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Non-linear and non-stationary relationships in the pelagic ecosystem of the Gulf of Riga (Baltic Sea)

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Estonian Marine Institute and Department of Zoology, Institute of Ecology and Earth Science, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers referred to in the text by their Roman numerals (**I–III**):

I. **Einberg, H.**, Klais, R., Rubene, G., Kornilovs, G., Putnis, I., and Ojaveer, H. 2019. Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea. ICES Journal of Marine Science, 76(7): 2427–2436.

II. **Einberg, H.**, Klais-Peets, R., Põllumäe, A., and Ojaveer, H. 2020. Taxon-specific response to the invasion of a pelagic invertebrate predator, revealed by comparison of pre- and post-invasion time series. Journal of Plankton Research, 42(6): 714–726.

III. Ojaveer, H., Klais-Peets, R., **Einberg, H.**, and Rubene, G. 2021. Spawning stock biomass modulation of environment – recruitment relationship in a marginal spring spawning herring (*Clupea harengus membras*) population. Canadian Journal of Fisheries and Aquatic Science, 78(12): 1805–1915.

AUTHORS' CONTRIBUTION

In addition to the leading papers **I** and **II**, I contributed to all papers (**I**, **II**, **III**) in all stages: the planning and design of the study, preparation of the data and selecting statistical methods, performed formal analysis as well as interpreted the results, preparation of figures and tables, and manuscript writing.

LIST OF ABBREVIATIONS

AIC	Akaike information criterion
BSI	Baltic Sea Index
EDF	Estimated degrees of freedom
EDM	Empirical dynamic model
EBFM	Ecosystem-based approach to fisheries management
GAM	Generalized additive model
GCV	Generalized cross validation
GoR	Gulf of Riga
GWA	Growing window analysis
NAO	North Atlantic oscillation
NIS	Non-indigenous species
R	Recruitment (addition of young fish to the parent fish stock)
SSB	Spawning stock biomass (parent fish stock)
SST	Sea surface temperature
SWA	Sliding window analysis
WS	Winter severity

1. INTRODUCTION

1.1. Types and shapes of the links in marine ecosystems

The response of species and populations to external variables can be either linear or non-linear. While linear systems behave additively, non-linear systems are non-additive (Fogarty *et al.*, 2016). Linear links are parametric, whereas non-linear links can further be divided into parametric and non-parametric. Parametric links can be described through a mathematical function, e.g. the growth rate response to ambient temperature (Crawley, 2012; Nisbet *et al.*, 2018). Other relationships, particularly those observed between population level variables (e.g. abundance, biomass) and their drivers of change, are more likely non-parametric, i.e. they cannot be easily approximated to any known mathematical function, and there is also no mechanistic reason why they should be. The reasons for this include the fact that most relationships observed in nature are empirical, apparent correlations or associations, driven by very complex interactions of different drivers (Sugihara *et al.*, 2012; Stige *et al.*, 2013; Ye *et al.*, 2015; Sguotti *et al.*, 2020). Further, whenever the word "relationship" is used, it refers to the ecological relationships between species, or species and the environment; whereas the term "link" always refers to an empirical correlation observed between variables in the data analysis.

Recent meta-analysis by Hunsicker *et al.* (2016) revealed that the majority of single driver links in the pelagic environment are non-linear and that the probability of finding non-linear links increases with the length and quality of the time series. Moreover, non-linearities are most common in relationships in which species biomass, abundance, growth, and body condition are the ecological responses and/or when e.g. pollution is the driver. Therefore, Hunsicker *et al.* (2016) suggest that when the type of link is unknown, it is safer to assume that it is non-linear, rather than linear.

There are various shapes of non-linear responses of species to external drivers. The simplest are the forms where only the effect size (per unit change in the driver) varies: e.g. the response to the one degree of temperature change being stronger at low temperatures, and then levelling off above a certain value i) Gulf of Riga herring (*Clupea harengus membras*) recruitment (R) and sea surface temperature (SST) link in Cardinale *et al.* (2009); or ii) common fish mean-weight at age growth curves (see Brunel and Dickey-Collas, 2010). More complex patterns include one single maximum or minimum along the variable's axis (dome- or U-shape), amongst which the most common is one maximum type of link (see Daskalov *et al.*, 1999; Cardinale *et al.*, 2009; Pörten and Peck, 2010), e.g. temperature effect on the individual growth rate of Atlantic cod (*Gadus morhua*; Björnsson *et al.*, 2001). It is common to find unimodal empirical relationships in marine environments when the data contains a wide range of different values (Daskalov, 1999). Hunsicker *et al.* (2016) also brings out more complex cases (splines) with several turning points (see also Otto *et al.*, 2014b), however such relationships are more difficult to explain ecologically, at least for single species communities. Complex patterns should be more often the case when the change over time is shown, since time (observation year) itself is not a real variable, and does not need a mechanistic explanation. Examples of the complex non-linear shapes with time as the explanatory variable include the long-term patterns in the diatom-dinoflagellate relationship shown in Klais *et al.* (2011), or species composition changes shown in Olli *et al.* (2011).

It is important to use more flexible models in identifying the appropriate shape for the relationships when investigating long-term changes or making future predictions (Cardinale and Arrhenius, 2000; Ottersen *et al*., 2004; Hunsicker *et al*., 2016). Assuming a linear link when an ecological response is actually complex and more likely non-linear, may be inappropriate and therefore may have unwanted consequences if potential management decisions are made based on the scientific evidence obtained on these grounds. For that reason, several previous studies have also criticized using only "well-behaved" linear (parametric) models instead of more appropriate (often non-parametric) ones or combining them to make accurate assessments and predictions, e.g. for fish stocks (Cardinale and Arrhenius, 2000; Perretti *et al*., 2013; Fogarty *et al*., 2016; Hunsicker *et al*., 2016; Sguotti *et al*., 2020). For example, Sguotti *et al.* (2020) compared the traditional parametric model to two non-parametric approaches to investigate stock-recruitment relationships of 20 Atlantic cod stocks. They found that the stocks that experienced abrupt and state-dependent dynamics are best modelled using non-parametric approaches; for others, traditional (e.g. Ricker) models can be used. They emphasized the importance and value of using multimodal approaches (Sguotti *et al*., 2020).

1.2. Stability of relationships

Marine ecosystems are complex and dynamic, and are affected by multiple variables (Perretti *et al*., 2013; Ye *et al*., 2015, Deyle *et al*., 2016). The environment strongly influences population dynamics as well as their responses to individual variables (Ottersen *et al*., 2004). The relationships between populations and the variables affecting them may either stay stable over time and space (i.e. be stationary), or change and break down as the ecosystem changes (i.e. be non-stationary) (Ottersen *et al*., 2013; Klais *et al*., 2017; Tamburello *et al*., 2019). Non-stationarity is understood here as temporal or spatial variability of the relationship, which can manifest itself in the change of the type (e.g. from linear to non-linear), direction (from positive to negative or vice versa) or strength (changes in explanatory power and significance) of the relationship.

Fluctuations in environmental conditions can be gradual or abrupt. They are often caused by changes in climate (e.g. temperature, salinity, oxygen content) or multiple anthropogenic pressures (e.g. exploitation of living resources, pollution), but often a combination thereof to a level not experienced before (e.g. Österblom *et al*., 2007). These are also the main reasons why the species-environment relationships may change over time. Changes might be caused by periodic fluctuations in some key variables, including e.g. fluctuations between milder vs harsher winters or saline vs less saline conditions (e.g. Ojaveer *et al.*, 1999; Raudsepp, 2001). Such fluctuations may determine the strength of the impact of the variable(s), as well as overall dynamics in species-specific relationships mediated through food web interactions.

1.2.2. Temporal dynamics

Only long-term time series, which enable to capture a wide range of variability of drivers and encompass different combinations of their relative roles, allow to learn both the type of the effect on the species or populations of interest, and the potential dynamics over time. For example, Myers (1998) investigated the stability of R-environment relationships of several fish stocks globally in a meta-analysis where he retested the correlations reported by previously published papers, using updated time series. He found that only 28 of the initially reported 74 R-environment relationships were valid (i.e. either stayed positive or negative), while most of them changed in direction. Stable relationships (i.e. those that remained the same) were primarily associated with species at their northern limit, showing almost always positive correlations with temperature. Another example of the changing relationship by extending the time series is given by Solow (2002). He found that the positive correlation between the R of Northeast Arctic haddock (*Melanogrammus aeglefinus*) and cod, and the North Atlantic Oscillation (NAO) index in 1973–1996 disappeared in the earlier part of the time series from 1945 to 1972 (Solow, 2002). Stige *et al*. (2013) found that the strength of the correlations of the R-environment relationship of several fish stocks in the Barents Sea, Gulf of Alaska and the Bering Sea showed substantial variations over multidecadal scales, with the relationship in some stocks reversing signs. For example, the correlation between walleye pollock (*Gadus chalcogrammus*, in the eastern Bering Sea) R and temperature were positive at first (1980 to the mid-1980s) and then became negative (Stige *et al*., 2013). Ottersen *et al*. (2013) reported that for many stocks (situated in e.g. Baltic Sea, North Sea, Barents Sea) R-temperature correlations have changed considerably over time. For example, there were increasingly strong positive correlations from around the 1960s onwards for populations of cod, herring and haddock in the Barents Sea region, but these weakened in the 1990s to 2000s, i.e. the strength of the relationship changed over time. Contrary, in the North Sea there is a pattern of increasingly negative correlations for several stocks (Ottersen *et al*., 2013). Klais *et al*. (2017) found that the species-variable relationship could also be dependent on the season i.e. long-term changes can differ depending on the specific month (May, June, July). In the first half of the time series (the late 1950s to the early 1980s), the effect of winter temperature on the abundance of the copepod *Acartia* spp. differed depending on a given month (i.e. fluctuated between strong positive or strong negative), but was replaced by a general weak positive effect for all three months in the early

1980s. Around the same time, the effect of the sea surface temperature on *Acartia* spp. abundance shifted from negative to positive (Klais *et al*., 2017).

