

TIMO ARULA

Ecology of early life-history stages
of herring *Clupea harengus membras*
in the northeastern Baltic Sea



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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Ichthyology and fisheries at the University of Tartu on 23.08.2012 by the Scientific Council of the Institute of Ecology and Earth Science, University of Tartu.

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Commencement: Room 301, Vanemuise St. 46 Tartu, on 23 October 2012 at
10.15 a.m.

Publication of this thesis is granted by Estonian Marine Institute and the Institute of Ecology and Earth Sciences, University of Tartu and by Doctoral School of Earth Sciences and Ecology created under the auspices of European Social Fund.



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ISSN 1024–6479

ISBN 978–9949–32–124–7 (print)

ISBN 978–9949–32–125–4 (pdf)

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University of Tartu Press

www.tyk.ee

Order No 450

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LIST OF ORIGINAL PUBLICATIONS

Current thesis is based on the following papers, which are referred in the text by Roman numerals:

- I. Arula, T., Ojaveer, H., Shpilev, H. 2012. Individual fecundity of the autumn spawning Baltic herring *Clupea harengus membras* L. *Estonian Journal of Ecology*. **61**, 2, 119–134.
- II. Ojaveer, E., Arula, T., Shpilev, H., Lankov, A., 2011. Impact of environmental deviations on the larval and year class abundances in the spring spawning herring (*Clupea harengus membras* L.) of the Gulf of Riga (Baltic Sea) in 1947–2004. *Fisheries Research* **107**, 159–168.
- III. Arula, T., Kotta, J., Lankov, A., Simm, M., Põlme, S. 2012. Diet composition and feeding activity of larval spring-spawning herring: importance of environmental variability. *Journal of Sea Research*, **68**, 33–40
- IV. Arula, T., Gröger, P., J., Ojaveer, H., Simm, M. Regime shifts in larval herring and the related marine environmental time-series: case study in the Gulf of Riga (Baltic Sea) for 1957–2010. Manuscript.

Author's contribution:

The author's contribution to papers **I**, **III** and **IV** was substantial including the generation of original idea and hypothesis, data collection, time-series assembling, data analyses and hypotheses testing, results interpretation and manuscript writing. As for publication **II**, the author's main tasks were participation in data collection and statistical analyses.

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I. INTRODUCTION

Fishes within the family *Clupeidae* form one of the most abundant fish populations in the world's oceans. Atlantic herring (*Clupea harengus* L. 1758) is one of the most important members of that family within the Atlantic Ocean. Its distribution ranges from the western Atlantic Ocean, reaching from the northern part of South Carolina up to Greenland, across to the eastern Atlantic coasts of Novaya Zemlya (Russia) and from Spitzbergen to the northern Bay of Biscay, including the brackish water of the Baltic Sea (fishbase.org; visited 26.07.2012). The Atlantic herring is both ecologically and economically a key species in many temperate marine ecosystems (Blaxter and Hunter 1982). It typically represents one of the main food items for marine top predators like cod *Gadus morhua* (Link et al. 2008) and, in turn, feeds upon the intermediate trophic levels (Blaxter and Hunter 1982).

Herring has historically been the most important commercial fish in the Baltic Sea. This species is probably the best adapted marine fish to the prevailing spatio-temporally varying heterogeneous environmental conditions of the Baltic Sea by forming several distinct populations (Ojaveer 1988). These populations show differences in migration and spawning patterns as well as morphological characteristics (Ojaveer 1988; Klinkhardt 1996). Various aspects of the local populations have been relatively well studied, including identifying the mechanisms behind the population dynamics (e.g., Ojaveer 1988; Cardinale et al. 2009).

On the basis of morphometric and meristic characters, two distinct groups – spring and autumn spawners – were distinguished in the Baltic Sea (Heincke 1898; Hessle 1931; Ojaveer 1962). While spring spawning herring generally constitute most of the herring landings in the Baltic Sea, the importance of the autumn spawners has varied over time (Ojaveer 1988). For instance, autumn spawners constituted the main part of herring catches about a century ago, which was often based on only a very few strong year-classes (Hessle 1931 and references therein). Unfortunately, our knowledge of the Baltic autumn spawning herring is limited compared to that of the spring herring and is almost completely lacking from the previous decades (Arula et al. 2012 and references therein). In terms of stock assessment and management, Baltic spring and autumn herring populations are not separated, and herring is nowadays divided into five different stock units: western Baltic (spawning grounds located in the Kattegat and the Belt Sea), central Baltic (including the Gulf of Finland), the Gulf of Riga, Bothnian Sea and Bothnian Bay. It is important to mention here, that previous studies have identified, for instance eleven different spring herring populations in the Baltic Sea (Ojaveer 1988).

One of the very distinct herring populations, considered extensively within this study, and which is also managed as a separate stock, is the Gulf of Riga spring herring population. This is a slow-growing fish characterized by one of the lowest mean length- and weight-at-age in the Baltic Sea. Gulf of Riga spring

herring does not undergo major migrations into the open sea and largely resides within the basin (Ojaveer 1988). Only a small component of the older herring leave the Gulf after the spawning season during the summer and autumn, but they tend to return to the Gulf. The extent of migration depends on stock size and on local feeding conditions. From the 1960s to the 1980s, in low stock conditions, the number of migrating fish was considered negligible. However, since the mid-1990s, the migration rate has increased, but the Gulf of Riga herring catch in the central Baltic never exceeded 6% of the total catch (ICES 2011).

Abundance of the early life history stages of fish varies over different spatio-temporal scales and their survival/mortality is considered as an important factor for influencing the abundance of fish populations through annual recruitment (see below). Early life history stages of fish are influenced by multiple external factors. For marine organisms with complex life cycles, characteristics of larvae, including their size, growth rate and mortality are considered to be most critical in determining larval survival and abundance of post-metamorphosed stages (Hamilton et al. 2008). Switching on exogenous feeding after the yolk-sac resorption is assumed to be a very critical phase during the pre-juvenile stages of fish (Houde 2008). For example, Blaxter and Hempel (1963) formulated the “point of no return” concept where they state, that the failure of the first feeding larvae to find suitable food leads to a point when the starved larvae are too weak to feed even though they are in an area of sufficient prey supply.

In addition to quantity of prey in the environment, abiotic factors such as temperature, salinity, turbidity, wind induced drift and oxygen supply as well as parental effects also play important roles in determination of larval feeding success, and therefore also its survival (Fogarty et al. 1991; Werner 2002). Temperature is considered the most important factor due to its influence on numerous processes taking place in early life stage, *inter alia* growth, development, metabolic rates, stage duration and condition. However, for other species preferred environmental parameter thresholds may vary because of adaptational preferences. For example, unfavourable conditions for larval herring in the environment will limit nutritional condition and thus reduce their growth rates and prolong stage duration (Cushing 1972). As herring larvae are visual predators, their feeding success is strongly related with light intensity which, in turn, depends on water turbidity. However, water turbidity may have the reverse effect on some larval fish species, whose prey contour will be better discernable in low light conditions. The “growth-mortality hypothesis” or “stage duration hypothesis” proposes a correlation between nutritional condition and the probability of mortality, *i.e.* an organism with a cheesy body condition and consequently decreased growth rate and size at age, undergoes a higher risk of mortality due to either predation or starvation (Ware 1975; Shepherd and Cushing 1980). Therefore, survival in the larval phase is directly linked to

growth, because mortality rates decrease with increasing larval body size (Peterson and Wroblewski 1984).

Advanced understanding in growth and feeding ecology of larval fish is important, given that this knowledge is essential to understanding spatio-temporal dynamics of the population (Costalago et al. 2011). Studies on larval fish feeding ecology aim to explain whether larval fish select their prey and to identify which prey is preferred. In general, some larval fish species are selective in their feeding and selection is based on both the taxonomy and size of a prey. Selectivity patterns change as larvae grow bigger, and as a rule, larger larvae consume larger prey as it is energetically more profitable (van der Meeren and Naess 1993). There is some evidence for optimization of feeding based on food abundance and prey type or size, but there are few data to suggest whether the choice of prey is based on species or size. Some species, including herring larvae, maintain fairly narrow size spectrum in the prey items they consume (Munk 1992; Arula et al. 2012). However, the effects of size and species composition of prey on feeding behaviour of fish larvae are generally poorly known, but considerable information is available on the feeding selectivity of larvae both in the laboratory (Frank and Leggett 1986) and in the field (Munk and Nielsen 1994). Laboratory studies have demonstrated that growth of larvae fed continuously on small-sized prey is depressed (Ehrlich and Blaxter 1976), compared to larvae where larger prey items are available. Still, there are various other biotic aspects related to feeding conditions that are also important, such as prey and predator abundance, prey shape and pigmentation, biochemical composition of the prey, prey movement and the species composition of the prey (Dower et al. 2002).

Several hypotheses have been proposed to explain variability in recruitment abundance of fish populations. About a century ago Hjort (1914) suggested in his “critical-period” hypothesis that the mortality rates of early life stages caused by starvation can influence a great extent of recruitment variations of fish populations. Cushing (1975) suggested that larval fish survival and, subsequently, recruitment success is a function of a temporal overlap between larval and prey production. His “match/mismatch” hypothesis states the importance of temporal coupling and decoupling of seasonal production maxima of fish larvae and plankton in determination of the year class strength of fish stocks. Lasker (1981) extended these observations by emphasizing the importance of oceanographic features and he concluded, that development of prey patches is regulated by stability of water masses. His “ocean stability hypothesis” assumed that potential planktonic food for fish larvae is dispersed, and that patchiness of prey concentration becomes lost, under turbulent ocean conditions arising from storms or wind-driven upwelling phenomena (Lasker, 1981). Only in appropriately calm water regions can suitable patches of food for effective successful feeding of fish larvae arise. Sinclair’s (1988) “member-vagrant hypothesis” focused more on the oceanographic conditions influencing drift and dispersal of the fish larvae instead of their prey. This theory illustrates

the causal link between retention of the early life stages within a beneficial environment (an area with sufficient food supply and favourable abiotic conditions) and spawning success. More recent theories focus on the impact of both larval growth rates and predation on the variability in survival of cohorts, over a significant portion of their pelagic stage (Bergenius et al. 2002). These theories emerged from observations that small changes in larval growth and mortality rates can generate order-of-magnitude or larger differences in annual recruitment (Shepherd and Cushing 1980). Besides all these bottom-up hypotheses explaining recruitment fluctuations, based on the physical environment and food supply, the top-down impact on the survival of fish larvae through predation is also thought essentially important and should be taken into account (Thompson and Harrop 1991).

