.682	3	4.838	0.012833 *
s(TEM)	3.000	3	14.857	5.03e-05 ***
s(BSI)	2.663	3	6.221	0.004698 **
s(SST8)	1.776	2	24.494	9.30e-06 ***
s(PM)	2.693	3	11.470	0.000228 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.843 Deviance explained = 91%  
GCV score = 0.028708 Scale est. = 0.015915 n = 31

---

Formula:

$Ra \sim s(WAA3pl, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.03760	0.03461	1.086	0.290

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	2.394	3	10.787	0.000171 ***
s(TEM)	2.912	3	3.952	0.022249 *
s(BSI)	1.910	3	3.565	0.031587 *
s(SST8)	1.862	2	8.704	0.001776 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.634 Deviance explained = 74.5%

GCV score = 0.055005 Scale est. = 0.037124 n = 31

Formula:

Ra ~ s(WAA3pl, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 4)

Parametric coefficients:

Estimate Std. Error t value Pr(&gt;|t|)

(Intercept) 0.03760 0.03369 1.116 0.277

Approximate significance of smooth terms:

edf Est.rank F p-value

s(WAA3pl) 2.411 3 11.218 0.000147 \*\*\*

s(TEM) 3.000 3 4.882 0.010264 \*

s(BSI) 1.837 3 3.529 0.033214 \*

s(SST8) 2.389 3 7.041 0.001979 \*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.653 Deviance explained = 76.5%

GCV score = 0.053562 Scale est. = 0.035183 n = 31

Formula:

Rs ~ s(SSB, k = 3) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(ACA, k = 3) + s(TEM, k = 4) + s(BSI, k = 3) + s(SST5, k = 3) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(SALD, k = 4)

Parametric coefficients:

Estimate Std. Error t value Pr(&gt;|t|)

(Intercept) 2.97146 0.02203 134.9 &lt;2e-16 \*\*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

edf Est.rank F p-value

s(SSB) 1.132 2 1.812 0.201829

s(BIOM5pl) 1.111 2 0.850 0.449515

s(WAA3pl) 1.634 2 4.561 0.031276 \*

s(ACA) 1.000 1 2.272 0.155338

s(TEM) 3.000 3 15.012 0.000155 \*\*\*

s(BSI) 1.380 2 2.158 0.154651

s(SST5) 1.000 1 0.250 0.625115

s(SST8) 1.000 1 20.244 0.000581 \*\*\*

s(PSE) 1.000 1 3.636 0.078610 .

s(PM) 2.589 3 9.981 0.001068 \*\*

s(SALD) 1.000 1 0.922 0.354243

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.88 Deviance explained = 94.6%

GCV score = 0.033196 Scale est. = 0.014554 n = 30

Formula:

Rs ~ s(SSB, k = 3) + s(WAA3pl, k = 3) + s(ACA, k = 3) + s(TEM, k = 4) + s(BSI, k = 3) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(SALD, k = 4)

Parametric coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept) 3.00536   0.02192  137.1 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Approximate significance of smooth terms:

```

      edf Est.rank    F p-value
s(SSB)  1.850      2 28.246 1.70e-05 ***
s(WAA3pl) 1.000      1 11.161 0.005214 **
s(ACA)   1.679      2  1.761 0.209927
s(TEM)   3.000      3 12.501 0.000374 ***
s(BSI)   1.691      2  3.524 0.059399 .
s(SST8)  2.019      3 15.352 0.000136 ***
s(PSE)   1.000      1  2.465 0.140099
s(PM)    2.425      3 11.701 0.000511 ***
s(SALD)  2.136      3  2.646 0.092298 .

```

```

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

R-sq.(adj) = 0.903 Deviance explained = 95.7%  
 GCV score = 0.034992 Scale est. = 0.014899 n = 31

Formula:

$R_s \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(TEM, k = 4) + s(BSI, k = 3) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(SALD, k = 4)$

Parametric coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept) 3.00536   0.02238  134.3 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Approximate significance of smooth terms:

```

      edf Est.rank    F p-value
s(SSB)  1.669      2 22.762 2.94e-05 ***
s(WAA3pl) 1.200      2  5.488 0.016362 *
s(TEM)   3.000      3 13.604 0.000152 ***
s(BSI)   1.463      2  2.807 0.092314 .
s(SST8)  2.102      3 14.669 0.000101 ***
s(PSE)   1.000      1  3.701 0.073668 .
s(PM)    2.464      3 13.230 0.000177 ***
s(SALD)  2.189      3  2.167 0.134695

```

```

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

R-sq.(adj) = 0.899 Deviance explained = 95%  
 GCV score = 0.032272 Scale est. = 0.015525 n = 31

Formula:

$R_s \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(TEM, k = 4) + s(BSI, k = 3) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept) 3.00536   0.02391  125.7 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Approximate significance of smooth terms:

```

      edf Est.rank    F p-value

```

```

s(SSB) 1.000 1 16.504 0.000790 ***
s(WAA3pl) 1.586 2 4.401 0.028568 *
s(TEM) 3.000 3 14.725 5.24e-05 ***
s(BSI) 1.502 2 3.648 0.047720 *
s(SST8) 2.246 3 16.360 2.74e-05 ***
s(PSE) 1.000 1 4.394 0.051115 .
s(PM) 2.425 3 12.526 0.000137 ***

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.884 Deviance explained = 93.3%  
 GCV score = 0.031873 Scale est. = 0.017726 n = 31

Formula:

$R_s \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(TEM, k = 4) + s(BSI, k = 3) + s(SST8, k = 4) + s(PSE, k = 4)$

Parametric coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept) 3.00536 0.03438 87.42 <2e-16 ***

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

```

      edf Est.rank  F p-value
s(SSB) 1.905 2 15.676 7.64e-05 ***
s(WAA3pl) 1.000 1 18.596 0.000329 ***
s(TEM) 1.000 1 0.028 0.868914
s(BSI) 1.871 2 8.731 0.001836 **
s(SST8) 1.898 3 3.346 0.039384 *
s(PSE) 2.026 3 3.238 0.043535 *

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.761 Deviance explained = 83.8%  
 GCV score = 0.055949 Scale est. = 0.03664 n = 31

Formula:

$R_s \sim s(SSB, k = 3) + s(WAA3pl, k = 3) + s(PSE, k = 4) + s(BSI, k = 4) + s(SST8, k = 4)$

Parametric coefficients:

```

      Estimate Std. Error t value Pr(>|t|)
(Intercept) 3.00536 0.03391 88.64 <2e-16 ***

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

```

      edf Est.rank  F p-value
s(SSB) 1.892 2 17.036 3.93e-05 ***
s(WAA3pl) 1.000 1 20.223 0.000196 ***
s(PSE) 2.057 3 3.209 0.043782 *
s(BSI) 2.013 3 6.366 0.003041 **
s(SST8) 1.915 3 3.414 0.036111 *

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.767 Deviance explained = 83.6%  
 GCV score = 0.052302 Scale est. = 0.035637 n = 31

>

---

**Gulf of Riga Herring**

Formula:

$\text{RECR} \sim \text{s}(\text{BIOM5pl}, k = 5) + \text{s}(\text{WAA2pl}, k = 5) + \text{s}(\text{ACA}, k = 5) + \text{s}(\text{EUR}, k = 5) + \text{s}(\text{BSI}, k = 5) + \text{s}(\text{SST5}, k = 5)$

R-sq.(adj) = 0.537 Deviance explained = 74.7%

GCV score = 0.19701 Scale est. = 0.14374 n = 28

$\text{RECR} \sim \text{s}(\text{BIOM5pl}, k = 5) + \text{s}(\text{BSI}, k = 5) + \text{s}(\text{ACA}, k = 5) + \text{s}(\text{EUR}, k = 5) + \text{s}(\text{SST5}, k = 5)$

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	3.600	0.0714 .
s(BSI)	1.000	1	0.154	0.6987
s(ACA)	1.000	1	0.265	0.6121
s(EUR)	1.000	1	3.563	0.0728 .
s(SST5)	1.653	4	1.504	0.2364

---

R-sq.(adj) = 0.55 Deviance explained = 74.9%

GCV score = 0.17964 Scale est. = 0.13696 n = 28

---

Formula:

$\text{RECR} \sim \text{s}(\text{BIOM5pl}, k = 5) + \text{s}(\text{ACA}, k = 5) + \text{s}(\text{EUR}, k = 5) + \text{s}(\text{SST5}, k = 5)$

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	4.577	0.0436 *
s(ACA)	1.000	1	0.590	0.4505
s(EUR)	1.000	1	3.616	0.0702 .
s(SST5)	1.705	4	4.167	0.0114 *