1.2.3. Spatial patterns

Although the temporal stability of the relationships is studied better and documented more often, the non-stationarity may reveal itself also at the spatial scale, both horizontally along an onshore-offshore gradient and vertically (Cardinale *et al*., 2009; Otto *et al*., 2014a). Spatial distributions can be controlled by internal (density-dependency) and/or external (i.e. environmental, and species interactions) variables (Planque *et al*., 2009; Cianelli *et al*., 2012), and therefore key variables affecting a given species can differ spatially. Below we provide a few examples from the pelagic realm in the Baltic Sea.

Cardinale *et al*. (2009) investigated R-environment relationships for five spring herring (*C. h. membras)* stocks (Gulf of Riga, Western Baltic, Bothnian Sea, Central Baltic and Bothnian Bay) and evidenced that: i) a positive relationship with R and SST was evident for three stocks (Central Baltic, Gulf of Riga and Bothnian Bay), ii) the type of the link between R-SST was non-linear for the Gulf of Riga and linear for the Bothnian Sea herring, iii) Baltic Sea Index (BSI) was the key variable for change in R for all stocks except the Gulf of Riga herring, and iv) R-prey biomass relationship was significant for two stocks (linear for the Central Baltic and non-linear for the Bothnian Sea herring). This emphasizes the occurrence of differences in the main regulation mechanisms in herring at relatively small spatial scales (Cardinale *et al*., 2009).

Investigation into the effect of different variables on zooplankton observed that the biomass dynamics of the copepod *Acartia* spp. in the central Baltic Sea was mainly affected by changes in atmospheric conditions (Otto *et al.,* 2014a). The effect of the BSI on *Acartia* spp. biomass in spring appeared to be positive and linear, but the strength of the relationship varied between the different basins investigated – Bornholm Basin, Gdansk Deep and Gotland Basin. In addition, the type and strength of the water temperature effect on *Acartia* spp. differed between the basins, being linear and weak in the Bornholm Basin, and non-linear and highly significant in the Gdansk Deep (Otto *et al.,* 2014a).

1.3. Causality and correlations

Causality means that one variable mechanistically affects another, i.e. defines the cause and effect relationship between two variables, regardless of whether the correlation in the given time is found or not. Pairs of these variables that are investigated are often identified by using correlations or regressions to see how they relate to each other, often assuming causality when a correlation is found (Munch *et al*., 2020). However, the use of correlation to identify causal links between variables can be misleading, producing both false positives (i.e.

correlation does not imply causation) and false negatives (i.e. lack of correlation does not imply a lack of causation) (Ye *et al*., 2015). In nature, false positives could be harder to detect, especially when not using suitable models or variables that do not interact with each other in the real world. For example, two individual populations are presumably strongly correlated, but actually do not interact with each other but are driven by a third shared component (e.g. environmental variable; demonstrated by Chang *et al*., 2017). False negative examples include mirage correlations, where e.g. two species can be positively correlated with each other for a period of time, negatively correlated in another, and then not correlated at all in yet another period of time, i.e. exhibiting non-stationarity (Sugihara *et al*., 2012; Deyle *et al*., 2013; Chang *et al*., 2017). In short, natural systems are usually too complex to understand using only linear approaches, especially when using observational data for analysis, thus are ill-posed for dynamic systems, where correlation can occur without causation and vice versa (Chang *et al*., 2017). Causality can be identified by: i) demonstrating that one time series is useful in forecasting another, this is termed as "Granger causality" (Granger, 1969; Sugihara *et al*., 2012); or ii) reconstructing the behavior of dynamic systems from time series data, which is a goal for empirical dynamic modeling (EDM, Sugihara *et al*., 2012).

Marine ecosystems are dynamic and complex, yet management strategies are often guided by a linear, stable perspective that excludes non-linearities and the possibility for evolution and adaptation (e.g. Griffith, 2020, and references therein). These approaches do not often allow identification of the underlying causal links between the possible driver of change and marine ecosystem parameters of interest. However, even if the driver is important in some period of time or another and causally related to the variable of interest, it does not mean that it is key to the management (Myers, 1998). Although finding causality between variables and key drivers is important, it is necessary to focus more on responsiveness to the drivers under changing conditions for management and assessment purposes.

1.4. Objectives of the study

This thesis analyses various relationships between biota and its variables in the pelagic ecosystem of the Gulf of Riga (GoR, Baltic Sea). Although biological systems are now believed to be rarely linear, still too often the methods used to analyze them assume linear and stationary relationships. Motivated by this concern, all papers (**I**, **II**, **III**) in this thesis started with the consideration that all links are likely non-linear and potentially also changing over time, and applied a suite of methods to detect such links. Further, this thesis aims to detect non-linear and non-stationary relationships in the GoR pelagic ecosystem using long-term monitoring data time series between 1958 and 2018 via application of an array of statistical approaches.

Each paper focused on different key species of the GoR pelagic ecosystem: i) long-term abundance dynamics of the arctic copepod *Limnocalanus macrurus*

(**I**); ii) changes in the abundance dynamics and alteration in the prey-environment relationship of the primary prey taxa of the non-indigenous predator cladoceran *Cercopagis pengoi* after the invasion (**II**); and iii) recruitment (R) dynamics of the local spring-spawning herring (*C. h. membras*) population (**III**).

In addition, a review of recently (2000–2020) published papers from the Baltic Sea was performed with the following aims: i) to evaluate how frequently the statistical methods that can detect non-linear or non-stationary relationships are used; ii) what the main methods applied were; iii) how many of these analyses detected non-linear and/or non-stationary relationships, and iv) which relationships were investigated (examples).

2. MATERIALS AND METHODS

2.1. Study area and ecosystem dynamics over time

The GoR (Figure 1) is a relatively shallow, semi-enclosed brackish water ecosystem in the Baltic Sea, and it is connected to the Baltic Proper via the Irbe Strait and the Väinameri Archipelago Sea by the Suur Strait. The surface area of the GoR is 16 333 km^2, and it receives fresh water from a huge drainage area (134 000 km^2), entering from the southern part of the basin. In most parts of the GoR the salinity is 5.0–6.5 PSU, but 0.5 to 2 PSU on surface water layers in Pärnu Bay, without a permanent halocline. Due to its shallowness, changes in air temperature directly influence the dynamics of the temperature regime of the GoR (Kotta *et al.*, 2009). A seasonal thermocline forms when the surface water temperature rises up to ~17–20 °C, reaches the maximum depth in August and disintegrates in September-October due to intensive wind-driven vertical mixing. The surface water cools down, and the deep-water temperature rises to 5–10 °C during autumn storms. Due to strong vertical mixing, dissolved oxygen concentrations are in most areas higher than 5 ml/l, while values below 2 ml/l have been found in the deepest part of the GoR (> 45m; Kotta *et al.*, 2008 and references therein).

The GoR ecosystem has faced several well-documented changes since the 1950s, influenced by climate change and increased anthropogenic impact (Kotta *et al.*, 2009; Arula *et al.*, 2014). While investigating the long-term dynamics of the GoR pelagic ecosystem, salinity increase until the mid-1970s, followed by a decline until the mid-1990s, and an increase since then have been reported by e.g. Raudsepp (2001) and Arula *et al.* (2014). Several previous studies have documented a general warming trend since the 1990s (Jurgensone *et al.*, 2011; Lehmann, 2011), and an increase in the frequency of milder winters since the late 1980s (ICES, 2020). In general, two climate-induced distinct ecosystem regimes have been observed in the GoR (1957–1983 and 1992–2010), separated by a smooth transition period (Arula *et al.*, 2014).

The main anthropogenic pressures included a substantial increase in the riverine nutrient loads from the 1960s to 1990s, which influenced the biogeochemical processes and led to severe and chronic eutrophication of the system. As a result, primary production of phytoplankton increased substantially during the 1970s and 1980s, reducing water transparency (Kotta *et al.*, 2008, and references therein). Since the 1960s, there have also been notable changes in the composition and abundance of mesozooplankton, also related to the changes in phytoplankton biomass as well as climate and modified food web interactions (Kotta *et al.*, 2004). For example, in the 1960s, mesozooplankton communities were dominated by copepods, the density of copepods started declining from the mid-1980s, but peaked again in the 1990s, dominated by *Acartia* spp. and *Eurytemora affinis* (Kornilovs *et al.*, 2004; Kotta *et al.*, 2004). The abundance of the cladocerans was low until the 1980s, followed by a short period of an increasing trend, before dropping again sharply at the beginning of the 1990s (Kotta *et al.*, 2004). Major changes in dynamics have been reported in the ecologically and commercially key pelagic fish in the basin – spring-spawning herring. A general decreasing trend and lower values in the mean weight-at-age of herring have been observed since the 1990s as compared to the 1980s. The GoR herring spawning stock biomass (SSB) was relatively low and stable from the 1970s to the late 1980s (40–50 thousand tons), followed by an abrupt increase until the mid-1990s (nearly 125 thousand tons) and stabilisation at notably higher levels recently (ICES, 2020).