The link between the early life stages of marine fishes and their recruitment is sufficiently well documented to justify a continued investment of efforts into investigations of the factors regulating the mechanism responsible behind the abundance and survival of the egg and larval stages (e.g., Leggett and DeBlois 1994). For example, it has been empirically shown that individual fecundity of fish is directly related to fish stock recruitment variation, suggesting thereby that fecundity is an important component of fish stock dynamics (Rickmann et al. 2000). Furthermore, the recruitment abundance of the Atlantic herring in the North Sea appears to be mostly determined by the abundance of larvae (Nash and Dickey-Collas 2005). Similarly, the abundance of large herring larvae determines the herring recruitment abundance in the Baltic Sea (Oeberst et al. 2009; Ojaveer et al. 2011). In addition, the variability in the production of larvae largely accounts for the major fluctuations in herring stock abundance in the North Sea (Nash et al., 2009). North Sea autumn spawning herring pre-larvae abundance is chiefly determined by the adult herring biomass, whereas the abundance of the post yolk-sac larvae mainly depends on the climate, indicating the importance of various processes during the larval stage (Gröger et al. 2009). To summarize, one of the major issues in fish and fisheries ecology and management has been to understand the mechanisms related to highly variable larval survival and linking this variation to recruitment of fish populations, which have major biological, ecological and socio-economic implications.

Abrupt ecosystem shifts, commonly termed as regime shifts, are changes between contrasting and persisting states of ecosystem structure and function. They are considered to be abrupt in the sense that the timespan during which the shift occurs is relatively short (1–2 years) in comparison to the duration of the different states (often decadal to multi-decadal). These events have been detected in atmospheric, terrestrial, freshwater and marine realms (e.g., deYoung et al. 2008; Scheffer et al. 2001). At present, the mechanics behind the marine ecosystem regime shifts have been explained as a result of multiple external causes, involving both natural and human-induced factors like climate variability and change, eutrophication and exploitation of living marine

resources (e.g., Collie et al. 2004; Österblom et al. 2007) with evidences in ecosystem abiotic properties as well as in multiple trophic levels. These include in the Baltic Sea, amongst others, salinity, copepod abundance and clupeid stock biomass (Casini et al. 2011). Disentangling the relative importance of different drivers in causing regime shifts is a challenge, especially due to co-occurring and often synergistic effects. However, the ability to separate these effects is of vital importance in developing management strategies to achieve sustainable use of marine ecosystems (Lindegren et al. 2010; Möllmann et al. 2011).

2. AIMS AND HYPOTHESIS

The general aim of the present study was to characterise the variability of the selected key parameters of the early life history stages of the Baltic herring and to identify which factors, and/or their combinations best explain the observed variability patterns. The findings were located into the ecosystem context. The study area is the Gulf of Riga, situated in the NE of the Baltic Sea, with the historical climate and marine ecological time-series available for the current study since the 1950s (see below).

The specific tasks of the present thesis were:

1. To identify factors influencing reproductive potential of the autumn spawning herring and determine potential differences in individual-level fecundity of the fish at different ecosystem regimes (I).

Compared to the spring-spawning herring, there is very little information available on the autumn herring in the Baltic Sea during the few last decades. Autumn herring have different adaptation capabilities and preferences/tolerances to the local environment compared to the spring herring, so extrapolation of results obtained for the spring herring is unfortunately not possible. We hypothesise (a) significant influence of individual growth-related parameters on fish fecundity and (b) age-specific fecundity differences between the recent (2000s) and historical (1959–1970) data as a function of changed ecosystem condition.

2. To investigate feeding ecology of the spring-spawning herring larvae in relation to environmental conditions and to apply this knowledge with regard to interpretation of the long-term dynamics of larval herring. For this purpose, we have applied selected key abiotic and biotic parameters to identify the effect of environmental factors (both uni- and multivariate) on the feeding activity and diet composition of larval herring (III).

Feeding success of fish during their early life history stages is one of the important pre-conditions for formation of abundant recruitment of fish populations. Significant decreases in larval herring abundance in the Gulf of Riga since the early 2000s, combined with environmental change (including decrease in water transparency, overall increase in prey densities and changed phenology of prey) lead us to initiate a study on the causal effect of multiple *in-situ* measured abiotic and biotic factors on larval herring feeding. We hypothesize, amongst others, that larval herring food intake might be affected by water transparency and changed prey field. For the study, we have used historical data from the 1970s and complemented those with more contemporary data from the 2000s.

3. By using larval spring spawning herring-relevant time-series to describe and analyse the long-term dynamics of different ecosystem components (abiotic and biotic) and identify causal links between the ecosystem change and larval herring abundance and phenology (**II, IV**).

The study was carried out by using the Gulf of Riga long-term time series (since the 1950s) by the following three main sub-goals: (a) to characterise the long-term performance of larval herring in relation to the climate and marine ecosystem variables; (b) to study the multivariate effect of the abiotic and biotic time-series on the long term abundance dynamics of larval herring, and (c) to seek options for herring year-class strength predictions, based on the fisheries-independent data – larval fish abundance.

3. MATERIAL AND METHODS

3.1. Study area

The current thesis is based on field studies conducted in the Gulf of Riga (GoR), supplemented by climate-related time-series (see below). Most of the data, including all larval herring data, originate from the NE part of GoR (Pärnu Bay) while fish fecundity studies were carried out in the northern GoR, south coast of Saaremaa (see also Fig. 1).

The GoR (area 16,330 km²) is a shallow, semi-enclosed sub-system in the northeastern part of the Baltic Sea. The GoR receives freshwater from a large drainage area (134,000 km²), primarily entering the southern part of the basin. The average salinity varies around 5.0–6.5 PSU with the absence of a permanent halocline. Due to its shallowness, the dynamics of both surface and deep-water temperatures are directly coupled with air temperatures. The oxygen regime is relatively good due to strong vertical mixing and in most areas, oxygen concentrations are higher than 5 ml l⁻¹ (Kotta et al. 2009 and references therein).

Pärnu Bay, located in the northeastern part of the Gulf of Riga, is a relatively enclosed and very shallow (average depth 5 m) sea area covering 700 km² with a volume of 2 km³. In most years, Pärnu Bay is covered by ice from December-January to March-April. In the warmest summers, the average surface water temperature has reached 22.0–23.8°C during July–August. The salinity of the bay fluctuates from almost freshwater to 7.5 PSU, with mean values of approximately 5 PSU. The hydrographic conditions are formed under the complex influence of ice conditions, freshwater inputs from the Pärnu River and the water exchange with the Gulf of Riga and therefore Pärnu Bay is very strongly influenced by freshwater inflows. Here the major structuring factor is the Pärnu River. Besides supplying a huge amount of nutrients to the area, the Pärnu River also affects Pärnu Bay through humic matter, changing the optical properties of the seawater and having a strong impact on light penetration (Kotta et al. 2009 and references therein). The bay suffers from extensive human pressures (recreation, eutrophication and fishing) (Kotta et al. 2009).

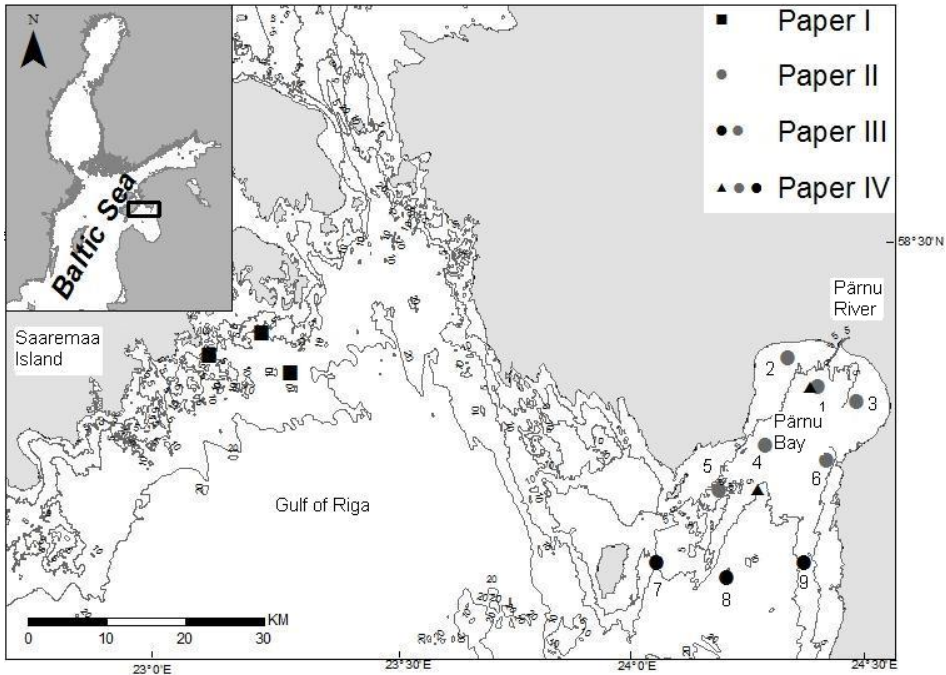


Figure 1. Location of the study area and sampling sites by individual papers in the Gulf of Riga (Baltic Sea).

3.2. Field sampling

Autumn herring samples for fecundity studies were taken from commercial catches on spawning grounds of a distinct autumn herring population (named as Saaremaa-Ventspils population; Ojaveer 1974) during 2008–2010 (Fig.1, black squares). For each fish, standard morphometric measurements were taken: total length (L, measured to the nearest 0.1 cm), total body weight (TW, measured to the nearest 0.1 g) and gonad weight (Gw, measurement precision 0.001 g). Fish age was determined from otoliths. The herring included in the fecundity analyses were all staged as maturing with maturity stage IV (similar with studies on the spring spawning Baltic herring) (Raid et al. 2010). Ovaries were removed by careful dissection, weighed fresh and preserved in 90% ethanol.