---

R-sq.(adj) = 0.567 Deviance explained = 74.8%

GCV score = 0.16487 Scale est. = 0.13128 n = 28

---

Formula:

$\text{RECR} \sim \text{s}(\text{BIOM5pl}) + \text{s}(\text{EUR}) + \text{s}(\text{SST5})$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	14.65776	0.06822	214.9	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	4.482	0.0451 *
s(EUR)	1.000	1	3.307	0.0819 .
s(SST5)	1.664	4	3.980	0.0133 *

---

R-sq.(adj) = 0.533 Deviance explained = 73.9%

GCV score = 0.15635 Scale est. = 0.13031 n = 28

---

Formula:

$\text{RECR} \sim \text{s}(\text{BIOM5pl}) + \text{s}(\text{SST5})$



Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	14.790	0.000776 ***
s(SST5)	1.962	4	8.097	0.000278 ***

---

R-sq.(adj) = 0.545 Deviance explained = 71.6%  
GCV score = 0.15984 Scale est. = 0.13722 n = 28

Family: gaussian  
Link function: identity

Formula:

$R_s \sim s(\text{BIOM5pl}, k = 5) + s(\text{WAA2pl}, k = 5) + s(\text{ACA}, k = 5) + s(\text{EUR}, k = 5) + s(\text{BSI}, k = 5) + s(\text{SST5}, k = 5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05705	59.73	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	0.008	0.9298
s(WAA2pl)	1.000	1	2.252	0.1504
s(ACA)	1.000	1	3.432	0.0801 .
s(EUR)	1.000	1	4.226	0.0543 .
s(BSI)	2.912	4	1.650	0.2045
s(SST5)	1.766	4	3.492	0.0276 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.637 Deviance explained = 75.4%  
GCV score = 0.13924 Scale est. = 0.091116 n = 28

Formula:

$R_s \sim s(\text{WAA2pl}, k = 5) + s(\text{BSI}, k = 5) + s(\text{ACA}, k = 5) + s(\text{EUR}, k = 5) + s(\text{SST5}, k = 5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05545	61.44	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA2pl)	1.000	1	2.658	0.1193
s(BSI)	2.974	4	1.817	0.1667
s(ACA)	1.000	1	3.727	0.0684 .
s(EUR)	1.000	1	4.648	0.0440 *
s(SST5)	1.805	4	3.752	0.0203 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.657 Deviance explained = 75.6%  
GCV score = 0.12541 Scale est. = 0.086096 n = 28

---

Formula:

$Rs \sim s(WAA2pl, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(SST5, k = 5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05936	57.4	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA2pl)	1.000	1	1.951	0.17634
s(ACA)	1.000	1	2.419	0.13405
s(EUR)	1.000	1	3.318	0.08204 .
s(SST5)	1.826	4	6.279	0.00155 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.607 Deviance explained = 67.7%

GCV score = 0.12456 Scale est. = 0.098646 n = 28

---

Formula:

$Rs \sim s(ACA) + s(EUR) + s(SST5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05983	56.94	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(ACA)	1.000	1	1.753	0.19856
s(EUR)	1.000	1	1.358	0.25594
s(SST5)	2.087	5	5.745	0.00141 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.601 Deviance explained = 66.1%

GCV score = 0.12249 Scale est. = 0.10023 n = 28

---

Formula:

$Rs \sim s(ACA) + s(SST5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05989	56.89	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(ACA)	1.000	1	0.600	0.446132
s(SST5)	2.158	5	7.003	0.000374 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.6 Deviance explained = 64.7%

GCV score = 0.11796 Scale est. = 0.10044 n = 28

---

Formula:

$R_s \sim s(SST5)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	3.40707	0.05994	56.84	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SST5)	2.001	5	8.828	6.25e-05 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.599 Deviance explained = 62.9%

GCV score = 0.11269 Scale est. = 0.10061 n = 28

>

---

### Bothnian Sea Herring

Formula:

$RECR \sim s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	15.28960	0.06894	221.8	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	0.039	0.84635
s(BIOM5pl)	1.000	1	0.061	0.80758
s(WAA3pl)	1.271	2	1.138	0.34070
s(BSI)	1.000	1	2.334	0.14248
s(SST6)	1.000	1	11.806	0.00266 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.443 Deviance explained = 66%

GCV score = 0.16287 Scale est. = 0.12359 n = 26

---

Formula:

$RECR \sim s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	15.28952	0.06726	227.3	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	0.027	0.86998
s(WAA3pl)	1.306	2	1.353	0.28033
s(BSI)	1.000	1	2.804	0.10907
s(SST6)	1.000	1	13.040	0.00167 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.469 Deviance explained = 66.1%  
 GCV score = 0.14779 Scale est. = 0.11763 n = 26

Formula:

RECR ~ s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	15.28954	0.06573	232.6	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA3pl)	1.322	2	1.568	0.231252
s(BSI)	1.000	1	3.544	0.073253 .
s(SST6)	1.000	1	16.908	0.000471 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.499 Deviance explained = 66.1%  
 GCV score = 0.13472 Scale est. = 0.11232 n = 26

Formula:

RECR ~ s(BSI) + s(SST6)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	15.29471	0.06743	226.8	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	1.128	3	1.47	0.248948
s(SST6)	1.000	1	19.26	0.000216 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.406 Deviance explained = 62.3%  
 GCV score = 0.1344 Scale est. = 0.11823 n = 26

Formula:

RECR ~ s(SST6)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	15.30152	0.07001	218.6	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SST6)	1	1	33.16	6.19e-06 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.395 Deviance explained = 57.4%  
 GCV score = 0.13804 Scale est. = 0.12743 n = 26

Formula:

Rs ~ s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.87111	0.06883	41.71	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	3.872	0.06339 .
s(BIOM5pl)	1.000	1	0.013	0.90949
s(WAA3pl)	1.000	1	0.412	0.52849
s(BSI)	1.374	2	2.570	0.10198
s(SST6)	1.000	1	8.202	0.00972 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.474 Deviance explained = 58.7%

GCV score = 0.16319 Scale est. = 0.12318 n = 26

Formula:

$R_s \sim s(SSB, k = 4) + s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.87111	0.06781	42.34	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	23.093	9.73e-05 ***
s(BSI)	1.195	3	2.009	0.14387
s(WAA3pl)	1.000	1	0.665	0.42390
s(SST6)	1.000	1	9.116	0.00657 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.489 Deviance explained = 57.5%

GCV score = 0.14941 Scale est. = 0.11956 n = 26

Formula:

$R_s \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST6, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.87111	0.06651	43.17	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.000	1	23.398	8.28e-05 ***
s(BSI)	1.484	3	2.049	0.1370
s(SST6)	1.000	1	9.474	0.0056 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.509 Deviance explained = 57.7%

GCV score = 0.13898 Scale est. = 0.11501 n = 26

---

Formula:

$R_s \sim s(SSB) + s(SST6)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.87111	0.04791	59.92	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	8.137	9	8.644	0.000376 ***
s(SST6)	4.107	9	6.125	0.002003 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.745 Deviance explained = 87%

GCV score = 0.12167 Scale est. = 0.059691 n = 26

>

---

### Bothnian Bay Herring

Formula:

$R_a \sim s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	0.003	0.955
s(WAA3pl)	1.000	1	0.114	0.739
s(BSI)	1.257	2	0.682	0.517
s(SST6)	1.000	1	1.599	0.221

R-sq.(adj) = -0.0787 Deviance explained = 11.3%

GCV score = 0.49676 Scale est. = 0.3923 n = 25

---

Formula:

$R_a \sim s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	1.596	3	1.050	0.392
s(WAA3pl)	1.043	3	0.706	0.559
s(SST6)	1.000	1	1.587	0.222

R-sq.(adj) = -0.00111 Deviance explained = 15.1%

GCV score = 0.44703 Scale est. = 0.36408 n = 25

---

Formula:

$R_a \sim s(SST6, k = 3) + s(BSI, k = 3)$

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SST6)	1.000	1	1.400	0.250
s(BSI)	1.516	2	1.048	0.368

R-sq.(adj) = 0.0238 Deviance explained = 12.6%

GCV score = 0.41312 Scale est. = 0.35501 n = 25

---

Formula: Model3

$Ra \sim s(SST6)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-0.0184	0.1194	-0.154	0.879

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SST6)	1	1	1.483	0.236

R-sq.(adj) = 0.0197 Deviance explained = 6.06%

GCV score = 0.3875 Scale est. = 0.3565 n = 25

>

---

Formula:

$Rs \sim s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.7352	0.1275	21.46	1.35e-14 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.024	3	0.952	0.436
s(BIOM5pl)	1.000	1	0.112	0.742
s(WAA3pl)	1.000	1	0.169	0.686
s(BSI)	1.344	2	0.765	0.479
s(SST6)	1.000	1	1.379	0.255

R-sq.(adj) = 0.332 Deviance explained = 48.2%

GCV score = 0.54489 Scale est. = 0.4061 n = 25

---

Formula:

$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.7352	0.1227	22.3	3.52e-15 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.139	3	2.179	0.124
s(BSI)	1.680	3	1.099	0.373
s(WAA3pl)	1.000	1	0.247	0.625
s(SST6)	1.000	1	1.558	0.227

R-sq.(adj) = 0.382 Deviance explained = 50.6%

GCV score = 0.49023 Scale est. = 0.37613 n = 25

---

Formula:

$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST6, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.7352	0.1204	22.72	7.05e-16 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.00	1	12.307	0.00218 **
s(BSI)	1.76	3	1.202	0.33423
s(SST6)	1.00	1	1.304	0.26685

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.404 Deviance explained = 49.7%  
GCV score = 0.44768 Scale est. = 0.36245 n = 25

---

Formula:

$R_s \sim s(SSB) + s(SST6)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.7352	0.1216	22.49	<2e-16 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1	1	17.451	0.000391 ***
s(SST6)	1	1	1.606	0.218305

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.392 Deviance explained = 44.3%  
GCV score = 0.42031 Scale est. = 0.36987 n = 25

---

Formula:

$R_s \sim s(SSB)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	2.7352	0.1232	22.20	<2e-16 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1	1	15.45	0.000668 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.376 Deviance explained = 40.2%  
GCV score = 0.41263 Scale est. = 0.37962 n = 25

>

---

### Baltic Sprat

Formula:

$R_a \sim s(BIOM5pl, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST5, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09789	0.155	0.879



Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	0.596	0.45065
s(WAA2pl)	1.000	1	2.569	0.12750
s(ACA)	1.000	1	3.198	0.09167 .
s(TEM)	1.000	1	1.015	0.32796
s(BSI)	2.371	3	5.356	0.00889 **
s(SST5)	1.000	1	0.005	0.94372
s(SST8)	1.000	1	3.480	0.07958 .
s(PSE)	1.000	1	4.485	0.04933 *
s(PM)	1.942	3	1.950	0.16008
s(CLA)	1.799	3	1.324	0.29944

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.439 Deviance explained = 68.4%

GCV score = 0.54523 Scale est. = 0.29703 n = 31

---

Formula:

$Ra \sim s(\text{BIOM5pl}, k = 4) + s(\text{WAA2pl}, k = 4) + s(\text{ACA}, k = 4) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 4) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4) + s(\text{CLA}, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09494	0.16	0.875

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BIOM5pl)	1.000	1	0.629	0.43803
s(WAA2pl)	1.000	1	2.792	0.11224
s(ACA)	1.000	1	3.631	0.07305 .
s(TEM)	1.000	1	1.057	0.31771
s(BSI)	2.408	3	5.910	0.00555 **
s(SST8)	1.000	1	3.721	0.06988 .
s(PSE)	1.000	1	4.905	0.04010 *
s(PM)	2.008	3	2.037	0.14518
s(CLA)	1.822	3	1.450	0.26192

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.472 Deviance explained = 68.8%

GCV score = 0.48765 Scale est. = 0.27941 n = 31

---

Formula:

$Ra \sim s(\text{WAA2pl}, k = 4) + s(\text{ACA}, k = 4) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 4) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4) + s(\text{CLA}, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09368	0.162	0.873

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA2pl)	1.000	1	2.977	0.10096
s(ACA)	1.000	1	3.368	0.08243 .
s(TEM)	1.000	1	0.929	0.34737
s(BSI)	2.614	3	7.594	0.00161 **
s(SST8)	1.000	1	3.022	0.09861 .
s(PSE)	1.000	1	6.101	0.02333 *
s(PM)	1.859	3	2.010	0.14726

s(CLA) 1.845 3 1.586 0.22639

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.486 Deviance explained = 68%

GCV score = 0.45146 Scale est. = 0.27206 n = 31

Formula:

$Ra \sim s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09222	0.164	0.871

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA2pl)	1.000	1	3.290	0.08516 .
s(ACA)	1.000	1	2.601	0.12293
s(BSI)	2.629	3	7.815	0.00128 **
s(SST8)	1.000	1	3.038	0.09715 .
s(PSE)	1.000	1	5.539	0.02925 *
s(PM)	2.061	3	2.130	0.12932
s(CLA)	1.855	3	1.720	0.19601

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.502 Deviance explained = 67.7%

GCV score = 0.42011 Scale est. = 0.26364 n = 31

Formula:

$Ra \sim s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09492	0.16	0.875

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(WAA2pl)	1.000	1	0.927	0.34686
s(ACA)	1.000	1	0.811	0.37826
s(BSI)	2.247	3	5.443	0.00644 **
s(SST8)	1.451	3	1.114	0.36631
s(PSE)	1.075	3	2.075	0.13477
s(PM)	2.634	3	2.253	0.11254

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.472 Deviance explained = 63.8%

GCV score = 0.42043 Scale est. = 0.27929 n = 31

Formula:

$Ra \sim s(WAA2pl, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09285	0.163	0.872

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
--	-----	----------	---	---------

```

s(WAA2pl) 1.000      1 0.438 0.51514
s(BSI)    2.225      3 6.485 0.00275 **
s(SST8)   1.668      3 1.280 0.30684
s(PSE)    1.116      3 2.261 0.11066
s(PM)     2.727      3 3.344 0.03841 *

```

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.495 Deviance explained = 64.2%  
 GCV score = 0.38966 Scale est. = 0.26727 n = 31

---

Formula:

$Ra \sim s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09278	0.163	0.872

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	2.254	3	6.395	0.00271 **
s(SST8)	1.592	3	1.133	0.35706
s(PSE)	1.000	1	6.742	0.01632 *
s(PM)	2.727	3	3.391	0.03564 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.496 Deviance explained = 62.3%  
 GCV score = 0.36889 Scale est. = 0.26687 n = 31  
 > summary(mod.r7)

Family: gaussian

Link function: identity

Formula:

$Ra \sim s(BSI) + s(PSE, k = 4) + s(PM)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09452	0.16	0.874

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	2.493	5	4.506	0.00502 **
s(PSE)	1.016	3	2.803	0.06186 .
s(PM)	2.921	6	2.054	0.09799 .

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.477 Deviance explained = 58.9%  
 GCV score = 0.36424 Scale est. = 0.27694 n = 31  
 > summary(mod.r8)

Family: gaussian

Link function: identity

Formula:

$Ra \sim s(BSI) + s(PSE)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.09452	0.16	0.874

(Intercept) 0.01517 0.07999 0.19 0.851

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	2.189	5	6.717	0.000759 ***
s(PSE)	7.436	9	4.252	0.003230 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.625 Deviance explained = 74.6%  
GCV score = 0.30179 Scale est. = 0.19835 n = 31

Formula:

$Ra \sim s(BSI) + s(PM)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.01517	0.10548	0.144	0.887

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(BSI)	2.102	5	2.676	0.0453 *
s(PM)	2.873	6	1.546	0.2043

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.349 Deviance explained = 45.7%  
GCV score = 0.42731 Scale est. = 0.34494 n = 31

>

Formula:

$Rs \sim s(SSB, k = 3) + s(BIOM5pl, k = 3) + s(WAA2pl, k = 3) + s(ACA, k = 3) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST5, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.41427	0.09591	46.02	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.682	2	4.066	0.03759 *
s(BIOM5pl)	1.000	1	1.161	0.29740
s(WAA2pl)	1.000	1	1.901	0.18719
s(ACA)	1.000	1	3.718	0.07196 .
s(TEM)	1.000	1	0.632	0.43830
s(BSI)	2.549	3	6.379	0.00485 **
s(SST5)	1.000	1	0.319	0.57997
s(SST8)	1.000	1	3.229	0.09145 .
s(PSE)	1.000	1	2.867	0.11002
s(PM)	1.000	1	0.933	0.34867
s(CLA)	1.946	3	1.883	0.17358

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.527 Deviance explained = 75.1%  
GCV score = 0.55867 Scale est. = 0.28516 n = 31