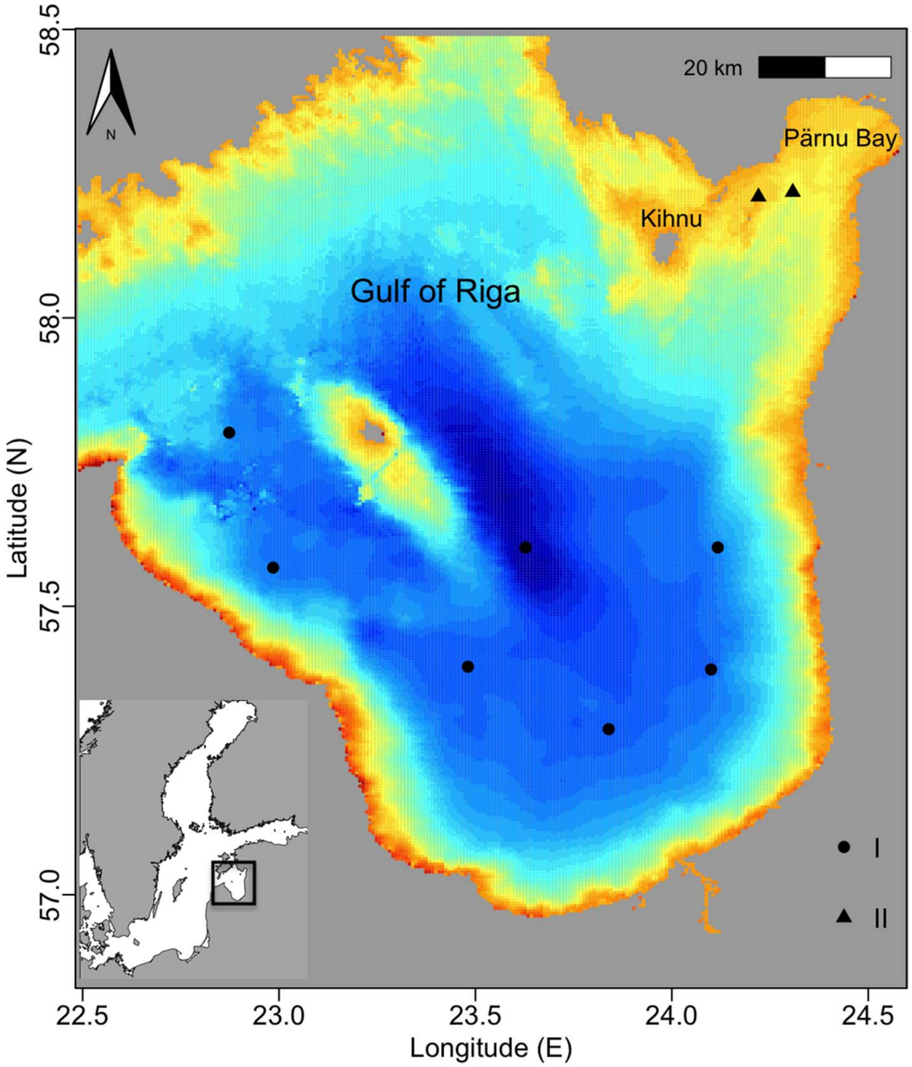

Figure 1. Location of sampling stations of papers **I** and **II** in the GoR and Pärnu Bay. Dark red indicates the shallower parts of the gulf and dark blue deeper parts.

The changes in the environmental conditions also have direct implications for the food web dynamics. For example, five periods with distinct food web characteristics were recently documented in the GoR during 1981–2014, separated by pronounced changes in the food web network properties. Likely explanations for the changes in food web functions were alterations in community structure as a response to changes in abiotic drivers, such as increases in temperature (Kortsch *et al.*, 2021).

There are several non-indigenous species (NIS) that are widespread, reach high abundances, and therefore pose significant ecosystem impacts in the GoR. The reported impacts include, amongst others: i) changes in the physio-chemical habitats of sediments and water; ii) declines in the abundance and biomass of native species; and iii) changes in food webs (Ojaveer and Kotta 2015; Ojaveer *et al.*, 2021). NIS impacting the GoR foodweb the most are the predatory cladoceran *C. pengoi* and the zebra mussel *Dreissena polymorpha* (Ojaveer *et al.*, 2021), while the impact of the polychaete *Marenzelleria* spp. is mostly confined to the abiotic environment (Ojaveer and Kotta, 2015). In this thesis, we have investigated the impact of *C. pengoi* (first detected in the GoR in 1992) on its prey abundance, seasonal dynamics and prey-environment relationships while considering the impact of likely confounding factors (**II**).

2.2. Data

2.2.1. Data origin

In this thesis, monitoring and assessment data from the GoR (Baltic Sea) was used from 1958 to 2018. Only the GoR time series data from stations with the highest sampling frequency and continuous time series were included.

Abundance data on zooplankton taxa were extracted from the database of the Institute of Food Safety, Animal Health and Environment, BIOR (**I**, **III**) and from the Baltic Sea zooplankton database (Klais *et al.*, 2016), collected by the Estonian Marine Institute of the University of Tartu and its predecessors (**II, III**); for details see papers **I**–**III**. For papers **I** and **II** samples were collected during monitoring cruises from seven and two stations in the GoR and Pärnu Bay, respectively (Figure 1). For paper **III** samples were collected from the open GoR covering the entire basin.

Data on recruitment (R) abundance (individuals at age 1) and spawning stock biomass (SSB, tons) of the GoR spring-spawning herring for 1958–2015 **(I**, **III)** was obtained from Ojeveer *et al.* (2004) and ICES (2020). The GoR autumn herring SSB (**I**) was obtained from Ojaveer (2003).

Environmental variables data were extracted from the Estonian Environmental Agency (**I**, **II**, **III**; 1958–2018). For papers **II** and **III** data was obtained from Kihnu weather station (58.09861 N, 23.97028 E, Figure 1). For paper **I** the data was obtained from a database of the Institute of Food Safety, Animal Health and Environment, BIOR (1963–2016).

2.2.2. Key variables and data preparation

Paper I

In paper **I**, data on the abundance of calanoid copepod *L. macrurus* abundance (individuals per m^2), the GoR herring SSB (thousand tons) of the previous year (autumn and spring herring together) and winter severity (WS, measured as a sum of negative daily mean air temperature from November to March) was used and covered the years of 1958–2016. Data on the temperature (°C), salinity (PSU) and oxygen (ml L^{-1}) content of the bottom water covered the years of 1963–2016, an average value was measured from the depth range of 30–50 m in August. For additional details see paper **I**.

Paper II

Abundance data on the predatory cladoceran *C. pengoi* (ind. m^{-2}) and its prey taxa – larvae of cirriped *Amphibalanus improvisus*, cladocerans *Bosmina* spp. and *Pleopis* spp., copepod nauplii (all species) and copepod *E. affinis* (for all prey taxa ind.m^{-2} or ln(ind.m^{-2}) covered the years of 1968–2018. Data was divided into pre- (<1992) and post-invasion periods of *C. pengoi*. To ensure the strongest possible contrast between the two periods, the post-invasion period was limited to the years when *C. pengoi* abundance had already reached the plateau and its full impact on the prey community (i.e. 1999–2018). Two variables were used to test the effect of hydroclimatic forcing: temperature proxy (°C) and storminess index (strong wind hours). Because the preliminary inspection of mean seasonal patterns of environmental proxies pre- and post-invasion indicated a notably higher air temperature in the post-invasion period, additional filtering of years was applied to ensure that both periods be represented by similar environmental conditions. Yearly mean daily air temperatures and mean daily strong wind hours during July-August were used to identify the overlapping range for both variables across both periods. This was done to minimize the likelihood that observed changes in prey taxa could be associated with factors other than the invasion of *C. pengoi*. For additional details, see paper **II**.

Paper III

Paper **III** investigated the dynamics of the GoR spring-spawning herring R (10^6 individuals) in relation to the main affecting variables. Data from 1958–2015 was used. Variables that were included in these analysis were: i) the annual data on spring herring SSB (thousand tons); ii) WS (sum of negative daily mean air temperatures from November to March) in two versions, before hatching and lagged series (WS0) of the first winter these individuals survived (WS1); iii) mean daily air temperature in May (°C); iv) copepod *E. affinis* abundance (ind. m^{-2}) both for the open GoR and Pärnu Bay, aggregating three different stages (copepodites I–III and IV–V, and adult copepods, ln(ind. m^{-2})). For additional details, see paper **III**.