Since the late 1940's stationary sampling stations (Fig. 1, black and grey circles no. 1–9) were historically chosen with the intention to take representative samples of spring herring larvae covering the whole larval herring retention area in the NE Gulf of Riga. Larval sampling cruises usually started in early May and were carried out on weekly basis until the end of the spring herring larvae distribution (late July). Due to the shallowness of the study area, the Hensen net was used for larval sampling and the same method has been applied throughout the whole study period until now. Mouth diameter of the

Hensen net is 800 mm and the mesh size 500 μm (170 μm in the sampler). The samples were taken in the surface layer (usually at 1–2 m depths from the surface) in daylight with the towing speed of about 2 mph and a duration of 10 minutes. Samples were preserved in weak formaldehyde solution. Herring larvae in the samples were counted and their length from the tip of the snout to the end of the chorda was measured to the nearest millimetre. In the case of large numbers of larvae in a sample, a random subsample of 100–500 individuals was measured and the results were extrapolated to the whole sample from the station.

Sampling of fish larvae for feeding activity and diet composition was performed weekly from May to July during daylight in 1973–1974 and 2004–2005. Samples were taken from stations 1–6 (Fig. 1) using the Hensen larval fish trawl with the same methodology as explained above. Altogether, the guts of 2748 herring larvae were analysed from 97 hauls. For analysis of feeding activity and diet composition, herring larvae were divided into three size groups: small (8.1–10.0 mm), medium (10.1–16.0 mm) and large (16.1–20.0 mm). The size group of the smallest larvae contains first-feeding larvae (Munk et al. 1989). The medium size group contains larvae that are dependent on a relatively narrow prey spectrum and are restricted in their swimming ability. The morphological development of the largest larvae, in particular the formation of fins, is considerably progressed. The spectrum of prey has become broader than for the other size groups, and the food availability is in general not as critical as in case of smaller larvae (Haslob et al. 2009).

Mesozooplankton was collected from two stations (at 7 m and 11 m depths, triangles in Fig. 1) during 1957–2010 which are considered spatially representative to characterize zooplankton dynamics in the study area. The mesozooplankton sampling was performed simultaneously to larval fish collection with a weekly resolution and was done by vertical hauls with a Juday net (opening area 0.1 m², mesh size 100 μm) through the whole water column from bottom to surface. Samples were preserved in formaldehyde solution and analysed by a routine method suggested by the Baltic Monitoring Programme (HELCOM 1988). Adults and copepodite stages of copepods were identified to a species levels. The major larval herring prey items (*i.e.*, copepods) were identified and counted by the following different developmental stages: *nauplii*, copepodites by stages from I to V and adults.

3.3. Other data

Time series (TS) on the selected and herring-relevant (Rannak 1971; Ojaveer 1988; Ojaveer et al. 2011; Arula et al. 2012; Greve et al. 2005) local hydroclimatic parameters; air and water temperature, timing of ice retreat, river inflow and wind speed were obtained from the Estonian Meteorological and Hydrological Institute (EMHI). To describe the winter severity, the sum of

monthly mean winter air temperatures was used. The monthly (May-July) mean values in sea surface water temperature in spring, summer and sea surface salinity were obtained from Omstedt 2011 (updated).

Data on the recruitment abundance (at age 1) of the GoR spring herring stock for 1977–2010 were obtained from ICES (2011) and for previous of 1951–1976 from Ojaveer et al. (2004).

All in all, we have collected and established 19 interannual time-series in Paper IV, based on data availability (since 1957) and relevance for larval herring ecology. Detailed description of the time-series used, their units and measurement details, together with the source, is given in the Table 1.

Table 1. Description of time series used in the current study. 1–7: abiotic environment, 8–13: copepod and herring phenology, 14–19: biotic environment. For more detailed description of variables please see Material and methods.

Variable	Abbreviation	Time	Measurement unit	Source
1. Winter air temperature	Winter	January-March	°C	EMHI*
2. Timing of ice retreat	Ice retreat	Annual	Week	EMHI
3. Sea surface temperature, spring	SST spring	April	°C	Omstedt, 2011
4. Sea surface temperature, summer	SST summer	May-July	°C	Omstedt, 2011
5. Sea surface salinity, summer	Salinity	May-July	PSU	Omstedt, 2011
6. Pärnu River inflow	River inflow	Annual	Km ³ *year ⁻¹	EMHI*
7. Water transparency	Transparency	May-July	Meter	Original data
8. Herring larvae onset	Onset	May-July	Week	Original data
9. Larval herring retention time	Retention	May-July	Day	Ojaveer et al., 2011 updated
10. Timing of maximum abundance of <i>Eurytemora nauplii</i>	En timing	May-July	Week	Original data

Table 1.Continuation

Variable	Abbreviation	Time	Measurement unit	Source
11. Timing of maximum abundance of <i>Eurytemora affinis</i> females	Eaf timing	May-July	Week	Original data
12. Timing of maximum abundance of herring larvae	Her timing	May-July	Week	Original data
13. Degree of mismatch between larval herring and <i>Eurytemora nauplii</i>	Mismatch	May-July	Week	Original data
14. Copepod <i>nauplii</i> , mean abundance	Cn mean	May-July	Ind.*m ⁻³	Original data
15. Adult <i>Eurytemora affinis</i> , mean abundance	Ea mean	May-July	Ind.*m ⁻³	Original data
16. <i>Eurytemora nauplii</i> , maximum abundance	Ean max	May-July	Ind.*m ⁻³	Original data
17. Female <i>Eurytemora affinis</i> , maximum abundance	Eaf max	Summer	Ind.*m ⁻³	Original data
18. Herring larvae, mean abundance	Her larvae	May-July	Ind.*10 min ⁻¹ haul	Ojaveer et al., 2011 updated
19. Herring recruitment	Her recruits	Annual	Number at age 1 (10 ³)	ICES 2011; Ojaveer et al., 2011

* Estonian Meteorological and Hydrological Institute

3.4. Statistical analyses

Several statistical softwares and approaches were used in the present thesis. These are summarised in the Table 2. below, together with the reason for the specific application.

Table 2. Most important statistical approaches applied in the thesis, together with a brief explanation on the purpose and reference to individual research papers. For more detailed description please see text below.

Statistical method	Purpose	Paper
Analyses of similarities (ANOSIM)	To test the significance of similarity of larval herring diet composition between different size groups and years	III
ARIMAX	To replace missing values in the long-term time-series	IV
BEST	To investigate the importance of different environmental variables on the diet composition of larval herring	III
Generalized additive model (GAM)	To relate the impact of environmental characteristics on larval fish and recruitment abundances	II
MULTIPLE REGRESSION	To study the effect of multiple independent variables on dependent variable	I, IV
Principal component Analyses (PCA)	Variable aggregation has been performed, by using the 1 st principal component (PC1) as this comprises most of the variation in the data, to generate the shiftogram	IV
Repeated measures analyses of covariance (RMA ANCOVA)	To study the importance of multiple time-varying covariates on dependent variable	I, III
Scree test	To order studied factors by variance, and plot the variance against the each factor	IV
Sequential t-test analysis of regime shifts (STARS)	To investigate presence and timing of regime shift(s) in herring larval abundance time-series	II
Shifting diagrams (SHIFTGRAM)	To investigate presence and timing of regime shift(s) in ecosystem time-series	IV
Similarity percentages (SIMPER)	To determine the contribution of individual prey items in larval herring gut	III

Missing values in the datasets (Paper IV) were replaced by making use of two information sources: internal information of the “spoiled” time series (i.e. the time series containing the missing values) to get the dynamic structure of it, plus information from outside to profit from its correspondence to other TS. Both approaches were combined here to give an integrated transfer function model (ARIMAX model) consisting of two model components. The dynamic structure of the “spoiled” time series data was identified by fitting an ARIMA model in terms of an intervention model (1st model component; see Schlittgen, 2001), external information has been implemented simply by looking at correlations between the “spoiled” time series and correlated other ones (2nd component).

The monthly aggregated data (Paper III) were analysed by the statistical software SPSS PASW (Predictive Analytics SoftWare) Statistics version 18 and R version 2.10.1. Repeated measures analysis of covariance (RMA ANCOVA) was used to analyse the time-effect. Sampling time was considered as repeated measures. Several independent characteristics were included in the analysis as time-varying covariates. RMA tests whether time factor has an effect on the dependent variable after removing the variance for which covariates account. In order to describe the diet composition of herring larvae, multivariate analyses were performed by the statistical program “PRIMER” version 6.1.5 (Clarke and Gorley 2006). Similarities between each pair of samples were calculated using a zero adjusted Bray–Curtis coefficient (a similarity equals to 0 means dissimilarity equals to 1). The coefficient is known to outperform most other similarity measures and enables samples containing no organisms at all to be included (Clarke et al. 2006). Analysis of similarities (ANOSIM) was used to test whether the diet composition significantly differ between larval size groups and years. If ANOSIM revealed differences between the studied factor levels, a similarity percentages (SIMPER) analysis was performed to determine the contribution of individual prey items to the average dissimilarity between treatments.

BEST analysis (BIOENV procedure) was used to relate the studied environmental variables to the density of different prey items in larval herring guts (Paper III). This analysis shows which environmental variables or their combination best predict the observed diet composition in larval herring guts. A Spearman rank correlation (Rho) was computed between the similarity matrices of abiotic environment (Euclidean distance) and different prey items (a zero-adjusted Bray–Curtis distance). For all statistical tests, alpha was set at 0.05 for all comparisons.

Predictive models for dependent factor were analysed by univariate linear regressions. The relationship was considered statistically significant when $p < 0.05$. Further, multiple regressions were applied to assess the major predictors (Paper I). The model, based on the lowest residual sum of squares, was run stepwise with subsequent runs excluding non-significant variables

($p > 0.05$, starting with the highest) until only significant predictors were included in the respective model.