---

Formula:

$$Rs \sim s(SSB, k = 4) + s(BIOM5pl, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.41427	0.09141	48.29	<2e-16 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.661	3	2.314	0.1153
s(BIOM5pl)	1.000	1	1.477	0.2421
s(WAA2pl)	1.000	1	2.799	0.1141
s(ACA)	1.000	1	3.630	0.0752 .
s(TEM)	1.000	1	0.750	0.3995
s(BSI)	2.398	3	6.092	0.0059 **
s(SST8)	1.000	1	3.989	0.0634 .
s(PSE)	1.000	1	2.397	0.1414
s(PM)	2.310	3	1.783	0.1915
s(CLA)	1.875	3	1.605	0.2281

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.57 Deviance explained = 77.4%  
GCV score = 0.50966 Scale est. = 0.25904 n = 31

---

Formula:

$$Rs \sim s(SSB, k = 4) + s(WAA2pl, k = 4) + s(BIOM5pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.41427	0.08823	50.03	<2e-16 ***

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.812	3	2.541	0.09204 .
s(WAA2pl)	1.000	1	2.843	0.11068
s(BIOM5pl)	1.000	1	1.420	0.25036
s(ACA)	1.000	1	2.938	0.10536
s(BSI)	2.437	3	7.135	0.00280 **
s(SST8)	1.000	1	3.761	0.06985 .
s(PSE)	1.000	1	2.216	0.15553
s(PM)	2.450	3	1.978	0.15702
s(CLA)	1.901	3	1.733	0.19963

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.6 Deviance explained = 78.1%  
GCV score = 0.45616 Scale est. = 0.24133 n = 31

---

Formula:

$$Rs \sim s(SSB, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
--	----------	------------	---------	----------

(Intercept) 4.41427 0.09031 48.88 <2e-16 \*\*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.714	3	2.226	0.120502
s(WAA2pl)	1.000	1	1.966	0.178072
s(ACA)	1.000	1	2.675	0.119468
s(BSI)	2.727	3	8.951	0.000778 ***
s(SST8)	1.000	1	2.639	0.121801
s(PSE)	1.000	1	4.644	0.045086 *
s(PM)	1.773	3	1.866	0.171934
s(CLA)	1.945	3	1.946	0.158756

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.581 Deviance explained = 75.1%

GCV score = 0.43925 Scale est. = 0.25281 n = 31

Formula:

$R_s \sim s(SSB, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.41427	0.08839	49.94	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.934	3	3.954	0.02531 *
s(ACA)	1.000	1	0.631	0.43736
s(BSI)	2.588	3	7.884	0.00150 **
s(SST8)	1.379	3	1.140	0.36017
s(PSE)	1.000	1	4.224	0.05490 .
s(PM)	2.663	3	2.423	0.09988 .
s(CLA)	1.705	3	1.037	0.40018

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.598 Deviance explained = 76.3%

GCV score = 0.42347 Scale est. = 0.24222 n = 31

Formula:

$R_s \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.41427	0.08578	51.46	<2e-16 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	2.050	3	4.261	0.019082 *
s(BSI)	2.540	3	8.807	0.000795 ***
s(SST8)	1.684	3	1.416	0.270143
s(PSE)	1.000	1	4.309	0.052277 .

s(PM) 2.774 3 3.813 0.027839 \*  
s(CLA) 1.668 3 0.965 0.430216

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.622 Deviance explained = 76.9%  
GCV score = 0.38676 Scale est. = 0.2281 n = 31

Formula:

$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

Estimate Std. Error t value Pr(>|t|)  
(Intercept) 4.41427 0.08777 50.29 <2e-16 \*\*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	2.097	3	3.641	0.03025 *
s(BSI)	2.285	3	7.149	0.00188 **
s(SST8)	1.709	3	1.391	0.27444
s(PSE)	1.000	1	3.470	0.07719 .
s(PM)	2.808	3	3.543	0.03307 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.604 Deviance explained = 73.5%  
GCV score = 0.36832 Scale est. = 0.23883 n = 31

Formula:

$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

Estimate Std. Error t value Pr(>|t|)  
(Intercept) 4.41427 0.09011 48.99 <2e-16 \*\*\*

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	F	p-value
s(SSB)	1.861	3	2.961	0.05456 .
s(BSI)	2.459	3	7.788	0.00101 **
s(PSE)	1.000	1	4.444	0.04667 *
s(PM)	2.754	3	3.792	0.02485 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.582 Deviance explained = 69.5%  
GCV score = 0.35592 Scale est. = 0.25173 n = 31

Formula:

$Rs \sim s(BSI, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$

Parametric coefficients:

Estimate Std. Error t value Pr(>|t|)  
(Intercept) 4.4143 0.1021 43.24 <2e-16 \*\*\*

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

---

	edf	Est.rank	F	p-value	
s(BSI)	2.344	3	5.699	0.00429	**
s(PSE)	1.000	1	10.922	0.00297	**
s(PM)	2.594	3	3.010	0.04990	*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.464 Deviance explained = 57%

GCV score = 0.41627 Scale est. = 0.32311 n = 31



## Annex 5: All models of the statistical analysis of environment-recruitment relationships

WB – Western Baltic Herring (DIIIa & SD22-24), MB – Main Basin Herring (SD25-29&32excl. GOR), GOR – Gulf of Riga Herring, BS – Bothnian Sea Herring (SD30), BB – Bothnian Bay herring (SD31), S – Baltic Sprat (SD22-32); bold rows – finally selected models; R – recruitment, Ra – recruitment anomalies, Rs – recruitment success.

Stock	Response	Model	GCV	Expl. Dev.
WB	Ra	$Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{SAL2}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$	0.073361	75.3
WB	Ra	$Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$	0.065461	67.5
<b>WB</b>	<b>Ra</b>	<b><math>Ra \sim s(\text{BIOM5pl}, k = 3) + s(\text{SST2}, k = 3) + s(\text{BSI}, k = 3)</math></b>	<b>0.063554</b>	<b>62.4</b>
WB	Ra	$Ra \sim s(\text{SST2}, k = 4) + s(\text{BSI}, k = 4)$	0.080334	31.5
WB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{SAL2}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$	0.09147	93.6
WB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$	0.084057	88.9
WB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{BSI}, k = 3) + s(\text{SST2}, k = 3)$	0.073749	86.7
WB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{BSI}, k = 3)$	0.064006	85.5
WB	Rs	$Rs \sim s(\text{SSB}, k = 4) + s(\text{WAA3pl}, k = 4)$	0.062696	82.0
<b>WB</b>	<b>Rs</b>	<b><math>Rs \sim s(\text{SSB})</math></b>	<b>0.059221</b>	<b>93.0</b>
MB	Ra	$Ra \sim s(\text{WAA3pl}, k = 4) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 4) + s(\text{SST8}, k = 4)$	0.05356	75.6
MB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{BIOM5pl}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{ACA}, k = 3) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 3) + s(\text{SST5}, k = 3) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4) + s(\text{SALD}, k = 4)$	0.03319	94.6
MB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{ACA}, k = 3) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 3) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4) + s(\text{SALD}, k = 4)$	0.034992	95.7
MB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 3) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4) + s(\text{SALD}, k = 4)$	0.032272	95
<b>MB</b>	<b>Rs</b>	<b><math>Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 3) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4) + s(\text{PM}, k = 4)</math></b>	<b>0.031873</b>	<b>93.3</b>
MB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{TEM}, k = 4) + s(\text{BSI}, k = 3) + s(\text{SST8}, k = 4) + s(\text{PSE}, k = 4)$	0.055949	83.8
MB	Rs	$Rs \sim s(\text{SSB}, k = 3) + s(\text{WAA3pl}, k = 3) + s(\text{PSE}, k = 4) + s(\text{BSI}, k = 4) + s(\text{SST8}, k = 4)$	0.052302	83.6
GOR	R	$\text{RECR} \sim s(\text{BIOM5pl}, k = 5) + s(\text{WAA2pl}, k = 5) + s(\text{ACA}, k = 5) + s(\text{EUR}, k = 5) + s(\text{BSI}, k = 5) + s(\text{SST5}, k = 5)$	0.19701	74.7