2.3. Key species

2.3.1. The native arctic copepod *Limnocalanus macrurus*

L. macrurus is an ecologically relevant but relatively poorly studied species in many marine and freshwater environments of the northern hemisphere, including the Baltic Sea. This large lipid-rich copepod has a high content of polyunsaturated fatty acids, serving thereby as a high-quality prey for fish (Hiltunen *et al.*, 2014). *L. macrurus* is considered a glacial relict in the Baltic Sea (Segerstrale, 1966), being the largest widely distributed copepod species (up to 3 mm in length) in the northern part: Gulf of Bothnia, Gulf of Finland, and GoR. As a cold stenotherm species (Van Hove *et al.*, 2001; Apollonio and Saros, 2013; Jackson *et al.*, 2013; Drits *et al.*, 2016) the distribution of *L. macrurus* is usually restricted to deeper colder water masses (Carter and Goudie, 1986), with the ability to penetrate the seasonal thermocline to the upper water layers at night when stratification is weak (Wells, 1960). The species is characterized by continuous and plastic feeding (Warren, 1985; Barbiero *et al.*, 2009; Dahlgren *et al.*, 2012; Jackson *et al.*, 2013), thereby efficiently exploiting the available food resource and transferring the energy from lower trophic levels to fish. Based on long-term records, this species was very abundant in the GoR before the 1980s but nearly disappeared in the late 1980s, allegedly due to milder winters which resulted in warmer water during the winter/spring period (Kornilovs *et al.*, 2004). In addition, abundance of *L. macrurus* has been suggested to change in relation to variations in salinity in the Bothnian Sea (Rajasilta *et al.*, 2014), where it may dominate in the copepod community most of the year, constituting often >50% of the biomass (Dahlgren *et al.*, 2010). It is also a highly preferred prey item for the most abundant pelagic fish species – herring – in both the Gulf of Bothnia (Flinkman *et al.*, 1992) and the GoR (Livdane *et al.*, 2016), while other abundant planktivorous fish consume *L. macrurus* only marginally (Ojaveer *et al.*, 1997).

2.3.2. The non-indigenous predatory cladoceran *Cercopagis pengoi*

The predatory cladoceran *C. pengoi* was first found outside of its native range (the Ponto-Caspian region) in the Baltic Sea and the North American Laurentian Great Lakes in the 1990s (Ojaveer and Lumberg, 1995; MacIsaac *et al.*, 1999). Since then, it has become a permanent integrative constituent of pelagic communities in these invaded marine and freshwater ecosystems (e.g. Lehtiniemi and Gorokhova, 2008; Makarewicz and Lewis, 2015). The food web interactions of the species have been fairly well studied, as well as potential consumption rates in the field and via controlled laboratory experiments (e.g. Laxson *et al.*, 2003; Simm *et al.*, 2006; Gorokhova and Lehtiniemi, 2007; Pichlová-Ptáčníková and Vanderploeg, 2009; Lankov *et al.*, 2010). However, quantifying the predatory effect of *C. pengoi* on natural plankton communities is challenging (e.g. Stewart *et al.*, 2010), and the long-term impact of the changes in relationships between its prey taxa and environmental variables remains to be investigated. Previous studies done in the US Laurentian Great Lakes and the Baltic Sea reported that *C. pengoi* is an opportunistic generalist predator primarily feeding on low motile and thereby easily captured small-sized prey but is also able to consume species with different sizes and escape abilities (Pichlová-Ptáčníková and Vanderploeg, 2009; Holliland *et al.*, 2012). *C. pengoi* is able to tolerate a wide range of temperatures and salinities. Moreover, it is facilitated by higher temperatures, *C. pengoi* usually appears in the zooplankton community in the GoR in the late spring when the sea surface temperature exceeds 12–13 °C (Simm and Ojaveer, 2006), but is inhibited by water column instability (Avinski, 1997; Ojaveer *et al.*, 2000). Inhibition by water column disturbance occurs along with higher densities: individuals can get tangled into masses by their long caudal appendages (often seen in fishermen's nets; Krylov *et al.*, 1999; MacIsaac *et al.*, 1999).

2.3.3. Gulf of Riga herring (*Clupea harengus membras*)

The Baltic herring is an important and very abundant commercial species in the GoR. Herring dominates in commercial catches, about 90% of total values, exploited by trawls and trap nets. There are two herring populations in the basin: spring- and autumn-spawning herring. Their growth dynamics are roughly similar and depend mainly on food availability, temperature, and salinity; however, these two populations differ in morphology and behavior (Ojaveer, 1988). The GoR spring herring does not undergo major migrations into the open Baltic Sea, with only a minor part of the older herring leaving the gulf after the spawning season but returning afterwards, and constitutes thus a local resident population, which is also managed as a distinct stock (ICES, 2020). The extent of migrating individuals depends on the stock size and the feeding conditions in the GoR (Ojaveer, 1988). In this thesis, the primary focus was on the GoR spring-spawning herring. Spring-spawning herring in the GoR spawns from the middle of May to mid-July at temperatures from 9 to 16 °C mainly in the eastern part of the gulf; the depth of the spawning grounds varies from 2–3 to 10–15 m. The larvae occur in late May to the end of July-beginning of August when the water temperature is 7–12 °C, and the last larvae hatch at 18–20 °C, and appear in depths of up to 20–25 m. They perform diurnal migration in the daytime, feeding on prey in the surface layer (Ojaveer *et al.*, 2011). Compared to the other spring-spawning herring stocks of the Baltic Sea, the GoR herring is characterized by the lowest mean weight-at-age values: the mean individual weight groups 1–8 of the GoR herring and other herring stocks of the Baltic Sea in 2019 were 19.9 and 22.4–31.1 g, respectively (ICES, 2020). The R for the GoR herring is reported for the year when the fish are one year old.

2.4. Statistical methods

Model selection should always be guided by the questions asked and the data used. In this thesis, most links were modelled using generalized additive models since often the aim was to determine non-linear links. In some cases, mostly using shorter time periods, simple correlation or linear models were used when the temporal behavior of model parameters was of interest. Also, the sliding window analysis was applied, an example seen in Beaugrand (2012) when studying the stationarity of the relationships, and extended further into a 'growing window analysis' (2.3.3.).

All the analyses and visualizations were done in RStudio (versions 1.1.442, 1.1.414, 1.3.1056, using *R* 3.4.0, 4.0.2).

A generalized additive model (GAM) is a generalized linear model with a linear predictor involving a sum of smooth functions of covariates (Wood, 2017). GAMs are useful in the detection of non-linear patterns that classic linear models can miss. Links between the predictive and dependent variables are captured through smooth functions that will be only as curvy as is justified by the data through internal cross-validation. The type of fit (linear vs non-linear) was evaluated from the "estimated degrees of freedom" (edf) returned by the *gam* function, where edf = 1 indicated a linear, and edf > 1 a non-linear link. The direction of the link, of course, needs to be evaluated visually, in contrast to parametric models (**I**, **II**, **III**). GAM also allows the use of interactions which gives the user information about whether two explanatory variables can explain the response variable better in a state-dependent manner, where the effect of one variable is changing as a function of the other explanatory variable (Wood, 2017). The GAM toolset used here also includes the test of concurvity, which can be viewed as a generalization of collinearity. Concurvity of a model gives estimates (worst, estimated and observed) between 0 and 1, with 0 indicating no problem, and 1 indicating the total lack of identifiability. The R library *mgcv* (1.8–20; 1.8–31) was used for fitting GAM models.

The sliding window analysis (SWA) refers here to the procedure of refitting the same model or performing a similar calculation to the small parts of a time series, where the parts are determined with a sliding time window. It is quite similar to the concept of constructing the moving average estimates of a time series. The results of SWA are usually presented as a time series of model parameters or the average value of the studied variable from observations within the time slot. SWA is inspired by Beaugrand (2012), similar methods, for example, have been used by Ottersen *et al.* (2013) and Klais *et al.* (2017). In this thesis, a chronological sliding window was used for papers **I** and **III**. For both studies, the window length was fixed to 15 years with an increment of one year. Linear models were fitted to the 15-year subsets of data, and slopes and p-values of the models fitted to these subsets were recorded. The subsets were selected with the sliding window of 15 years, moving stepwise from the start to the end of the time series (e.g. 1959–1973;1960–1974; ...; 2002–2016). SWA can be used to detect and visualize the non-stationarity in the relationships between the selected variables, and test changes in strength and direction of the relationships over time, based on the R^2 or p-values of the models in every step.

The growing window analysis (GWA) is an approach that we have not seen being used in other analyses, i.e. we did not find any previous papers that have used a similar approach. GWA was used to test whether the shape link, direction or the strength of it changes when gradually extending the time period used in the analysis (**III**). In GWA, univariate GAMs were fitted to the gradually growing subsets of data, starting with a fixed number of datapoints (n), e.g. years, and then adding n+1 at each step. This method mimics the real-world situation of adding new data to the time series and retesting the previously known relationships in a gradual and continuous manner.

Out of sample prediction skill can be used as an additional measure of a model's performance (**III**). In this thesis, the sample size was relatively small (yearly mean values of up to 60 years) (**III**). For small sample sizes, leave-one-out cross-validation (2011) can be used, i.e. if we have n = 50 data points (e.g. year), the model is fitted 50 times, excluding each year once, and predicting with the model the selected variable (x) to the year excluded from the model training data. The skill is measured as the adjusted R^2 of the linear model: observed x ~ predicted x. Out of sample prediction skill is a generic validation procedure that provides a more realistic evaluation of models' performance than the adjusted R^2 of the model and is often used as performance criteria for time series forecasts.