To provide an integrated view on the status and long-term trend of the GoR ecosystem, shift detection analyses were conducted on the available multiple time-series. Part of the concept was to study whether a global approach with all variables included gives the same picture as an individual approach with all variables being split into three categories/subsets: biotic, abiotic and phenological factor groupings. Individual analyses were therefore performed to reflect the three major dimensions (regimes), assuming that this type of separation leads to a more detailed shift pattern. As described in detail in Gröger et al. (2011) the shift detection algorithm can be summarized as follows: while iteratively moving a potential shift point t_0 over the TS using a specifically defined structural break model (by incrementing t_0 by 1 year each step), per each iteration relevant decision criteria described below are recorded. These results are displayed in a compound diagrammatic illustration that was termed as a “shiftoqram” (Gröger et al. 2011). A shiftoqram consists of a set of elementary diagrams (plots) that summarize graphically the results of all relevant decision criteria (quality-of-fit criteria, marginal p values) each of which are synchronized over the same time scale.

4. RESULTS AND DISCUSSION

4.1. Variability and change in individual fecundity of the autumn-spawning herring

Absolute individual fecundity (AF) of fish is known to vary over time and space (Kennedy et al. 2007; Morgan and Rideout 2008). In many cases, these variations have been linked to food availability, which in turn is affiliated by hydroclimatic conditions and affects energy reserves, both at the individual fish and stock level (Kjesbu et al. 1991). In the Baltic Sea, periodic climate fluctuations have been linked to several principal changes, like milder winters that have favoured survival of young herring (II). A distinct change in the main environmental conditions and ecosystems of the Baltic Sea was recorded in the 1970s–1980s with the cycle of years with mild winters starting in the early 1970s (Alheit et al. 2005; Ojaveer and Kalejs 2010). Another climate-driven feature of the Baltic Sea is sea salinity change. The high-frequency period of saltwater intrusions ended in the late 1970s with a general decrease in salinity of the sea starting in the 1980s (IV). Amongst others, this has manifested itself in a decrease of distribution area and densities of organisms of marine origin, including large marine copepods like *Pseudocalanus acuspes*, which is an important energy source for herring in the Baltic Sea. The most human-induced environmental change in the Baltic Sea affecting the ecosystem status in general is eutrophication, which has broadly resulted in an increase of general biological production during the past 50 years (HELCOM 2009a, b). As a result of eutrophication, several changes in physical characteristics (e.g., decrease in water transparency) contributed to important biotic alterations (e.g., species composition and size structure of communities) affecting essential ecosystem properties directly related to pelagic fish.

Autumn herring absolute individual fecundity was studied in three consecutive years from 2008–2010 and compared with historical findings, derived from 1959–1970s. Large and significant inter-annual differences were observed in the present study in the relative fecundity of the fish, while interannual differences in the AF values remained insignificant during the recent period (I). Differences in AF might be related to seasonally varying hydroclimate and prey availability between years during the maturation process in May–July and associated energy allocations for reproductive growth (I, IV). For example Kennedy et al. (2011) found that because of fluctuations in prey field, annual values in fecundity for Norwegian spring spawning herring differed by up to 18% annually. Although we do not have data and information on inter-annual dynamics of autumn herring prey on its feeding grounds, we have found highly variable copepod abundances in the NE GoR (IV). Knowing that spatio-temporal distribution and abundance of mesozooplankton in GoR is patchy (Ojaveer et al. 1997) and annually variable (IV), high variability of the prey field characteristics of autumn herring in its feeding areas are very likely. In

addition to fish length and individual body mass, which were both strongly coupled to individual fecundity (Oskarsson et al. 2002), body condition factor is also very often used in fish fecundity studies (Stares et al. 2007). However, while all variables mentioned were important as single predictors, only fish length and condition factors were the major predictors for fecundity in multiple regression (**I**). Fish condition, in turn, may be dependent on several, often interconnected, factors such as density dependence (Casini et al. 2011), hydro-climatic conditions and selective fishing (Vainikka et al. 2009). Signs on the density-dependent relationship in herring are supported by the most recent findings in a nearby herring population, the spring spawning herring of the GoR. Under the conditions of high population abundance and spawning stock biomass, their individual-level fecundity has shown substantially lower values, associated with reductions in individual growth and body condition of the fish (Raid et al. 2010). At this stage we lack information on the potential changes in the individual growth and body condition of the autumn herring (**I**). However, the observed differences in individual fecundity by different age groups between 1959–1970 and 2008–2010 may indicate size-selective density-dependent regulation as a function of prey availability (**I**).

Major changes in the mesozooplankton species composition and abundance/biomass between the 1950s–1970s and the 1990s–2000s included replacement of the large-sized copepods (*e.g.*, *Pseudocalanus acuspes*, *Limnocalanus grimaldii*), which are the preferred food for herring, by small-sized and energetically less profitable taxa (like *E. affinis*, *Acartia* spp.) (Sidrevics et al. 1993; Möllmann et al. 2008). Those changes are suggested to have initiated reduction in the individual growth in the spring spawning herring (*e.g.*, Rönkkönen et al. 2004). Thus, herring prey field, both in terms of species composition and abundance/biomass, for especially older herring is presently much worse compared to the 1960s, while younger herring should now be benefit from the elevated production of the small-sized copepod species (**I**, **IV**).

We found that younger age-groups of the autumn herring are nowadays more fecund than historically and older fish are now substantially less fecund than during 1950–1970s. This might have resulted from the changed prey field, as described above, which have favored condition of younger individuals (**I**, **IV**). In other words, growth of younger age-classes is currently facilitated by abundantly occurring prey items, while the older age classes are probably forced to eat a less energetically profitable small-sized diet as the preferred large-bodied copepods densities are scarce. These trophic changes might have caused period- and age-specific shifts in individual growth of fish with measurable differences in individual absolute fecundities. However, the potential food-web effect on the weight-at-age of the fish needs future studies and the proposed link with AF evaluated afterwards. In turn, very recent findings for the spring herring have concluded, that on the contrary to the historical findings, diet of the young and old herring in the GoR overlap significantly nowadays, probably because of changed prey availability

associated with very low abundance of large-bodied copepods (Lankov et al. 2010). This suggests that prey availability may play a crucial role in pelagic fish performance dynamics.

Casini et al. (2011) demonstrated recently for the Baltic Sea, that the most abundant clupeoid species, spring herring and sprat, both can induce density-dependent effects. Unfortunately, we lack estimates for the spring herring and sprat abundance/biomass for the Saaremaa-Ventspils autumn herring distribution area in 1959–1970 to speculate on probability of density-dependency on autumn herring. In general, pelagic fish abundance is currently high and they strongly dominate in the Baltic main basin. Therefore, both these clupeoid species can potentially cause density effects on growth and fecundity on autumn herring via food competition. From a purely autumn herring perspective, potential negative effect of food shortage on fish fecundity may be compensated for by proportionally decreased fish abundance.

4.2. Long term variability in the environment and abundance of the early life-history stages of spring spawning herring

We have recorded several clear and distinct long-term patterns in several single hydro-climatic parameters of GoR. Amongst those, the mean SST in spring (April) and summer (May-July) slightly decreased until the late 1980s, however, with substantially higher, but also more variable values during the past two decades. Surface salinity consistently increased until the mid 1970s (to about 6.2 PSU), followed by a sharp decrease until the mid 1990s (around 5.1 PSU) and have recently increased again to over 5.8 PSU. River runoff has increased from below 1 m^{-3} per year in the 1960s to a level of 2.5 m^{-3} at the end of the 1980s. In the early 1990s, river inflow dropped sharply, but has increased again in the 2000s. Water transparency displayed generally higher values (max 2 m) in the 1960s and 1970s and followed by a sharp decline in the early 1980s. Since then annual water transparency values very seldom exceed 1.5 m (IV).

Larval herring abundance displayed the lowest values in the beginning of the observation period in the 1950s and the 1960s, increased thereafter and reached its peak level at the end of the 1990s (II, IV). This increase has been accompanied by substantial interannual variability. In the 2000s, larval herring abundance has clearly dropped, and is currently generally at a level similar to the 1960s and the 1970s. Several very abundant herring recruitment have occurred since the early 1990s, when the abundance of herring larvae also reached its peak. During the past few recent years, herring recruitment has dropped to a level of about half of the maximum values (II, IV).

Thermal conditions during the preceding winter significantly influenced the abundance of larval and recruitment of herring. In general, winters have become milder over time and this has resulted in an elevated abundance of herring

larvae and recruitment in GoR (II, IV). The positive relationship between winter severity and larval herring abundance was especially pronounced during the period of milder winters in 1973–2004. Earlier studies by Rannak (1971) confirmed that the abundance of the spring spawning herring recruitment in GoR was influenced by the thermal regime in spring, as shown by significant correlation between recruitment and the surface water temperature in April. In addition, our results showed that thermal conditions can also modify the relationship between different herring population parameters: after mild winters, a slightly stronger significant correlation was found between SSB and recruitment as well as SSB and abundance of herring larvae (II).

In terms of practical applicability of the fisheries-independent herring data, our results clearly indicate that the correlation between the larval herring abundance and the recruitment improves from the small towards the large larvae and a significant relationship was found between the abundance of large larvae and recruitment of the herring stock (II). Therefore, abundance of large larvae can be used as a preliminary estimate, with a certain confidence, on the potential recruitment abundance of the Gulf of Riga spring-spawning herring population already a few months after the spawning event has occurred. In addition to remarkable fluctuations in GoR herring recruitment that are related to winter severity by enhanced survival in milder winters (see above), the abundance of herring larvae in medium and large size groups was also found to be linked to thermal conditions in winter (II, IV).

We found the main prey item for larval herring – copepod *nauplii* – (III) to display a dome-shaped abundance pattern over time with high values until the late 1960s, followed by a decrease until the mid-1980s and increase since then. Despite the very high prey abundance in the 1960s (II), a high degree of mismatch between larval fish and their prey (Fig. 2) has resulted in very low larval fish abundance during this time (II, IV). However, larval abundance increased and retained a high level in the conditions of decreased/low prey abundance, accompanied by a higher match between fish larvae and their prey (II, IV, Fig. 2). A significant drop in the larval herring abundance since the early 2000s occurred during the conditions of relatively high prey densities (IV) with a relatively good match between the larval herring and their prey (Fig. 2). However, it should be considered here, that the analysis on the degree of mismatch between larval fish and their prey was carried out for one station only (station number 1, see also Fig. 1), for which zooplankton data exist and, that herring larvae are also very abundantly present elsewhere than in this station only (Fig. 3).