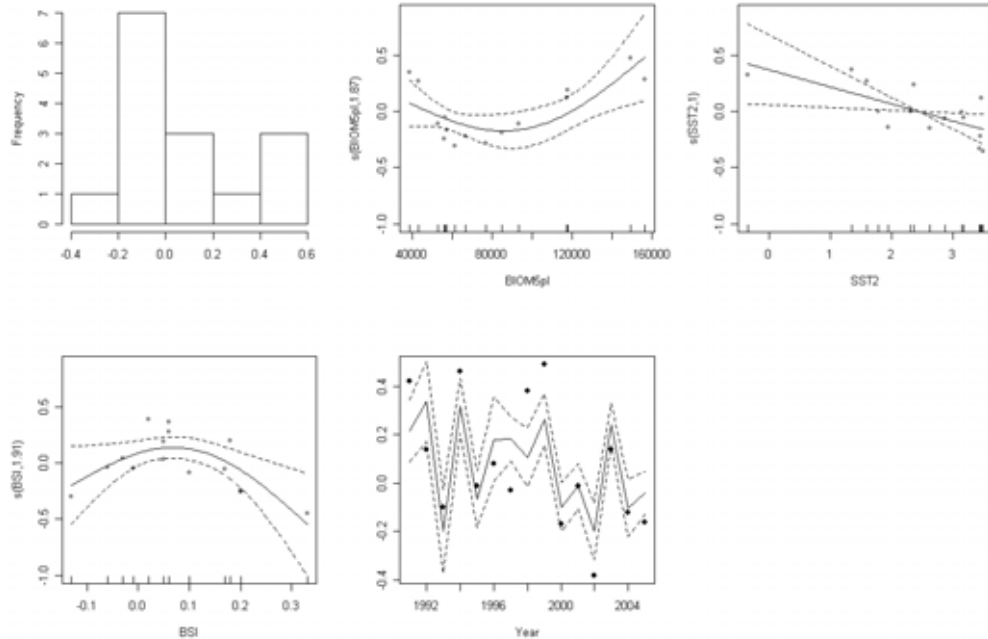
Stock	Response	Model	GCV	Expl. Dev.
GOR	R	$RECR \sim s(BIOM5pl, k = 5) + s(BSI, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(SST5, k = 5)$	0.17964	74.9
GOR	R	$RECR \sim s(BIOM5pl, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(SST5, k = 5)$	0.16487	74.8
<b>GOR</b>	<b>R</b>	<b><math>RECR \sim s(BIOM5pl) + s(EUR) + s(SST5)</math></b>	<b>0.15635</b>	<b>73.9</b>
GOR	R	$RECR \sim s(BIOM5pl) + s(SST5)$	0.15984	71.6
GOR	Rs	$Rs \sim s(BIOM5pl, k = 5) + s(WAA2pl, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(BSI, k = 5) + s(SST5, k = 5)$	0.13924	75.4
GOR	Rs	$Rs \sim s(WAA2pl, k = 5) + s(BSI, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(SST5, k = 5)$	0.12541	75.6
GOR	Rs	$Rs \sim s(WAA2pl, k = 5) + s(ACA, k = 5) + s(EUR, k = 5) + s(SST5, k = 5)$	0.12456	67.7
GOR	Rs	$Rs \sim s(ACA) + s(EUR) + s(SST5)$	0.12249	66.1
GOR	Rs	$Rs \sim s(ACA) + s(SST5)$	0.11796	64.7
<b>GOR</b>	<b>Rs</b>	<b><math>Rs \sim s(SST5)</math></b>	<b>0.11269</b>	<b>62.9</b>
BS	R	$RECR \sim s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.16287	66.0
BS	R	$RECR \sim s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.14779	66.1
BS	R	$RECR \sim s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.13472	66.1
<b>BS</b>	<b>R</b>	<b><math>RECR \sim s(BSI) + s(SST6)</math></b>	<b>0.1344</b>	<b>62.3</b>
BS	R	$RECR \sim s(SST6)$	0.13804	57.4
BS	Rs	$Rs \sim s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.16319	58.7
BS	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$	0.14941	57.5
BS	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST6, k = 4)$	0.13898	57.7
<b>BS</b>	<b>Rs</b>	<b><math>Rs \sim s(SSB) + s(SST6)</math></b>	<b>0.12167</b>	<b>87.0</b>
BB	Ra	$Ra \sim s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.49676	11.3
BB	Ra	$Ra \sim s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$	0.44703	15.1
BB	Ra	$Ra \sim s(SST6, k = 3) + s(BSI, k = 3)$	0.41312	12.6
<b>BB</b>	<b>Ra</b>	<b><math>Ra \sim s(SST6)</math></b>	<b>0.3875</b>	<b>6.1</b>
BB	Rs	$Rs \sim s(SSB) + s(BIOM5pl, k = 3) + s(WAA3pl, k = 3) + s(BSI, k = 3) + s(SST6, k = 3)$	0.54489	48.2
BB	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(WAA3pl, k = 4) + s(SST6, k = 4)$	0.49023	50.6
BB	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST6, k = 4)$	0.44768	49.7
BB	Rs	$Rs \sim s(SSB) + s(SST6)$	0.42031	44.3
<b>BB</b>	<b>Rs</b>	<b><math>Rs \sim s(SSB)</math></b>	<b>0.41263</b>	<b>40.2</b>
Sprat	Ra	$Ra \sim s(BIOM5pl, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST5, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.54523	68.4
Sprat	Ra	$Ra \sim s(BIOM5pl, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.48765	68.8

Stock	Response	Model	GCV	Expl. Dev.
Sprat	Ra	$Ra \sim s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.45146	68.0
Sprat	Ra	$Ra \sim s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.42011	67.7
Sprat	Ra	$Ra \sim s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$	0.42043	63.8
Sprat	Ra	$Ra \sim s(WAA2pl, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$	0.38966	64.2
Sprat	Ra	$Ra \sim s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$	0.36889	62.3
<i>Sprat</i>	<i>Ra</i>	<i><math>Ra \sim s(BSI) + s(PSE, k = 4) + s(PM)</math></i>	<i>0.36424</i>	<i>58.9</i>
<b>S</b>	<b>Ra</b>	<b><math>Ra \sim s(BSI) + s(PSE)</math></b>	<b>0.30179</b>	<b>74.6</b>
S	Ra	$Ra \sim s(BSI) + s(PM)$	0.42731	45.7
S	Rs	$Rs \sim s(SSB, k = 3) + s(BIOM5pl, k = 3) + s(WAA2pl, k = 3) + s(ACA, k = 3) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST5, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.55867	75.1
S	Rs	$Rs \sim s(SSB, k = 4) + s(BIOM5pl, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(TEM, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.50966	77.4
S	Rs	$Rs \sim s(SSB, k = 4) + s(WAA2pl, k = 4) + s(BIOM5pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.45616	78.1
S	Rs	$Rs \sim s(SSB, k = 4) + s(WAA2pl, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.43925	75.1
S	Rs	$Rs \sim s(SSB, k = 4) + s(ACA, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.42347	76.3
S	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4) + s(CLA, k = 4)$	0.38676	76.9
S	Rs	$Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(SST8, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$	0.36832	73.5
<b>S</b>	<b>Rs</b>	<b><math>Rs \sim s(SSB, k = 4) + s(BSI, k = 4) + s(PSE, k = 4) + s(PM, k = 4)</math></b>	<b>0.35592</b>	<b>69.5</b>
S	Rs	$Rs \sim s(BSI, k = 4) + s(PSE, k = 4) + s(PM, k = 4)$	0.41627	57.0

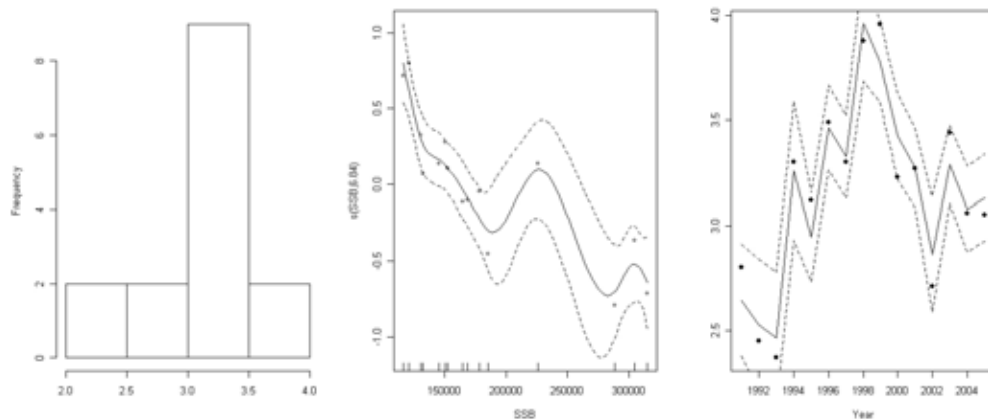
For codes of the variables see Annex 3.