A forward selection procedure of the models was guided by either the Akaike information criterion (AIC or AICc) or generalized cross validation (GCV) (**I**, **III**). AIC is used to compare different possible models and determine which one best fits the tested data (Akaike, 1974). The best fitting model based on AIC is the one that explains the greatest amount of variations using the fewest possible independent variables. For an example of AICc for a small sample size, see paper **I**. The models are ranked from best to worst based on the empirical data at hand (Burnham and Anderson, 2004) – the lower the value, the better the model. Cross-validation is a technique that predicts a subset of known data from the remaining data, similar to the out of sample prediction skill. GCV is a useful criterion for model selection and parameter estimation, particularly with small to moderate datasets. It is valuable also in comparing alternative models (Marcotte, 1995).

The Mann-Whitney U test is a non-parametric alternative to a commonly used t-test, which can be used to compare outcomes between two independent groups. This non-parametric test is necessary when the data distribution is asymmetrical, i.e. not a normal distribution. This test has a great advantage with sample sizes (**II**; Nachar, 2008).

2.5. Review

Additionally, a review was conducted from published papers in 2000–2020 that applied non-linear or non-stationary methods. Only papers that i) covered at least a 10-year time period; ii) investigated the type of links or changes in type, strength or direction of the relationships (e.g. species-environment); and iii) used monitoring/observation data on the Baltic Sea ecosystem (i.e. the paper had to be based on an empirical field study; laboratory and field experiments were left out), were included.

The published sources were identified from the Scopus and Web of Science databases. The search terms "Baltic Sea", "linear", "non-linear", "stationary", "non-stationary", "relationship", "marine", "change", "long-term", were used; each term was separated using the Boolean/phrase operator "and" and "or". In the Scopus database the search criterion of "all fields" or "titles", abstract, keywords" and in the Web of Science "all fields" or "topic" (for all keywords). The search was not limited to the pelagic ecosystem. References from suitable studies were also looked over to detect if there are more publications that were "lost in the database noise".

First, the titles were evaluated, and non-relevant studies were removed. Next, the abstracts and material and methods were evaluated. All the suitable papers were gathered in one table together with the following information: i) article title, authors and publishing year; ii) length of the time series; iii) names of applied method(s) and whether these were suitable for detecting non-linear or non-stationary relationships; iv) variables used; v) evidence(s) of non-linear/non-stationary relationships.

3. RESULTS AND DISCUSSION

This thesis focused on the detection and analysis of non-linear and non-stationary relationships in the GoR pelagic ecosystem through the application of different statistical methods to long-term multidecadal data. In the following sections, I will discuss and describe the main finding of my research. First, I will explore the type and stability of the relationships found in the analysis carried out for this thesis by interpreting the results of each paper (**I**, **II**, **III**). Secondly, I will interpret the results of the review. Thirdly, I will examine the importance and relevance of these results on the assessment and management of the GoR ecosystem. Further, I will elaborate on data availability, methodological innovations and limitations in results interpretation. Lastly, I will discuss the prospects for further analysis and possibilities.

3.1. Type of the links

In this thesis, both the type and direction of the links between the abundance/biomass of selected key species in the pelagic realm of the GoR and their potential variables were investigated. Paper **I** focused on the long-term variability of *L. macrurus*. The abundance of this species in springtime was linearly (negatively) related to herring SSB in the previous year, and unimodally to two environmental variables, both proxies of thermal conditions – WS and bottom water temperature in the preceding summer (**I**). The negative linear link to the predator implies top-down control of *L. macrurus* by herring, considering not only that *L. macrurus* is a preferred prey for herring (Livdane *et al.*, 2016), but also the spatial overlap with adult herring (both inhabit deeper water) and the key reproductive trait – the species produces only one generation per year. The shape and direction of the link between *L. macrurus* abundance in spring with the WS and bottom water temperatures found in our study verified the previous knowledge (e.g. Kornilovs *et al.,* 2004): higher abundances were to be found after harsh and medium winters, and lower abundances after milder winters. The link with water bottom temperature was also unimodal, with one single maximum around 4 °C. Similar non-linear and unimodal links are quite common in nature, describing links between fishes or zooplankton abundance/biomass and environmental variables (e.g. temperature, salinity, oxygen) where there is one environmental optimum for a species (e.g. see Cardinale *et al.*, 2009; Pörtner and Peck, 2010; Musialik-Koszarowska *et al.*, 2019). For example, Arula *et al.* (2015) found a non-linear dome-shape link between the number of post-flexion spring herring larvae and sea surface temperature in the GoR. Also, Otto *et al.* (2014b) observed a dome-shaped link between the abundance of the large-bodied copepod *Pseudocalanus acuspes* (early stages) and summer water temperature in the open Baltic Sea.

Paper **II** investigated how the invasion of *C. pengoi* may have influenced the relationships between the environment and the typical native prey of *C. pengoi*. Compared with the terrestrial environment, evidence of the impact of NIS in the marine realm is generally very limited (Pyšek and Richardson, 2010; Ruiz *et al.*, 2011). The most common reason is that long-term pre-and post-invasion data sets for investigating how NIS may have impacted native marine organisms are relatively rare. Several previous studies have found a preliminary negative effect of *C. pengoi* on its prey taxa (Leppäkoski *et al.*, 2002; Ojaveer *et al.*, 2004), but broader impacts of the species are still insufficiently understood and require future quantifications (Leppäkoski *et al.*, 2002; Katsanevakis *et al.*, 2014).

Out of the 20 cases (for details see section 2.2.2.), linear links were found in 11 cases (6 of them were significant) and non-linear links in 9 (4 of them were significant) (**II**, Table 1). Most prey-temperature links were linear, which indicates that rising temperatures affect prey within the observed temperature ranges either positively (*Bosmina* spp. post-invasion) or negatively (*E. affinis* in both periods). Larvae of *A. improvisus* exhibited the typical dome-shaped link in both periods, with one maximum in the most favorable temperature range which then turned negative as the temperature increased (Figure 6). The fact that nearly half of the links between prey abundance and environmental variables were non-linear further signifies the importance of using models and tools that have the capability of detecting the potential deviation from linearity.

Table 1. The effect of temperature proxy and storminess index on the abundance of five zooplankton taxa in Pärnu Bay (GoR) in the summer period (June-August) during the years of similar environmental conditions pre- and post-invasion of *C. pengoi*. Note that the value given in the parameter column is the estimated degree of freedom in the case of non-linear fit, and the slope parameter in the case of linear fit (**II**).

Variable	**Taxon**	**Pre-invasion** (n=303)			**Post-invasion** (n=109)		
		type of fit	**para-meter**	**p-value**	**type of fit**	**para-meter**	**p-value**
Temperature proxy	*A. improvisus* larvae	non-linear	2.95	**<0.001**	non-linear	2.83	**<0.001**
	Bosmina spp.	non-linear	2.80	**<0.001**	linear	0.29	**<0.001**
	Copepod nauplii	linear	–0.04	0.06	linear	–0.08	**0.02**
	E. affinis	linear	–0.09	**0.021**	linear	–0.30	**<0.001**
	Pleopis spp.	non-linear	2.92	**<0.001**	linear	–0.35	**<0.001**
Storminess index	*A. improvisus* larvae	linear	0.01	0.2	non-linear	1.84	0.1
	Bosmina spp.	linear	0.02	**0.002**	linear	0.01	0.1
	Copepod nauplii	non-linear	2.18	0.2	non-linear	1.29	0.8
	E. affinis	linear	0.003	0.7	linear	–0.01	0.4
	Pleopis spp.	non-linear	1.72	0.09	non-linear	1.78	0.07

3.2. Stability of relationships

Changes in the types, direction or strength of the relationships (i.e. detecting non-stationarity) can be tested either by i) looking at the entire time period; ii) gradually extending the time period; or iii) comparing two or more sub-periods. Revisiting the relationships with increased length of the time series and assessing the relevance of the variables over time and space by applying various data analysis techniques has been suggested to gain deeper insight into the patterns of change and identify likely mechanisms responsible for a change (Zimmermann *et al*., 2019).

Paper **I** evidenced non-stationary relationships between the spring abundance of *L. macrurus* and the key variables investigated (Figure 2). A weak positive relationship between *L. macrurus* abundance and herring SSB was found at the beginning of the time series, i.e. when herring SSB was low and *L. macrurus* abundance high (until the mid-1970s). This was followed by a negative and often stronger effect of SSB on *L. macrurus* abundance, during the period a rapid increase was evident in herring SSB (Figure 2a). This pattern indicated an increased predation pressure along with an increasing gradient of SSB. Kornilovs *et al*. (1992) proposed that the decline of the abundance of *L. macrurus* during that period could have been caused by both an increase in the stock size of the GoR herring and changed hydrological conditions. The effect of WS on *L. macrurus* abundance appeared to be weak in any of the sliding window steps, although the slopes became more negative after the mild winters (between the mid-1980s to the early 2000, Figure 2b).