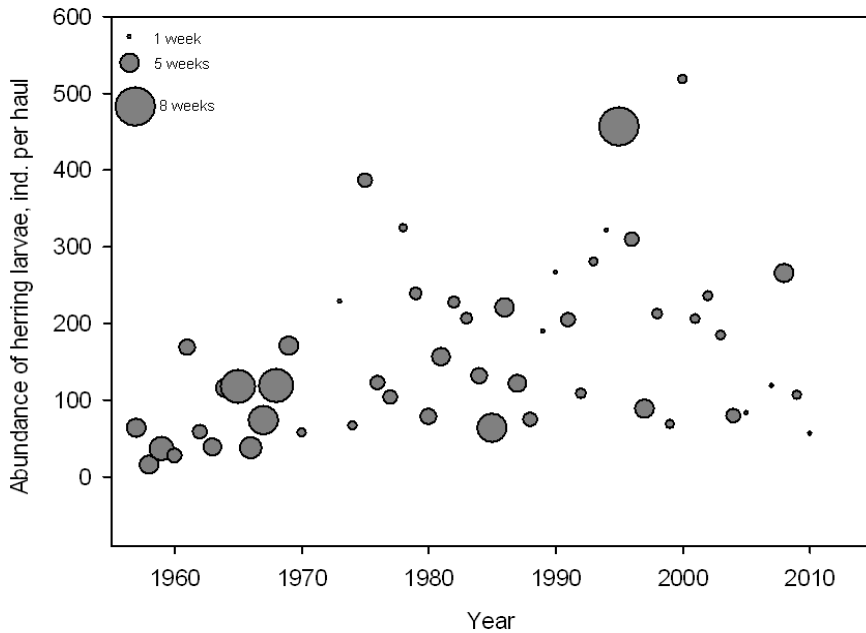


Figure 2. Long-term dynamics of the mismatch (1–8 weeks) between the larval herring and its main prey (*nauplii* of the copepod *Eurytemora affinis*) at one station (no. 1, please see Fig. 1) plotted against the abundance of herring larvae during 1957–2010. Larger bubble refer to a weaker match between larval herring and its prey.

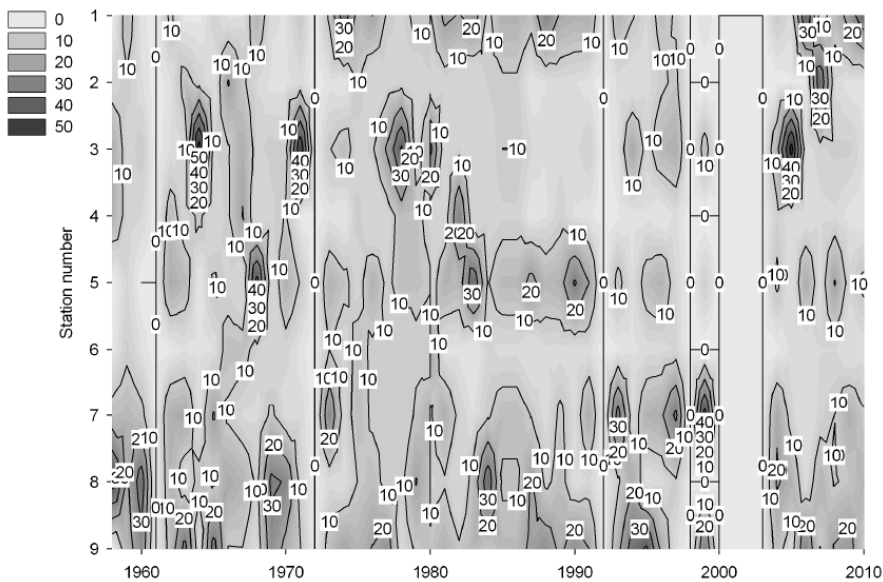


Figure 3. Distribution of herring larvae by sampling stations (1–9), expressed as a percent of individuals from annual total abundance, in the NE Gulf of Riga during May–June from 1958–2010. Note that data for seasonal spatio-temporal distribution of herring larvae in 1961, 1972, 1992, 1998, 2000–2003 are missing. For location of station numbers, please consult Fig. 1.

4.3. Feeding ecology of larval spring herring in relation to environmental variability and implications to larval fish abundance dynamics

The recruitment (year-class) strength of marine fish species can vary by orders of magnitude between years and is normally governed by feeding conditions that affect growth and mortality rates during the first year of life (Houde 2008). For example, changes in prey availability, resulting from spatio-temporal matches with their prey, can alter larval growth rates and consequently the duration of the pre-recruit period when larvae are particularly susceptible to predation mortality (Bailey and Houde 1989). Therefore, starved and weakened larvae may be more vulnerable to predation (Skajaa et al. 2004).

The main prey items of herring larvae are copepods, however rotifers, especially *Keratella quadrata*, are highly dominant in the zooplankton community during May-July. Although rotifers have been shown to be an important prey item for the first-feeding herring larvae elsewhere in the Baltic Sea (Margonski et al. 2006), our findings confirm the opposite results (III). The remaining two zooplankton groups, cladocerans and meroplankton had substantially lower densities during the presence of herring larvae. Amongst the main prey of herring larvae (*i.e.* copepods), their most abundant life-history stage was *nauplii*. Density of *nauplii* is the lowest in the beginning of the larval herring distribution season (May), increases thereafter and displayed a slight decrease in July (III).

Direct methods to describe and quantify the phenomenon of larval fish starvation include observations on feeding success including analyses of gut content (Bochdansky et al. 2008). In general, the share of herring larvae with prey items in the gut can vary greatly, from only a few to around 60–70% (Blaxter 1963). We found that the feeding activity of larval herring by the three distinct length groups varied between years and prey density in the field explained best these variations (III). However, differences in prey availability can affect small and large larvae differently because of the size-based variations in the prey encounter rates and capture efficiency (Miller et al. 1992). Diet composition of herring larvae was significantly different amongst the smallest size group compared to that of the medium and large larvae in the 1970s, but not in the 2000s. We hypothesize, that because of different prey field in terms of the developmental stage of prey and the mean annual abundance of copepod *nauplii* (IV), the smallest larvae were more likely forced to ingest more diverse prey and switch to consume larger sized prey in the 2000s earlier in their life than in the 1970s (III). However, small larvae (especially those with a length less than 10mm) are more likely to have serious difficulties in capturing large prey (*i.e.*, advanced stages of copepods) (Ehrlich and Blaxter 1976) and this may substantially decrease survival of the first-feeding herring larvae. This, in turn, may contribute to the decreased larval herring abundances (II, IV).

Furthermore, a seasonally variable climate governs to a great extent the timing of important developmental and behavioral events of organisms (Edwards and Richardson 2004). These commonly occur as a result of changes in phenology where rising temperatures cause the reproduction of the prey to shift towards earlier in the year, while the reproduction of the predator remains unaffected (Edwards and Richardson 2004). We found that the first appearance of herring larvae and degree of mismatch between herring larvae and their prey had one major synchronous shift in the mid-1990s (IV). This is in accordance with earlier studies which demonstrated that since the late 1980s and the early 1990s, most zooplankton species in GoR significantly changed their seasonal dynamics (Kotta et al. 2009). These changes in seasonality manifested as a result of eutrophication and climate variability (Kotta et al. 2009), associated with invasion of the non-native predatory cladoceran *Cercopagis pengoi* (Ojaveer et al. 2004). It is likely that one of the factors shaping the annual-scale variability in larval herring diet composition and feeding activity is inter-annual changes in seasonality of copepods, through their spatio-temporal match and mismatch (III, IV). This is also confirmed by differences in the dietary composition of larvae amongst all size groups, being larger between than within the decades (III). This could be partly caused by annual-scale variability in the degree of mismatch between larval herring and their major prey items – copepod *nauplii* (IV). Hence, irrespective of larval herring size-groups, abundance of copepod *nauplii* was the dominating factor in the model when combining all abiotic and biotic factors that determine larval herring feeding patterns (III).

The question of what factors regulate patterns of feeding in larval fish has remained a focus of fisheries oceanography for several decades (Dower et al. 2002). It is still crucial to describe how different environmental factors such as, water temperature, wind strength, light climate and prey field, interactively affect prey ingestion of larval fish (Fox et al. 1999; MacKenzie and Kjørboe 2000). Also, because of the development of the dorsal fin and thus improved swimming abilities, the relative effect of environmental forcing on prey consumption of larval herring varies by size groups. Environmental conditions, such as wind-induced currents, sea surface temperature, visibility, prey density and individual condition of larvae, might not necessarily have a direct effect on larval feeding activity. Nevertheless, our findings indicated that water transparency significantly affected medium-sized larval fish feeding. In the shallow study area, visibility is tightly related to wind, primary production, river runoff and density of small particles and is very variable both, in seasonal and long term perspective (III, IV). In light of the current study, long term changes in the GoR ecosystem (*i.e.* impoverished light conditions) may include larval herring being forced to eat more advanced developmental stages of copepods, presumably due to limited ability to detect smaller prey items (III). This, in turn, might give rise to an elevated dietary overlap within the local planktonic food web and result in increased density-dependent mortality amongst herring

larvae. Nevertheless, we found that out of the all investigated abiotic and biotic factors, water transparency appeared to be the most influential factor in determining the feeding activity of the medium-sized larvae with lower feeding activity at lower water transparency values (III).

4.4. Major reorganisations in the herring-relevant environment of the Gulf of Riga

While most of the regime shifts in the marine environment have been studied in larger spatial scales (*e.g.*, Beaugrand et al. 2003; deYoung et al. 2004; Lindegren et al. 2010) relatively little attention has focussed on coastal areas. Coastal areas and river estuaries fulfill important key functions of marine ecosystems *e.g.*, act as a nursery grounds for several commercial fish stocks and thus modify the size of future fish stocks. We have focussed in this study on nineteen long-term time-series relevant for the early life history of the most important commercial fish species in GoR – herring. To ensure provision of an integrated view on this, the newly developed shift detection method (Gröger et al. 2011) was applied. Part of the concept was to study whether a global approach with all variables included gives the same picture as an individual approach with all variables being split into three subsets: biotic, abiotic and phenological factor groupings. Individual analysis was thus performed to reflect the three major dimensions (regimes), assuming that this type of separation leads to more detailed information being available (IV).