## Annex 6: Diagnostic plots of the finally selected environment-recruitment models

### Western Baltic Herring

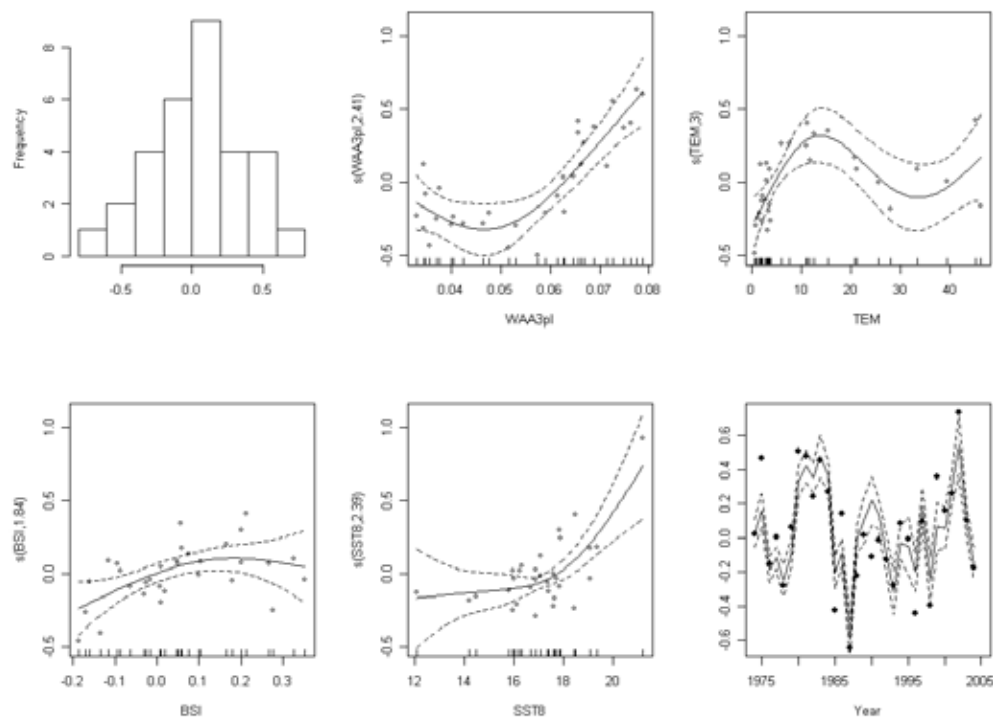


a) Diagnostic plots of the finally selected environment-recruitment models using Ra (hier model); from left to right: distribution of residuals, parental effect of older individuals (BIOM5pl – biomass of age-groups 5+), effect of surface salinity in February (SST2), effect of the Baltic Sea index (BSI), predicted (lines with 95% confidence limits) vs. observed (points) Ra.

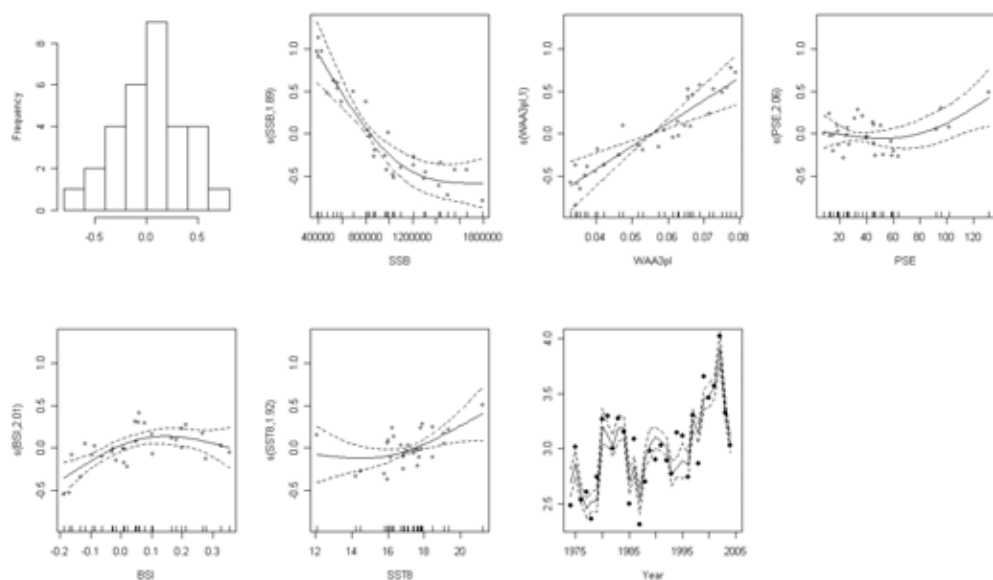


b) Diagnostic plots of the finally selected environment-recruitment models using Rs (hier model); from left to right: distribution of residuals, effect of spawning stock biomass (SSB), predicted (lines with 95% confidence limits) vs. observed (points) Rs.

# Main Basin Herring

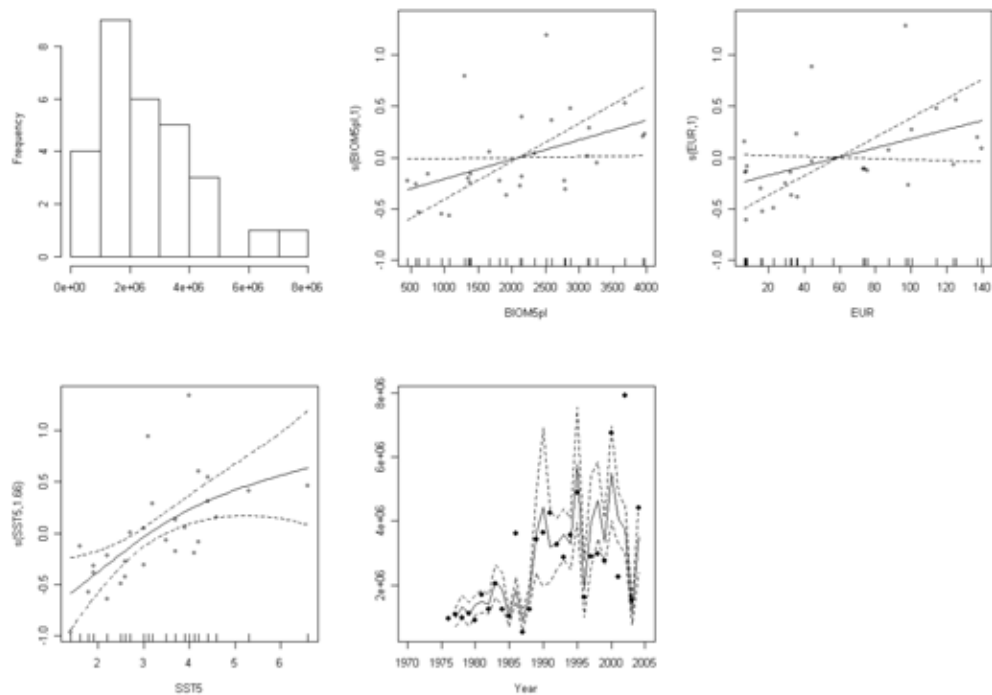


a) Diagnostic plots of the finally selected environment-recruitment models using Ra (hier model); from left to right: distribution of residuals, effect of individual weight (WAA3pl – mean weight of age-groups 3+), effect of T. longicornis biomass (TEM), effect of the Baltic Sea indec (BSI), effect of SST in August (SST8), predicted (lines with 95% confidence limits) vs. observed (points) Ra.

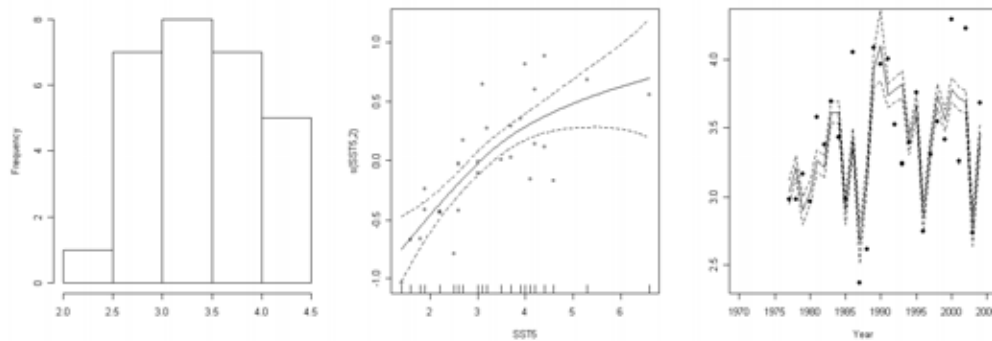


b) Diagnostic plots of the finally selected environment-recruitment models using Rs (hier model); from left to right: distribution of residuals, effect of spawning stock biomass (SSB), effect of individual weight (WAA3pl – mean weight of age-groups 3+), effect of P. acuspes biomass (PSE), effect of the Baltic Sea indec (BSI), effect of SST in August (SST8), predicted (lines with 95% confidence limits) vs. observed (points) Rs.