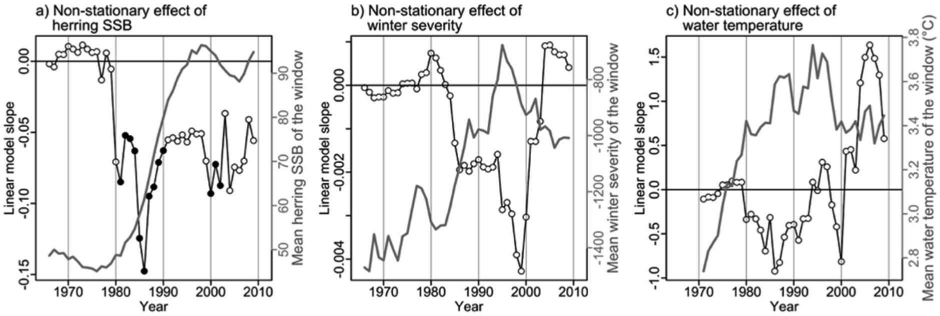

Figure 2. Results of the chronological sliding window analysis (SWA): time trends in linear slopes of *L. macrurus* abundance (ln(ind. m^{-2})) with herring SSB (thousand tons) in previous year (a), winter severity (mean air temperature during November–March) (b), and the bottom water temperature (°C) in the summer of the previous year (c). Filled points denote values where the slope was significant at $p<0.05$. The grey line indicates the mean values of the respective explanatory variable in each 15-year subset (1958–1972, 1959–1973, . . ., 2002–2016). On the x-axis is the middle year of each 15-year subset (**I**).

During the period of cold winters, until the mid-1980s, and since the mid-2000s, the effect of WS on *L. macrurus* abundance was weak and often positive (Figure 2b). The effect of bottom water temperature in the preceding summer on *L. macrurus* abundance became more negative during warm periods (Figure 2c). Kornilovs *et al.* (2004) also suggested that the decrease in the biomass of *L. macrurus* in GoR since the 1980s was probably a result of increasing water temperatures. In addition, previous studies have also documented an increase in the abundance of cladocerans and smaller copepods since the 1980s after a decrease in *L. macrurus* (Sidrevics *et al.*, 1993).

The main variables that were related to the variability of herring R were the severity of the first winter these individuals survived (WS1) and the abundance of the copepod *E. affinis* (stage IV–V) (**III**, $R^2 = 0.52$). In contrast to our findings, several previous studies have reported SSB as an important driver for herring R (Cardinale *et al.*, 2009; Margonski *et al.*, 2010). However, the inclusion of SSB improved the model's explanatory power, which included the prey abundance and WS1 ($R^2 = 0.62$), indicating a combined effect of these three variables in explaining herring R dynamics. The R-prey abundance relationship was positive and linear, i.e. herring R increased with prey abundance (**III**). When adding the interaction with SSB, the highest herring R values coincided with the high levels of SSB combined with high prey abundance (Figure 3a), indicating a density-dependent function where only very rich food resources together with a high parent stock level secured the formation of abundant herring R.

The link between herring R and WS1 was unimodal, with a peak at average winter temperatures and lower herring R for both very mild and harsh winters (**III**). Winter severity can influence herring survival, spawning timing, and abundance of the prey, and therefore food resources. For example, the preceding winter air temperature influences the timing of herring spawning and the first appearance of larvae, e.g. the spawning season begins up to six weeks earlier after milder winters compared to colder winters (Arula *et al.*, 2019). Moreover, climate (winter air temperature and spring SST) significantly affects the seasonal dynamics of the main prey of herring – *E. affinis* – via modulation of the timing of annual reproductive processes and abundance levels in the GoR (Kornilovs *et al.*, 2004; Klais *et al.*, 2017). Thus, climate is indirectly affecting interannual abundance dynamics of herring R through food web dynamics. Since milder winters increase biological productivity in surface layers and thus result in improved feed conditions for larvae and young herring, and support their higher survival (Ojaveer *et al.*, 2011), more positive effects of milder winters on herring R would have been expected. The likely reason for obtaining a deviating outcome is a match/mismatch between the temporal dynamics of larvae and their preferred prey, which is achieved at intermediate winter temperatures. In addition, elevated levels of herring R were detected in combination with low SSB and average winter temperatures (Figure 3b), pointing to the possible involvement of density-dependent processes in the formation of herring R (see also below).

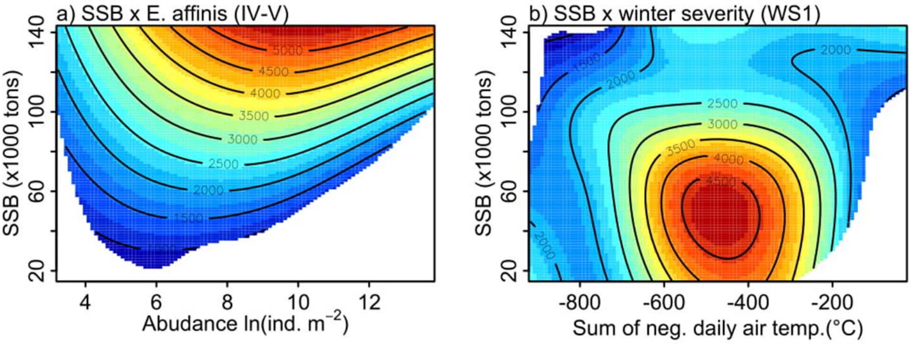

Figure 3. Generalized additive model (GAM) output with spawning stock biomass (SSB, thousand tons) interaction to describe the (a) partial effect of the interaction between SSB and abundance of *E. affinis* in open GoR (copepodites stages IV–V, ln(ind. m^{-2},)), and (b) partial effect of the interaction between SSB and winter severity (WS1, sum of negative daily temperatures, °C) on the GoR herring recruitment (R, 10^6 individuals) during 1958–2015. The color scale and contour lines indicate the R values predicted by the final model ($R^2 = 0.62$, **III**).

Time series of sufficient length are prerequisites for unravelling the relative roles of different factors affecting whether the same factors remain dominant over longer periods (Hjort, 1914). Ideally, the observation period should cover at least one prominent environmental cycle to allow the detection of non-linear or non-stationary relationships. Figure 4 displays how different lengths of time series influence and determine the type of fit. The type of herring R-SSB link appeared to be unimodal during about the first 25 years, peaking at around 30–40 thousand tons of SSB. When the time series was further extended, the unimodal link was abruptly replaced with a more linear and positive link (Figure 4a), coinciding with about a two-fold increase in the adjusted R^2 (from around 0.15 to 0.30, Figure 4b). Addition of the last 5 years to the time series (i.e. 2010–2015) revealed a new maximum of herring R at a high SSB level (ca. 90 thousand tons). While herring R-prey abundance link becomes more linear and more positive over time and is overall strong (R^2~0.3–0.6; Figure 4c, d), winter severity has only a marginal effect on herring R, at least when it is considered as a single variable in the model (Figure 4e, f). This indicates that the prey *E. affinis* abundance explains most of the model's power; the effect of WS1 becomes important only when combined with the main prey. Previous studies conducted in different marine ecosystems and involving various taxa have reported different results (in the type of fit or in strength and direction) of the links depending on the length of the time series used in the analysis. Overall, these relationships were either changed when extending the time series (e.g. Myers, 1998; Solow, 2002; Stige *et al*., 2013) or remained unchanged (e.g. sprat R-temperature relationship; MacKenzie and Köster, 2004).

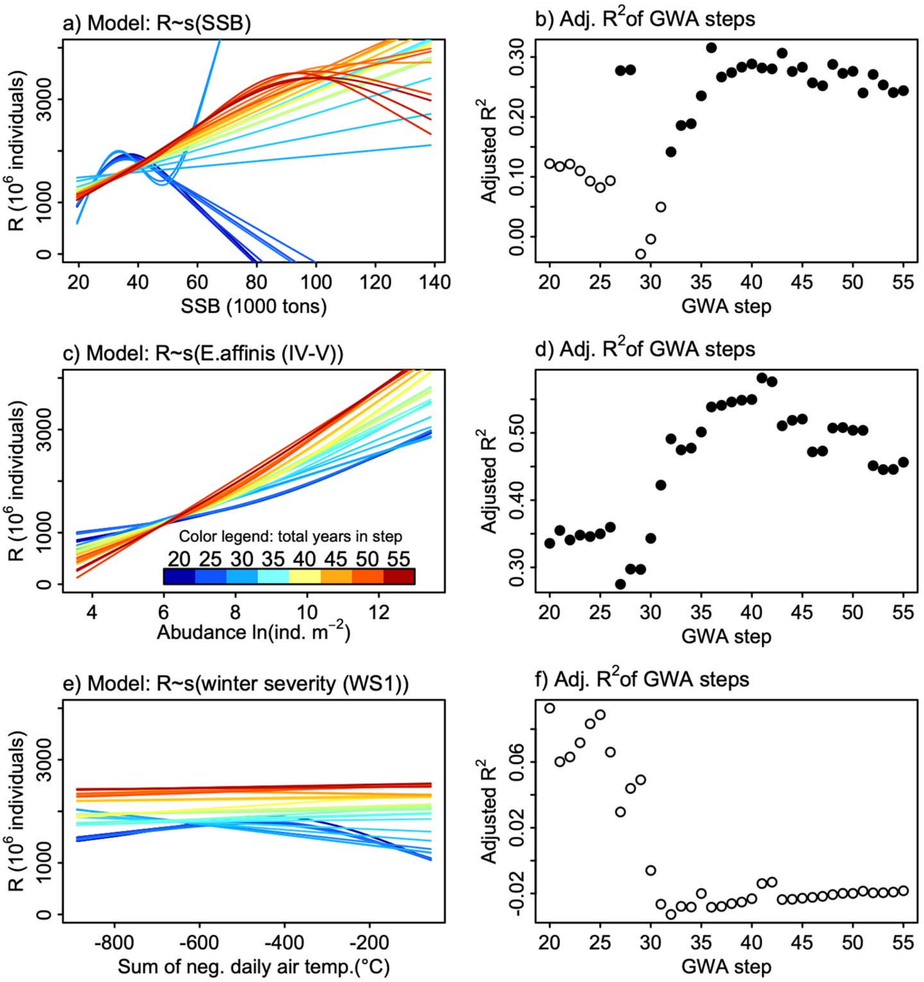

Figure 4. Growing window analysis (GWA) to test the changes in the type (linear or non-linear), direction (positive or negative) and strength (R^2) of the link between the GoR spring-spawning herring recruitment abundance (R) and (a–b) spawning stock biomass (SSB, thousand tons), (c–d) abundance of *E. affinis* in open GoR (copepodites stages IV–V, ln(ind. m^{-2})), and (e–f) winter severity (WS1, sum of negative daily temperatures, °C). Left panel: the type and direction of the links between R and the respective explanatory variable over an increasing observation period. The colors of the lines indicate the number of years included in each step, corresponding to the legend in panel c. Right panel: adjusted R^2 values for each time-step; filled points denote values where the step model was significant at $p<0.05$ (**III**).