Analysis for single variables were performed for the following herring TS: larval herring mean abundance, herring recruitment abundance, larval herring retention time, onset of herring larvae and the degree of mismatch between larval herring and *Eurytemora affinis nauplii*. We found that two phenological parameters – onset of herring larvae and larval herring retention time – displayed similar patterns over time and exhibited only one shift with the timing in the mid-1990s. In both cases, the shift pattern is also the same: level-changing type. Annual mean abundance of herring larvae and the degree of mismatch between larval herring and *E. affinis nauplii* displayed two shifts over time with very different timings: two years 1975 and 2000; and two time periods – late 1960s and mid-1990s, respectively. While larval herring phenology-related data series displayed a significant shift one or two times throughout the studied period, herring recruitment abundances had three shifts (in 1969, 1974 and 1989). Although we cannot confirm and directly affiliate changes in abiotic parameters or species phenologies to the timing of regime shifts in the single herring-related biotic scores, linking abiotic conditions to the studied single herring related variables may be justified. For instance, shifts in herring univariate parameters, which occurred in the mid-1990s, might have been triggered by thermal conditions and mediated through altered species phenologies. Onset of herring larvae, their retention time and degree of mismatch

between larval herring and *E. affinis nauplii* changed significantly at that time. However, when applying a slightly different approach, i.e. variable clustering, herring larvae and recruitment abundance were located in the same cluster with salinity and water transparency. This might indicate, that early life stages of herring are mostly influenced by local hydroclimate while food availability seems not to be the primary factor limiting abundance of this marine species in the NE Baltic Sea (see also Fig. 4) (IV).

For the abiotic environment, a scree test (Cattell 1966) identified four principal components (PCs) from the seven standardized abiotic variables (IV). The eigenvalues of the correlation matrix indicated that the first principal component (PC1) alone explains 47.57% of the total variance. High values of 0.4693, 0.4432 and 0.4652 of the abiotic PC1's eigenvector for sea surface temperature (SST) in spring and summer as well as winter air temperature reflect that these three were the strongest variables linked to PC1, thus predominantly describing the abiotic environment. This is confirmed by the fact that spring SST and summer SST plus winter air temperature are significantly and positively correlated with PC1, while salinity and timing of ice retreat were significantly negatively correlated with PC1 ($r = 0.86; 0.81; 0.85$ respectively, $n = 54, p < 0.01$). All these significantly correlated factors showed a similar temporal pattern over time when also applying hierarchical variable clustering. Hence, it is likely that these abiotic drivers are responsible for one clearly expressed RS in the study area. The transition zone from the negative to the positive values of PC1 scores had a smooth pattern lasting from the late-1980s until the early 1990s with the transition zone centre being located approximately in 1989 (IV).

With regard to phenological changes in larval herring and its prey over time, a scree test identified three PCs from the six phenological variables. The eigenvalues of the correlation matrix indicated that among all PCs generated, PC1 explains 34.43% of the total variance. High values of 0.5317, 0.6025 and 0.4775 of the phenological PC1's eigenvector for herring larvae onset, timing of maximum abundance of herring larvae, and degree of mismatch between larval herring and *E. affinis nauplii* reflect that these three variables were the strongest ones linked to PC1 which thus predominantly describe the phenological aspect. This result is also reflected by the fact that larval herring onset, timing of maximum abundance of herring larvae, and degree of mismatch between larval herring and *E. affinis nauplii* were the main variables being significantly positively correlated with phenological PC1 ($r = 0.76; 0.87; 0.69$ respectively, $n = 54, p < 0.01$), while all other variables explained only marginal part of temporal variation of PC1. Based on phenological changes over time, two RS can be identified, one of them taking place in the early 1970s and the second one during the mid-1990s (IV).

To analyse long-term performance of the biological environment, six different herring and copepod abundance time-series were used, from where a scree test identified four PCs. The eigenvalues of the correlation matrix

indicated that the biotic PC1 explains 30.71% of the total variance among all other PCs of this variable complex. High values of 0.3944, 0.6183 and 0.6420 of the biotic PC1's eigenvector for herring recruitment abundance, maximum abundance of *E. affinis nauplii* and maximum abundance of *E. affinis* females reflect that these three variables were the strongest linked to biotic PC1, thus predominantly describing the biotic environment. Whilst this is also confirmed by their correlations with biotic PC1 being all positive and highly significant ($r = 0.54; 0.84; 0.87$ respectively, $n = 54, p < 0.01$), all other variables remained insignificant. In difference from the abiotic and phenological component, the biotic environment seems to have retained a high stability since the beginning of the time-series until 2003, when the single significant shift took place (IV).

The multivariate shiftogram pooling all nineteen (see Table 1) larval herring-relevant parameters identified two distinct ecosystem states in the GoR. The first state of ecosystem lasted from 1957–1985, followed by a smooth transition period (1986–1991) and entering into a new phase from 1992 onwards. The main signal for the general regime shift came from abiotic components that were related to thermal regime (sea surface temperature in spring and summer, winter temperature and timing of ice retreat) while the importance of phenological aspect and biotic environment was negligible (timing of maximum abundance of herring larvae, larval herring onset and mean abundance of *E. affinis* adults) (Fig. 4) (IV). The existence and timing of the ecosystem regime shift identified in the current study was also confirmed by previous investigations, however, with several additional shifts with variable timing in the mid 1970s and late 1990s (Diekmann and Möllmann 2010; ICES 2012). Although these other abrupt changes are not clearly evident in the current analysis, there seems to be some evidence of a potentially weak shift in the 1970's (IV). In summary, compared to other studies in the Baltic Sea and in several cases elsewhere in marine ecosystems, there are three features which make the current study specific. These are: 1) we have used time-series that has been running for a relatively long period – since 1957, 2) we have also included several phenological time-series, which is not the case for other similar studies elsewhere, and 3) we have focussed our study on the pelagic ecosystem mostly related to the major commercial fish – herring. In general, timing of the abrupt changes found in the present study coincide with similar events observed in other areas, e.g. the Canadian Eastern Scotian Shelf (Choi et al. 2005), the U.S. Continental Shelf (Link et al. 2002), the North Pacific (Hare and Mantua 2000), the North Sea (Beaugrand 2004; Weijermann et al. 2005), and the Baltic Sea (Möllmann et al. 2008).

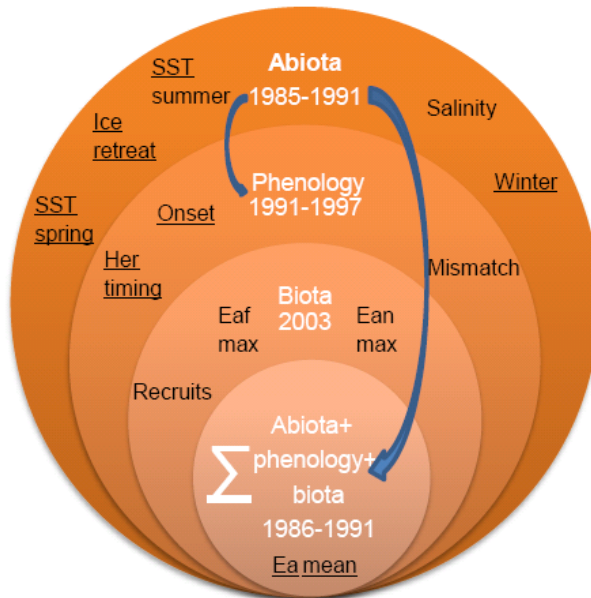


Figure 4. Schematic representation of significant factors that contributed to regime shifts in the Gulf of Riga, by using larval herring relevant time-series for the period of 1957–2010 by different specific categories/sub-sets (abiota, phenology, biota) and jointly for the system. Years referred to under different categories/sub-sets indicate timing and the duration of a regime shift within this particular category. Arrows indicate the suggested causal link between the discriminated categories. All individual factors displayed by different categories contributed significantly to the first principal component of this particular sub-set while the underlined parameters contributed significantly at the ecosystem level. For abbreviation explanations please see paper **IV**.

5. CONCLUSIONS

1. Absolute fecundity of the Baltic autumn-spawning herring varied between *ca.* one order of magnitude. While interannual variation in relative fecundity was significant, variability in absolute individual fecundity remained insignificant at an annual scale. Absolute fecundity correlated significantly with the total body length and weight of fish, while fish age was an insignificant factor both in single and multivariate models. Presumably due to changed ecosystem conditions and related trophic impacts on fish somatic growth, younger fish had a slightly higher fecundity in the 2000s than in the 1959–1970 time frame, while the opposite pattern was valid for older fish.
2. Earlier studies indicated that the first-feeding of small herring larvae was consumption of small-sized prey (mostly copepod *nauplii*) only. We have found that small herring larvae can also eat relatively advanced developmental stages of copepod prey and this may be linked to changed prey phenology and/or alterations in other ecosystem properties (like water transparency). Larval herring diet composition appeared to be mainly influenced by prey (copepod) density, whilst other environmental forcing seems to be less important.
3. Larval herring abundance has displayed two abrupt changes in the Gulf of Riga over the last 60 years with the high abundance level lasting for about three decades (since early 1970s until the early 2000s). The number of large larvae correlated significantly positively with the recruitment abundance of the GoR herring population. This might have importance as an additional fishery-independent indicator for stock predictions.
4. The multivariate shiftogram pooling nineteen herring early life-history stages relevant variables identified two distinct states in the studied variables. The first state occurred during the period 1957–1985, followed by a smooth transition period, lasting from 1986–1991 and has entered into a new phase from 1992 onwards. The GoR (herring-relevant) ecosystem seem to be mainly regulated by abiotic conditions related to the thermal regime while phenological aspect and biotic components had a substantially minor role.

SUMMARY

Fishes within the family *Clupeidae* form one of the most abundant fish populations in the world's oceans. Atlantic herring (*Clupea harengus* L. 1758) is one of the most important members of that family within the Atlantic Ocean. The Atlantic herring is both an ecologically and economically key species in many temperate marine ecosystems. Herring has historically been the most important commercial fish in the Baltic Sea and is probably the best adapted marine fish species to the prevailing spatio-temporally varying heterogeneous environmental conditions of the Baltic Sea by forming several distinct populations. These populations show differences in migration and spawning patterns as well as in morphology.