### Gulf of Riga Herring

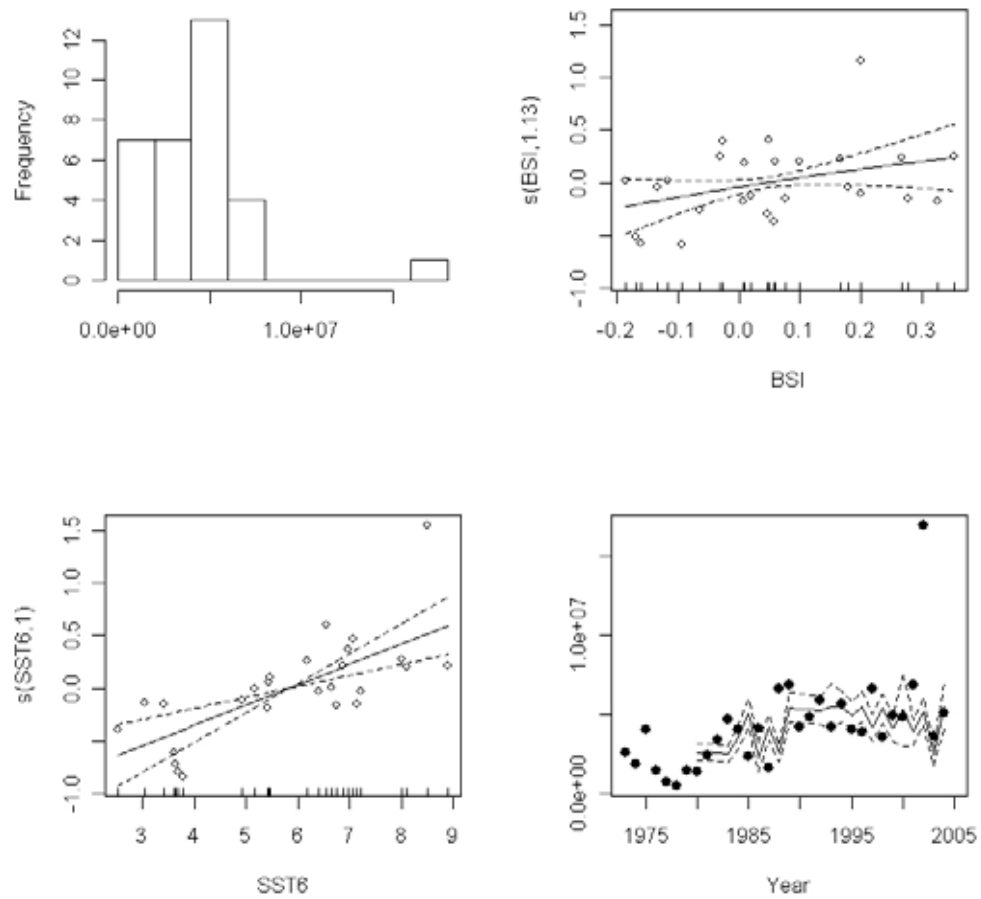


a) Diagnostic plots of the finally selected environment-recruitment models using R (hier model); from left to right: distribution of residuals, parental effect of older individuals (BIOM5pl – biomass of age-groups 5+), effect of *E. affinis* biomass (EUR), effect of SST in May (SST5), predicted (lines with 95% confidence limits) vs. observed (points) R.

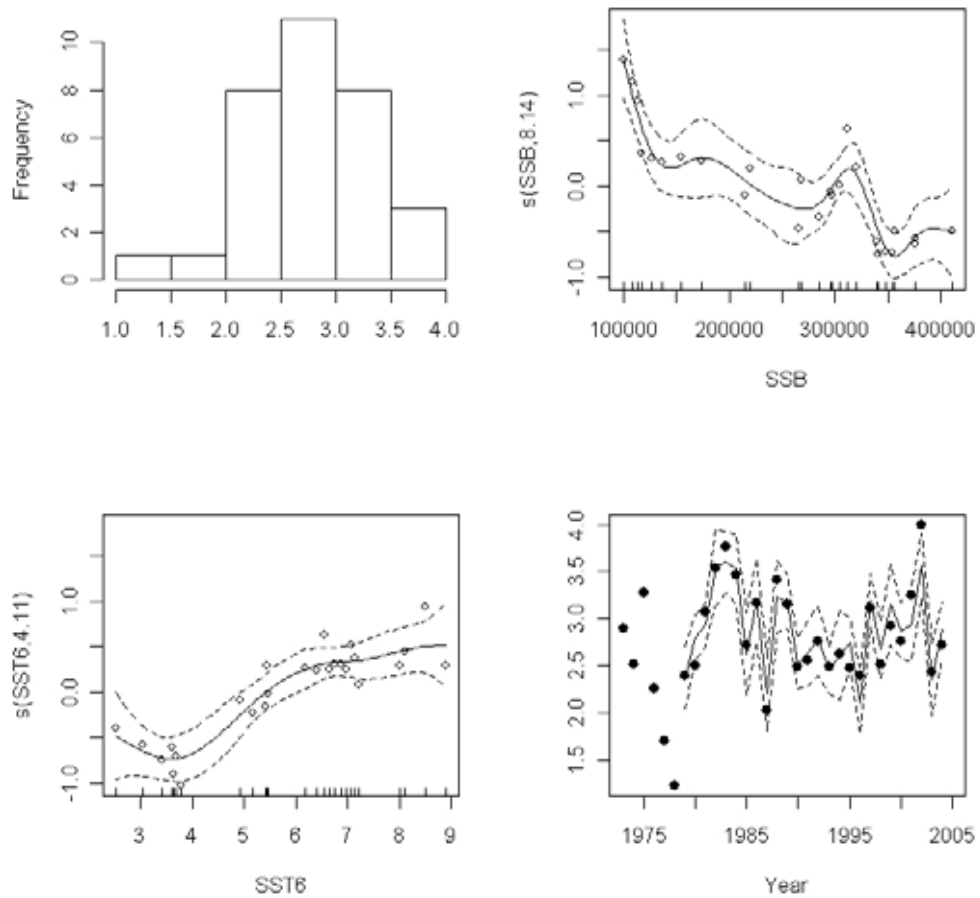


b) Diagnostic plots of the finally selected environment-recruitment models using Rs (hier model); from left to right: distribution of residuals, effect of SST in May (SST5), predicted (lines with 95% confidence limits) vs. observed (points) Rs.

### Bothnian Sea Herring



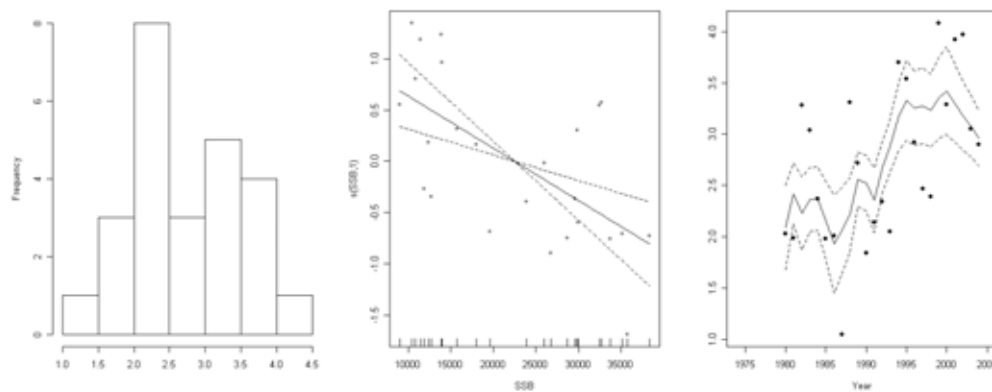
a) Diagnostic plots of the finally selected environment-recruitment models using R (hier model); from left to right: distribution of residuals, effect of the Baltic Sea Index (BSI), effect of effect of SST in June (SST6), predicted (lines with 95% confidence limits) vs. observed (points) R.



b) Diagnostic plots of the finally selected environment-recruitment models using  $R_s$  (hier model); from left to right: distribution of residuals, effect of spawning stock biomass (SSB), effect of SST in June (SST6), predicted (lines with 95% confidence limits) vs. observed (points)  $R_s$ .