With the exception of the 1970s, the herring R-SSB relationship was positive from the beginning of the time series until the mid-1990s, with a few most positive and significant relationships recorded for the middle/second-half of the 1980s. The relationship gradually declined and weakened from these peak values and remained negative until recently (Figure 5a, b). This contrasts with several previous studies, which have established significant positive herring R-SSB relationships, though at different time scales and/or applying other methods than in our research (Cardinale *et al.*, 2009; Margonski *et al.*, 2010; Ojaveer *et al.*, 2011). The relationship between herring R and prey abundance was stationary, i.e. remained positive during the whole study period and was in most cases significant, with a gradual increase in the slope since the 1980s. The herring R-prey abundance relationship was strongest from the early 1980s to the mid-1990s (adj. R^2 was 0.6–0.8; Figure 5c, d). This is probably due to increasing prey abundance since the 1990s when *E. affinis* exhibited several higher peaks compared to the period before that (see in **III** Figure 1). The relationship between herring R and WS1 has been mostly negative and insignificant throughout the entire period, except the 1980s, followed by a gradual decrease in the early 2010s. This points to a generally unimportant role of WS1, as a single variable, in the formation of herring R (Figure 5e, f).

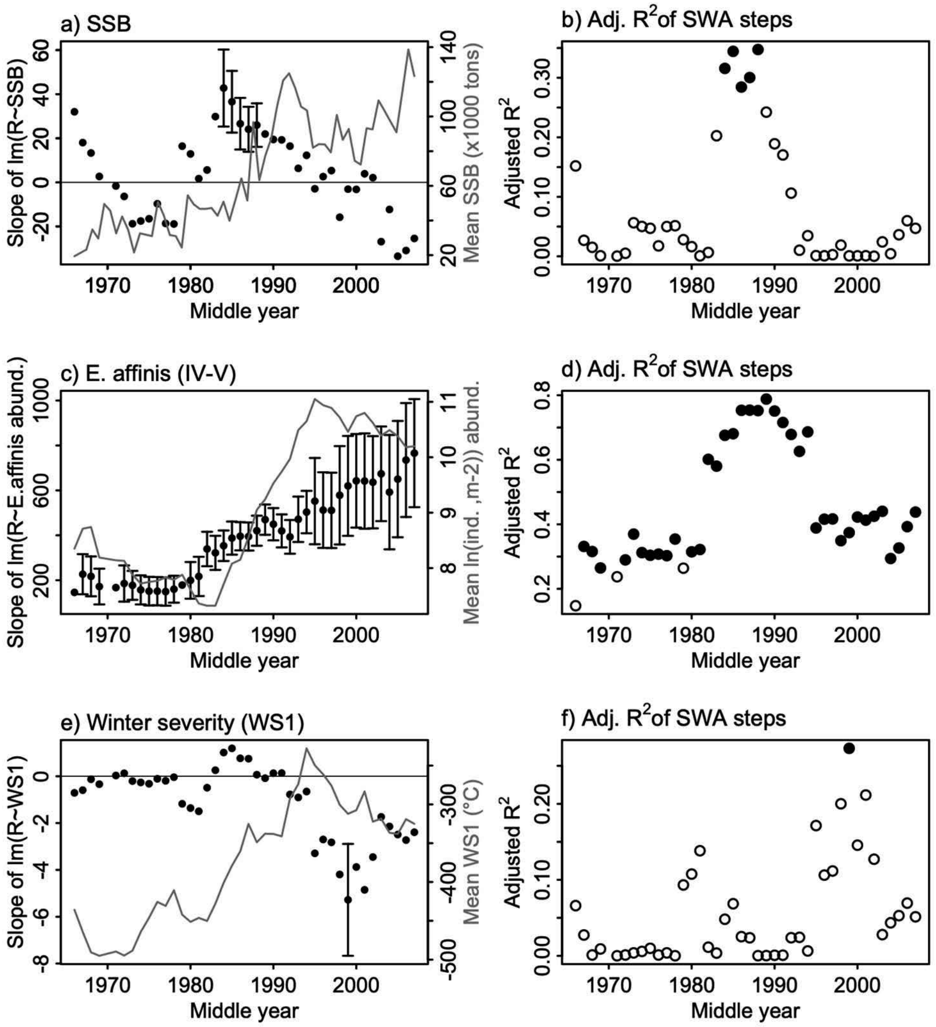

Figure 5. Sliding window analysis (SWA) to test the stepwise changes in direction (positive or negative) and strength (R^2) of the linear links between the GoR spring-spawning herring recruitment abundance (R) and: (a–b) spawning stock biomass (SSB, thousand tons), (c–d) abundance of *E. affinis* in open GoR (copepodites stages IV–V, ln(ind. m^{-2})), and (e–f) winter severity (WS1, sum of negative daily temperatures, °C). Left panel: slope of the linear model (points) and mean value of the respective explanatory variable (grey line), fitted to each 15-year subset of data. Error bars show the standard error of the slope for subsets where the slope was significant at $p<0.05$. Right panel: adjusted R^2 of the linear model fitted in every step. Filled points show the steps where the model was significant at $p<0.05$ (**III**).

Two major non-stationary effects were observed in association with the invasion of the predatory cladoceran *C. pengoi* (**II**). The type of the link changed over time between i) the abundance of two small-sized cladoceran prey (*Bosmina* spp. and *Pleopis* spp.) and temperature proxy from non-linear pre-invasion to linear post-invasion; and ii) the abundance of *A. improvisus* larvae and storminess index from linear to non-linear (Table 1). Overall, we expected that the relationship with the temperature proxy would change for all prey taxa towards negative post-invasion and with the storminess index towards positive. Both expectations were based on the effects that these environmental variables have on the abundance dynamics of *C. pengoi* (see section 2.2.2.). The direction of the prey abundance-temperature relationship changed for three prey taxa (*Bosmina* spp., *E. affinis* and *Pleopis* spp.), towards more negative post-invasion. For the prey taxa abundance-storminess relationship however, the results of our analysis unanimously rejected the hypotheses (Figure 6). Therefore, we suggest that the study area, a shallow coastal environment sheltered from the predominating westerly winds, likely prevented the water column instability at a level that would have affected the *C. pengoi* population sufficiently to reduce predation mortality and induce a measurable increase in prey abundance. However, we could expect such an effect in onshore open areas affected by winds. Further, there is general evidence on the negative effect of wind speed and the number of storm days on zooplankton in the GoR (Kotta *et al.*, 2009). Our failure to detect any significant negative relationships between prey abundance and the storminess index does not mean a contradiction with findings by Kotta *et al.* (2009), since we were looking at a very short time period before each sampling event, whereas Kotta *et al.* (2009) used annual values of storminess.

Associated with the *C. pengoi* invasion, and likely through predation, there was also a notable decline of prey abundances at higher temperatures: for *Bosmina* spp. and *E. affinis* from 15 °C and for *Pleopis* spp. from 20 °C (Figure 6, paper **II**). This is critical, bearing in mind the future perspective of climate warming in the region (Meier *et al.*, 2012) and may point to a potential further relative decrease in these native taxa in the future. As there is no seasonal thermocline in the study area, the prey of *C. pengoi* cannot escape to the cold deeper water below the thermocline, as reported in other areas in the Baltic Sea (Põllumäe and Väljataga, 2004; Lehtiniemi and Gorokhova, 2008).