On the basis of morphometric and meristic characters, two groups – spring and autumn spawners – were distinguished in the Baltic Sea. While the spring spawning herring generally constitute most of the herring landings in the Baltic Sea, the importance of the autumn spawners has varied over time. For instance, autumn spawners constituted the main part of herring catches in the Baltic Sea about a century ago but currently remain at a very low level and comprise less than 1% in commercial catches. Unfortunately, our knowledge of the Baltic autumn spawning herring is limited compared to that of the spring herring and almost lacking over the past decades. In terms of stock assessment and management, the spring and autumn herring populations are not separated. As fish stock recruitment abundance is related to individual fecundity, one of the aims of the thesis was to investigate individual fecundity of the currently depressed autumn herring in relation to somatic parameters and compare the most recent observations with the historical data from the period when the fish was abundant.

Absolute individual fecundity (AF) of clupeoid fish is known to vary over time and space. In many cases, these variations have been linked to food availability, which in turn is affiliated by hydroclimatic conditions and affects energy reserves, both at the fish individual and population level which in turn determines species reproduction potential. On the contrary, reproduction potential is important factor determining spatio-temporal dynamics of fish stock. Autumn herring absolute individual fecundity was studied in three consecutive years from 2008–2010 and compared with historical findings, derived in the 1960s and 1970s. AF varied between 11,838 and 108,093 oocytes per fish. Substantial (24–33%) and significant inter-annual differences were observed in the relative fecundity of the fish, while interannual differences in the absolute individual fecundity remained insignificant. However, while all mentioned variables were important as single predictors, only fish length and condition factor were the major predictors for fecundity in multiple regression. In addition, the obtained results on AF were compared with historical findings from 1959–1970, when the commercial catches of autumn spawners occasionally contributed to around 40% of the herring catch. Remarkable differences in

the AF between the two time periods by age groups were found, with higher fecundity amongst younger age-groups and lower amongst older age-groups in the 2000s compared to that during 1959–1970 (I).

Development of larval herring since the hatching and until the metamorphosis takes place in a very variable environment and their mortality is considered to be mostly related to availability of suitable prey. Feeding environment is determined by both abiotic as well as biotic conditions, which influence prey composition and feeding activity of larval herring. Advanced understanding of the combination of these factors has remained as a challenge until present. For better understanding of spring spawning herring abundance dynamics in the GoR, it is essential to understand which factors and the extent to which these influence feeding behaviour and patterns of larval herring. In the present thesis, feeding ecology of the larval spring-spawning herring was studied in relation to selected abiotic and biotic parameters in the shallow sheltered Pärnu Bay (Gulf of Riga) in the 1970s and the 2000s. The copepod *Eurytemora affinis* was the strongly dominating dietary item during all years while other prey was ingested only sporadically. Feeding activity of herring larvae was affected by different environmental variables and the relationships varied among the size classes of herring larvae. The studied abiotic (*i.e.*, wind speed, water temperature, water transparency) and biotic variables (*i.e.*, density of copepod *nauplii*, copepodite stages I–V and adults of *E. affinis*, mean developmental stage of copepods and density of fish larvae) had no significant effects on the feeding activity of small (< 10 mm) larvae. The feeding activity of medium (10–16 mm) larvae was only affected by water transparency and that of large (> 16 mm) larvae by a combination of water temperature, wind speed and the structure of local copepod community, respectively. On the other hand, the diet composition of all herring larvae was best described by the density of copepod *nauplii*. In addition, the density of fish larvae improved the diet composition model of small larvae and the density of adult copepods that of medium larvae, respectively (III).

Larval herring abundance studies in the GoR were started in 1947 and have continued until the present day. This dataset allowed us to establish long-term dynamics of larval herring abundance and investigate it in relation to hydro-climate and the biotic environment. Larval herring abundance was lowest at the beginning of the observation period in the 1950s and started to increase in the 1960s, reaching its peak at the end of the 1990s (II, IV). In the 2000s, larval herring abundance has clearly dropped, and is currently generally at a level similar to the 1960s and the 1970s. While the first increase is most probably related indirectly with a general increase in sea productivity, the second increase is probably favoured by mild winters. This is confirmed with the result, that thermal conditions during the preceding winter appeared to have a significant positive effect on the abundance of herring larvae and recruitment of the stock (II).

The link between the early life-history stages of marine fishes and recruitment is sufficiently well documented to justify a continued investment of efforts into investigations of the factors regulating the mechanism responsible behind the abundance and survival of the egg and larval stages. Despite considerable efforts made, several uncertainties are still evident in this field. We have found that the abundance of large larvae can be used for a preliminary estimation of the year class strength of the GoR spring spawning herring population. This should be considered as an important finding in practical terms **(II)** as it allows preliminary estimations to be made much earlier than the availability of the stock assessment results.

Sustainable management of marine fisheries resources require advanced understanding on the ecology of the early life-history stages of fish, including considering the fact that relationship and processes between different ecosystem components might change at different ecosystem regimes. The multivariate shiftogram approach by pooling nineteen different herring early life-history stages relevant variables was applied to identify a) whether and when the abrupt changes (also called as regime shifts) take place in the herring-relevant data series in the GoR ecosystem, b) which factors or their combination are responsible for the observed ecosystem-level changes and c) whether changes at the ecosystem level appeared synchronously with those observed in phenology and abundance-related single time series of larval herring. It appeared that two distinct ecosystem states of the GoR could be identified. The first state occurred between 1957–1985, followed by a smooth transition period, lasting from 1986–1991 and has resulted in a new ecosystem phase since 1992 onwards. The GoR ecosystem seem to be mainly regulated by abiotic conditions, especially those related to the thermal regime (sea surface temperature in spring and summer, winter air temperature and timing of ice retreat) while phenological and biotic time-series (timing of maximum abundance of herring larvae, onset of herring larvae and mean abundance of *Eurytemora affinis* adults) had a substantially minor role. While the regime shift in the abiotic environment was followed by a shift in the phenological cluster referring potentially to causality, shift in the herring-related biotic environment was evident much later than expected from the causality chain. Compared to other studies in the Baltic Sea and in several marine ecosystems elsewhere, there are three major features which make the current study specific. These are: 1) we have used a relatively long time-series – since 1957, 2) we have also included several phenological time-series, which is not the case for other similar studies elsewhere, and 3) we have focussed our study on the pelagic ecosystem mostly related to the major commercial fish – herring. In general, timing of the abrupt changes found in the present study coincide with similar events observed in other areas like the Canadian Eastern Scotian Shelf, North Pacific and North Sea **(IV)**.

SUMMARY IN ESTONIAN

Räime *Clupea harengus membras* varajaste elustaadiumide ökoloogia Läänemere kirdeosas

Sugukond heeringlased on üks arvukamaid kogu maailmameres ning Atlandi heeringas (*Clupea harengus* L. 1758) on üks arvukamaid liike selles sugukonnas Atlandi ookeanis. Läänemeres elav räim (*Clupea harengus membras*) on Atlandi heeringa kääbustunud vorm, kes on kohastunud elama riimveelise Läänemere väga varieeruvates keskkonnatingimustes. Räim on olnud Läänemeres ajalooliselt kõige olulisem tööduskala ning moodustab siin mitmeid asurkondi, mis erinevad üksteisest muuhulgas individuaalsete parameetrite kui ka ökoloogia poolest (nt. kudekäitumine, ränded, toitumine).

Morfoloogiliste tunnuste alusel eristatakse Läänemere räimel kahte erinevat sesoonset kudemistüüpi – kevad ja sügiskudu räim. Kui kevadräime osakaal on kaasajal räimesaakides valdav, siis sügisträime osatähtsus saakides on erinevatel aegadel suuresti varieerunud. Läänemere räimevarude suuruse hindamine ja nende majandamine toimub lähtuvalt kevadräimest ning sügisträime ei majandata eraldiseisva(te) varuühiku(ten)na. Sügisträime varu langes pikaajalisse madalseisu juba mitu aastakümnet tagasi ja veenvaid märke sügisträime taastumisest ei ole, kuivõrd sügisträime osakaal saakides jääb senini alla 1%. Kuna kalavaru täiendi arvukus seostub asurkonna absoluutse individuaalse viljakusega, oli doktoritöö üks eesmärgi selgitada madalseisu oleva sügisträime individuaalset viljakuset sõltuvalt kala somaatilistest parameetritest ning võrrelda leitud varasemate tulemustega perioodist, mil sügiskuderäime oli oluliselt rohkem Läänemeres.

Heeringlaste individuaalne absoluutne viljakus on väga varieeruv nii ajas kui ruumis ning seda varieeruvust on peamiselt seostatud toitumistingimustega, mis paljuski sõltub regionaalsetest hüdro-kliimaatilistest tingimustest ning mis omakorda määrab asurkonna paljunemispotentsiaali. Seevastu asurkonna paljunemispotentsiaal on oluline tegur, mis mõjutab nii noorkalade arvukust kui ka asurkonna suuruse dünaamikat ajas. Käesolevas töös analüüsisime Läänemere kirdeosas ajalooliselt eristatud sügisträime asurkonna absoluutset individuaalset viljakust (AF) kolmel järjestikusel aastal (2008–2010). AF varieerus vahemikus 11 838 ja 108 093 ootsüüti isendi kohta kusjuures erinevus aastate vahel ei olnud statistiliselt oluline. AF seostus statistiliselt oluliselt ning positiivselt kala kehamassi ja -pikkusega, kuid mitte kala vanusega. Üldjoontes oli kõrgema konditioonifaktoriga isendite AF suurem. Siiski väljendus korrelatsioon nõrgalt ja oli kahel üksikul aastal statistiliselt ebaoluline. Erinevus kalade suhtelises viljakuses oli kõigi kolme aasta vahel statistiliselt oluline, erinedes üksteisest 24–33%. Lisaks eelnevale võrdlesime me käesoleva töö tulemusi varasematega ajaperioodist 1959–1970, mil sügisträim oli arvukas ning ta osa räimesaakides märkimisväärne ning küündis 40%-ni. Ilmnes, et vanusrühmade lõikes erines

sügisräime AF kahel uuritaval perioodil (1959–1970 ja 2008–2010) märkimisväärselt, samas kui kehamassi kaupa AF-s erinevust periooditi ei leitud (I).