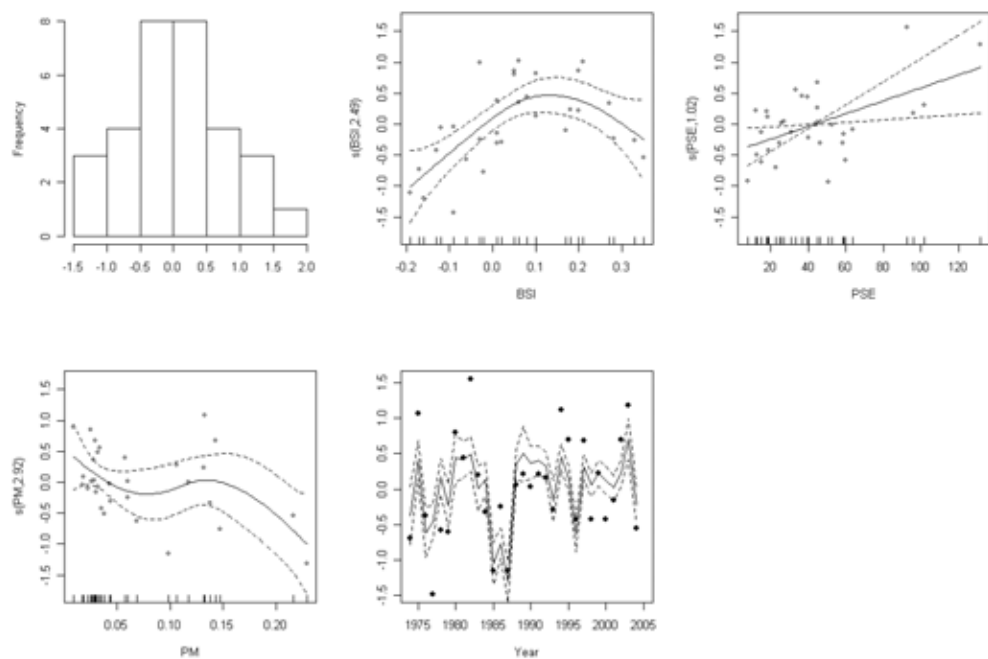


### Bothnian Bay Herring

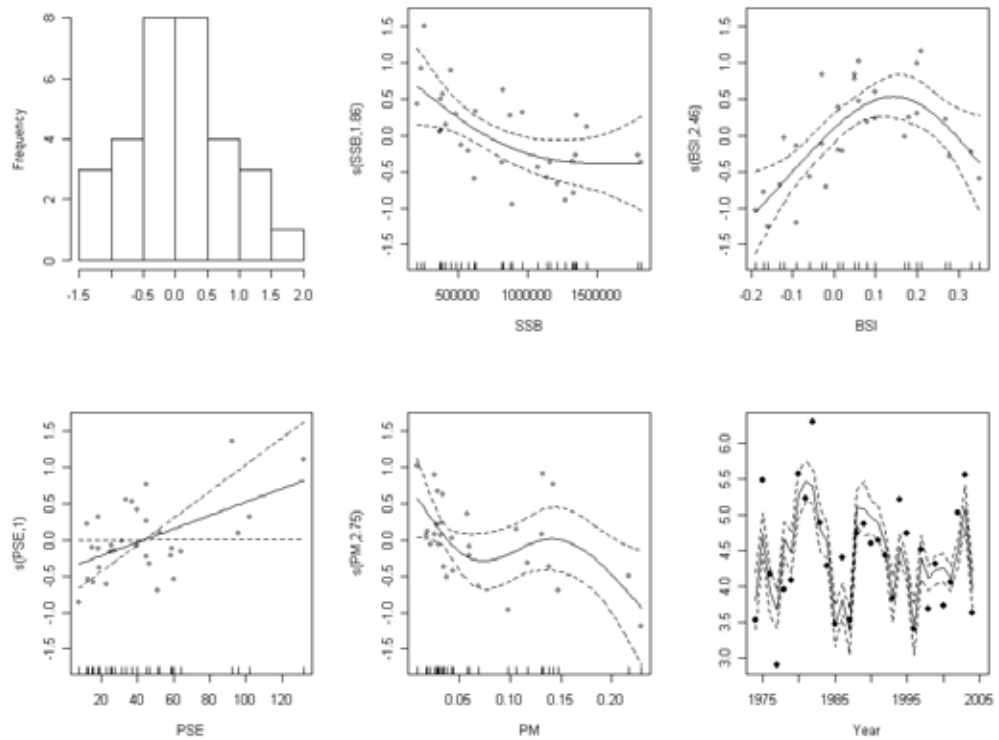


a) Diagnostic plots of the finally selected environment-recruitment models using  $R_s$  (hier model); from left to right: distribution of residuals, effect of spawning stock biomass (SSB), predicted (lines with 95% confidence limits) vs. observed (points)  $R_s$ .

### Baltic sprat



a) Diagnostic plots of the finally selected environment-recruitment models using  $R_a$  (hier model); from left to right: distribution of residuals, effect of the Baltic Sea Index (BSI), effect of *P. acuspes* biomass (PSE), effect of cod predation (PM), predicted (lines with 95% confidence limits) vs. observed (points)  $R_a$ .



b) Diagnostic plots of the finally selected environment-recruitment models using  $R_s$  (hier model); from left to right: distribution of residuals, effect of spawning stock biomass (SSB), effect of the Baltic Sea Index (BSI), effect of *P. acuspes* biomass (PSE), effect of cod predation (PM), predicted (lines with 95% confidence limits) vs. observed (points)  $R_s$ .

## Annex 7: WKSSRB terms of reference for the next meeting

An ICES/BSRP **Workshop on Developing and Testing Environmentally-Sensitive Stock-recruitment Relationships of Baltic Herring and Sprat stocks** [WKSSRB] (Chair: M. Cardinale, Sweden and C. Möllmann, Germany) will meet in Ponza, Italy from 25–28 March 2008 to:

- a) Review the work on environment-recruitment relationships for Baltic herring and sprat stocks, especially by WKHRPB;
- b) Construct stock-recruitment relationships including environmental variables;
- c) Evaluate the performance of environmentally-sensitive stock-recruitment relationships in stock projections;
- d) Develop stock-specific strategies for including environmental information into the work of WGBFAS.

WKSSRB will report by 30 April 2008 to the attention of the Baltic Committee.

### Supporting Information

<b>PRIORITY:</b>	This Workshop aims at incorporating environmental information into stock-recruitment relationships (SRRs) of Baltic herring and sprat stocks. It further will test the ability of environmentally-sensitive SRRs to improve stock projections in the assessment process.
<b>SCIENTIFIC JUSTIFICATION AND RELATION TO ACTION PLAN:</b>	The Workshop contributes to Actions 1.2, 1.3, 1.6, 1.7, 1.12, 3.2, 3.5, 3.15, 4.11, 4.15, 5.3, 5.6. of the ICES Action Plan. Herring is an essential component of the Baltic ecosystem, being a food item for cod and exerting predation pressure on zooplankton populations. The different populations are of considerable commercial value for the countries bordering the Baltic. While growth of herring has been intensively studied, studies on recruitment processes of Baltic fish stocks have in recent decades been exclusively directed to cod and sprat. However, recruitment trends drive a large proportion of the dynamics of the different stocks, which are partly of opposite direction. The work of WKHRPB has shown that these trends in recruitment are due to direct (e.g. temperature) and indirect effects (e.g. food availability) of climate. Reliably predicting recruitment is essential for proper stock management and environmentally-sensitive stock recruitment relationships are essential for implementing precautionary and ecosystem approaches. The workshop will thus build on the result of WKHRPB and model environmentally sensitive stock-recruitment relationships, evaluate their performance in stock projections, and suggest stock-specific strategies for including environmental information into the work of WGBFAS.
<b>RESOURCE REQUIREMENTS:</b>	Assistance of the secretariat in maintaining and exchanging information and data to potential participants.
<b>PARTICIPANTS:</b>	This Workshop is expected to attract 10-15 participants working on Baltic herring stocks, contributing data and expertise. Further, experts from other areas should be encouraged to participate.
<b>SECRETARIAT FACILITIES:</b>	None.
<b>FINANCIAL:</b>	No financial implications.
<b>LINKAGES TO ADVISORY COMMITTEES:</b>	ACFM
<b>LINKAGES TO OTHER COMMITTEES OR GROUPS:</b>	BCC, LRC, SG/WGs related to Baltic Sea issues, HAWG, WGIAB, WGLESB
<b>LINKAGES TO OTHER ORGANIZATIONS:</b>	Baltic Sea Regional Project (BSRP), HELCOM
<b>SECRETARIAT MARGINAL COST SHARE:</b>	