Räimevastsete areng alates marjast koorudes kuni metamorfoosini leiab üldjoontes aset väga varieeruvates keskkonnatingimustes. Kalavastsete suremuse peamiseks põhjuseks peetakse sobiva suurusega toiduobjektide nappust ajahetkel mil vastne asub toituma väliskeskkonnas leiduvast. Toitumise juures on oluline kogu toitumiskeskond, st. eluta- ja eluskeskkond, mis mõjutab nii kalavastsete toitumisaktiivsust kui ka toiduobjektide valikut. Just erinevate tegurite koostoime on jäänud paljuski selgusetuks kuni kaasajani. Seega, mõistmaks uurimise all oleva Liivi lahe kevadräime asurkonna arvukuse dünaamikat on eelnevalt vaja muuhulgas selgitada millised keskkonnategurid ning mil määral mõjutavad räimevastsete toitumist. Käesolevas töös on analüüsitud räimevastsete toitumisaktiivsuse ja nende sooltorust leitud saakloomade dünaamikat ning leitud on seostatud valitud eluta- ja eluskeskkonna teguritega madalaveelises Liivi lahe kirdeosas 1970ndatel ja 2000ndatel aastatel. Räimevastsete toidus oli selgelt valdavaks liigiks aerjalgne *Eurytemora affinis*, kusjuures kõikide teiste liikide isendeid leiti vastsete sooltorudest vaid juhuslikult. Räimevastsete toitumisaktiivsus seostus erinevate keskkonnateguritega, ning seosed varieerusid sõltuvalt räimevastse pikkusest. Ükski uuritud eluta- (tuule tugevus, veepinna temperatuur, vee läbipaistvus) ega eluskeskkonna (aerjalgsete erinevate argengustaadiumide arvukus, aerjalgsete keskmine arengustaadium ega kalavastsete arvukus) tegur ei seletanud väikeste (>10mm pikkuste) räimevastsete toitumisaktiivsust. Keskmise suurusega räimevastsete (10–16mm) toitumisaktiivsust mõjutas vee läbipaistvus ning suurte vastsete (<16 mm pikkuste) toitumisaktiivsust vee temperatuuri, tuule kiiruse ja erineva arengustaadiumiga aerjalgsete arvukuse koosmõju. Räimevastsete sooltorudest leitud toidu koosseisu kirjeldas sõltumatult pikkusrühmast kõige paremini aerjalgsete vastsete arvukus keskkonnas. Kõige väiksemate räimevastsete toidu koosseisu kirjeldas lisaks aerjalaliste vastsete arvukusele veel ka kalavastsete arvukus, mis võib viidata võimalikule toidukonkurenttsile. Keskmise suurusega räimevastsete toidu koosseisule oli määrav lisaks aerjalgsete vastsete arvukusele veel ka arenenumate aerjalgsete arvukus (staadiumid I–V) keskkonnas. Selline tulemus on ootuspärane, kuivõrd suuremad räimevastseted vajavad energeetiliselt toitvamaid ja seega suuremaid toiduobjekte (III).

Juba alates 1947. aastast regulaarselt läbiviidavate välitööde käigus kogutavad räimevastsete proovide analüüsi tulemusel selgus, et räimevastsete arvukus suurenes alates 1960ndatest aastatest, arvukuse kasv aeglustus 1970ndail ning suurenes taas 1980ndail aastail. Kui esimest järsku arvukuse suurenemist võib kaudselt seostada mere toitelisuse tõusuga, siis teise kiire kasvuperioodi põhjuseks on ilmselt sel perioodil oluliselt soojenenud talved. Seda kinnitab ka fakt, et räimevastsete arvukus seostus statistiliselt usaldusväärselt ja positiivselt talve õhutemperatuuridega. Samuti seostus talve õhutemperatuur statistiliselt usaldusväärselt noorkalade arvukusega, soosides seeläbi soojematele talvedele järgnevalt arvukamat noorkalade hulka (II).

Kalade varajaste elustaadiumite arvukuse dünaamika uuringute üks praktilisi väljundeid on juba möödunud sajandist alates seostunud kalavaru täiendi suuruse hindamisega. Vaatamata pingutustele ei ole selles valdkonnas väga suuri edusamme saavutatud. Käesolevas töös leiti, et suurte räimevastete arvukuse alusel on võimalik usaldusväärselt anda esialgne hinnang räimevaru täiendi suurusele. See on oluline kalandusandmetest mitte-sõltuv lisanäitaja hindamiseks räimevaru täiendi suurust oluliselt varem kui varu suuruse hinnang seda võimaldab (II).

Mere tööndukalade varude säästlik majandamine eeldab kala erinevate elustaadiumide ökoloogia head tundmist kusjuures mereökosüsteemi erinevates seisundites võivad selle eri komponentide vahelised suhted varieeruda. Käesolevas töös käsitletud üheksateistkümmne Liivi lahe kevadräime varajaste elustaadiumidega seonduva teguri pika-ajalisel analüüsil (perioodil 1957–2010) selgitasime a) kas ja millal on toimunud radikaalsed pöördumatud muutused (ehk nn. režiiminihked) Liivi lahe ökosüsteemis, b) millised tegurid või nende kombinatsioon mõjutavad oluliselt ökosüsteemi muutusi ning c) kas olulised muutused süsteemis toimusid sünkroonselt muutustega räime varajaste elustaadiumide käitumises. Liivi lahe ökosüsteemis saab eristada kahte teineteisest erinevat seisundit. Esimene neist kestis perioodil 1957–1985, millele järgnes sujuv, suhteliselt pikka aega kestnud üleminek (1986–1991) uude seisundisse, alates 1992 kuni tänapäevani. Tugevaim signaal keskkonnaseisundi muutustele pärines eluta keskkonnast ning seostus mere termilise režiimi muutusega (veepinna temperatuur kevadel ja suvel, talvine õhutemperatuur ja jääpäevade kestvus). Sealjuures nii fenoloogiliste kui eluskeskkonna komponente koondavate aegriidade olulisus režiiminihkele oli vähemtähtis. Nimetatud komponentide üksikteguritest osutusid statistiliselt olulisteks räimevastsete ilmumise aeg ja nende suurima arvukuse sesoonne ajastatus, ning aerjalgse *E. affinis* aastane keskmine arvukus. Eluta keskkonnas toimunud režiiminihe kandus lühikese ajalise nihkega edasi eluskeskkonna fenoloogilisse režiiminihkesse, kuid ei põhjustanud olulist muutust süsteemi eluskeskkonnas. Kuigi käesolevas töös rakendati pika-ajaliste andmeridade analüüsil uudset meetodit, on leitud ökosüsteemi režiiminihke ajastus üldiselt kooskõlas mitmetes teistes töodes leituga nii Läänemere kui muu maailmamere piirkondadega (nt. Kanada idarannik, Vaikse ookeani põhjaosa, Põhjameri). Võrrelduna teiste sarnaseid probleeme käsitlevate artiklitega võib käesoleva töö puhul esile tõsta kolme erisust: 1) käesolev töö kattis pikema ajaperioodi, 1957–2010, 2) kaasatud oli liikide fenoloogilisi muutusi käsitlevad aegread, 3) töö oli fokusseeritud ökosüsteemi peamise töönduskala ja pelaagilises süsteemis olulisema tarbija – räime, varajastele elustaadiumitele (IV).

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ACKNOWLEDGEMENTS

There are several people whose direct or indirect contribution improved this work, often with the small things or tips, which helped to clarify insights and improved the focus of this work. I am especially grateful to my supervisors, Dr. Henn Ojaveer and Prof. Toomas Saat, for helping me organise my PhD study, especially its research component, for all their patience, guidance, continuous support and confidence in me. Their great competence and long experience guided me into the world of (larval) fish ecology and increased my curiosity in this subject, which eventually became close to my heart. Their fastidiousness and knowledge in this work enabled me to develop an understanding for the subject. I am deeply grateful that you found time in your busy days to revise and provide feedback on my scientific papers and dissertation in details.

I wish to express my sincerest thanks to Dr. Sci. Evald Ojaveer, whose great experience, superb expertise and unmeasurable contribution in the field of herring and marine ecosystem investigations in the Baltic Sea firstly initiated feelings that there is nothing more to discover and that everything is already achieved. However, numerous telephone conversations that often lasted several hours appeared to have the most significant influence in the configuration of my scientific hypotheses and the multiple different ways testing those. I am grateful for your cooperation and appreciate your in-depth discussions at every occasion.

Thanks to all my present and former colleagues at the Estonian Marine Institute, University of Tartu whose assistance and professional guidance resulted in this thesis. I would like to express my eternal gratitude to Dr. Ain Lankov, Dr. Mart Simm, Dr. Jonne Kotta, Dr. Maria Pöllupüü and Mrs. Heli Shpilev. I would also like to thank Prof. Joachim P. Gröger from the Institute for Sea Fisheries, von-Thünen Institute (Germany) and Riina Klais (University of Tartu) in assistance of long-term data analysis and results interpretations. I want to thank the R/V “VILMA” staff for creating a pleasant working atmosphere on board the research vessel during the hundreds of hours I spent at sea collecting various different samples. I am grateful to Margret Sisask, Virve Käärrik and the staff of the Department of Zoology of the Institute of Ecology and Earth Science for creating an agreeable working space. I am also indebted to Dr. Bhavani Narayanaswamy for revising the English of the current thesis.

I want to give my thanks to all my family members, friends and relatives. I will not name all my supporters because the list of the names would be way too long, however I really appreciate their support and presence. My very special gratitude belongs to my consort Jana Galadi whose patient mind gave me a lot support at times when I most needed it and gave me a lot of motivation for writing the thesis. Without all of them this thesis definitely would not have been written.

I want to thank the following for supporting my work financially: the Estonian Ministry of Education and Research (grant no. SF0182579s03 and SF0180005s10), Estonian Science Foundation (grant no. 8747), European Community's Framework Programmes European Network of Excellence for European Ecosystem Analysis (EUR-OCEANS, FP6, Contract No. 511106 NoE) and Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS, FP7, Grant Agreement No. 266445).

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