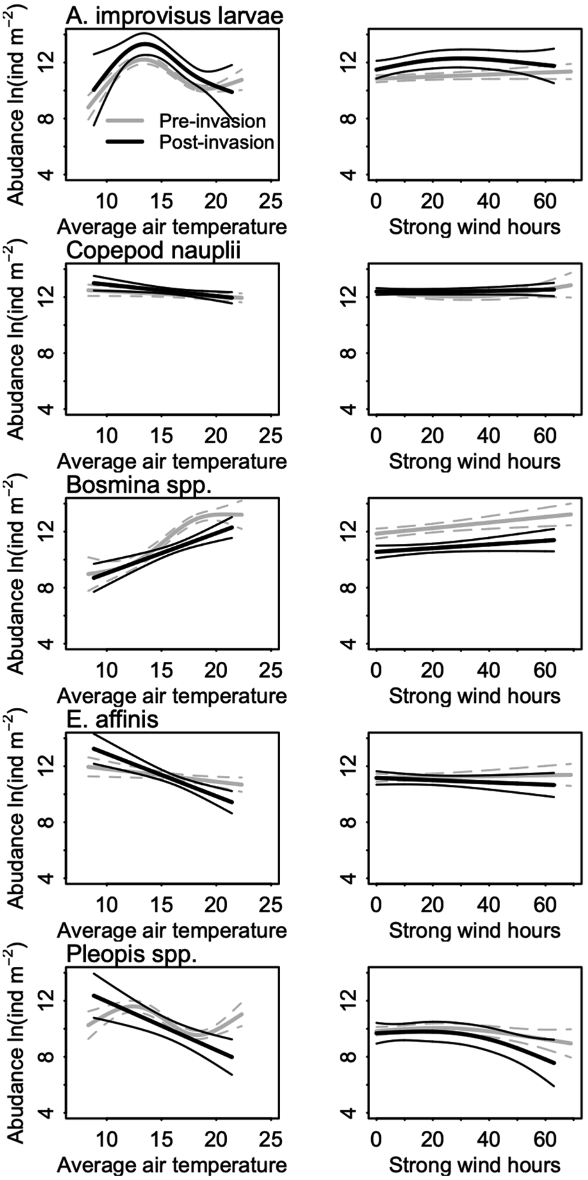

Figure 6. Pre- and post-invasion (of *Cercopagis pengoi*) links between the abundance (ln(x+1)-transformed, ind. m^{-2}) of five zooplankton taxa, and temperature proxy and storminess index in Pärnu Bay (GoR) during the years of similar environmental conditions estimated with GAM models. Grey dotted lines and black solid lines around pre- and post-invasion lines are 95% confidence intervals of the predicted line (i.e. SE) (**II**).

3.3. Review of the non-linear and non-stationary relationships in the Baltic Sea

In total, 69 previously published papers dealing with long-term changes in the Baltic Sea ecosystem, were assessed in this review to investigate the temporal tendencies in the use of methods that can identify non-linear and/or non-stationary relationships. Out of the 69 papers, 39 used methods that can detect non-linearity and/or non-stationarity. It appears that considering non-linear and non-stationary relationships in the studies of the Baltic Sea ecosystem started in the late 2000s (Figure 7a). While the cumulative number of studies has increased over time (since 2008), no increase in the annual rate is evident (Figure 7a). The length of the time series used varied between 10 and 59 years.

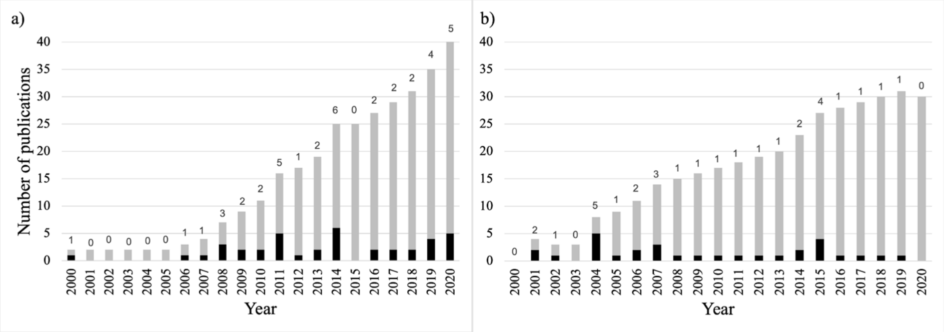

Figure 7. Annual and cumulative number of publications that used: a) methods that can detect non-linear and non-stationary relationships affecting the dynamics of biotic properties of the Baltic Sea and b) methods that could not detect these relationships. Grey bars: cumulative numbers of studies. Black bars and the numbers above the bars: cumulative number of studies done in the given year.

Studies that already considered the non-linearity or non-stationarity in this analysis focused on either the type or stability of the links in the different Baltic Sea ecosystems. The dependent variables were most often fishes (26 studies), but also zooplankton (9) and phytoplankton (4). Variables tested were either abiotic (e.g. temperature, salinity, NAO, depth, etc.), biotic (e.g. abundance/biomass of prey or predators) or both. Most of the studies included both abiotic and biotic variables (66.7%), 30.7% of papers used only abiotic and 2.6% only biotic variables.

The most used methods to test the type or stability of the relationships were GAM, SWA and moving window analysis, non-linear regression analysis, generalized additive mixed models, and threshold GAM. Less frequently used models were EDM, stochastic cups model, multivariate simplex projection, delta GAM. Most of the studies used a combination of different methods. The types of the links found were: i) non-linear slightly curved, e.g. proportion of cladocerans abundance in the zooplankton community and water temperature in the GoR

(Jansson *et al*., 2020); ii) dome-shaped, e.g. spring-spawning herring R-BSI links for several stocks in different parts of the Baltic Sea (Cardinale *et al*., 2009); iii) spline-shaped, e.g. *Acartia* spp. spring biomass-water temperature in Gdansk Deep (Otto *et al*., 2014a). Stationarity of the relationships was investigated in several papers, primarily for fish and plankton, e.g. Stige *et al.* (2006); Ottersen *et al.* (2013); Klais *et al.* (2017); Orio *et al.* (2017).

3.4. Relevance for assessment and management

Understanding the causes of and variability in marine systems in space and time is essential for their assessment and management. Long-term data collection through monitoring programs along with research and experience helps us to assess the status of and trends in the environment, and improve the understanding of ecosystem functioning. The core of this thesis was zooplankton monitoring data, which is one of the most extensive datasets on zooplankton species composition and abundance/biomass in the Baltic Sea (Jansson *et al*., 2020). It provides fundamental information not only on the dynamics of various zooplankton taxa under different external forcings and ecosystem regimes, but also facilitates advanced understanding of the response of trophically related taxa (including pelagic fish).

3.4.1. Non-indigenous species

Despite the rate of NIS introductions globally (also in the Baltic Sea) has declined during the past decade (Bailey *et al*., 2020), NIS are considered as one of the major drivers of change in marine ecosystems. In general, information on the effects of NIS on invaded marine ecosystems is poor (Pyšek and Richardson, 2010), which is a major concern. Therefore, improvement of the knowledge base through quantified evidence of NIS impacts is very much required for the assessment of environmental status and to inform management measures. The results obtained within this thesis are primarily of a high relevance in the context of the European Union Marine Strategy Framework Directive (EC, 2008). The revised Commission Decision of the MSFD Directive (EC, 2017) requests are not only to quantify the impacts caused by NIS (Descriptor 2 criterion 3 "*Proportion of the species group or spatial extent of the broad habitat type, which is adversely altered due to non-indigenous species, particularly invasive non-indigenous species*"), but also to use the information on NIS impacts in the assessments of several criteria under the D1 ("*Biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions*"). In addition, as food web impacts of NIS can compromise the MSFD D4 overall objective ("*All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term* *abundance of the species and the retention of their full reproductive capacity*"), our results also contribute to D4.

There is already multiple evidence available showing how much and by which mechanisms NIS have affected native species, communities and habitats (e.g. Ojaveer *et al.*, 2021). However, confounding factors potentially affecting the outcomes are considered relatively rare, resulting in a high uncertainty of the overall conclusions. In this thesis, the food web effect of the non-indigenous predatory cladoceran *C. pengoi* on the abundance of its main prey taxa was quantified, together with the assessment of the change in the prey taxa-environment relationship by comparing the pre- and post-invasion time series (**II**). As there were substantial differences in key abiotic variables likely affecting both predator and prey (air temperature and wind conditions), preliminary selection of the years was done before conducting the analysis. Our analysis clearly suggests that variability and/or alterations in environmental conditions may significantly affect the measured effect size and should therefore be considered in the impact assessments of NIS.

3.4.2. Fish stocks

Although the ecosystem-based approach to fisheries management (EBFM) has formally been widely adopted at least conceptually about 25 years ago, implementation of EBFM is explicitly mentioned as a requirement in the revised Common Fisheries Policy of the European Union (EU, 2013). Fish stock assessment and tactical management still takes very little account of ecosystem processes, implicitly ignoring that fish stock production depends on the physical and biological conditions of the ecosystem (Skern-Mauritzen *et al.*, 2016). One of the reasons lies in the limited ability to predict R from environmental factors even if the principal mechanisms are understood (Myers, 1998; Dickey-Collas *et al.*, 2010).

Despite over half a century of investigations, environment-based forecasts are still less reliable than other approaches for the GoR spring herring assessment on a regular basis, and the short-term forecasts for the GoR herring are currently based on the geometric mean of year classes from 1989 corresponding to the period of improved reproduction conditions and prevalence of mild winters (ICES, 2020). The environmental data of mean water temperature (0–20 m water layer) and biomass of the main prey of the GoR spring herring, *E. affinis* were included in the GoR spring herring stock forecasts until 2011 (ICES, 2020). When only the data after 2000 were used, the biomass of *E. affinis* in May, and Fulton's condition factor for ages 2–5 proved to be good predictors of herring R. However, incorporating these variables into herring assessment models also failed due to a high variation ratio (ICES, 2020). Our SWA (**III**) showed that the abundance of the main prey *E. affinis* (copepodites stage IV–V) described the dynamics of herring R fairly well (small standard error) until 1995 (incorporating the years 1987–2011), but the standard error of the relationship increased sharply since then and has remained high until the end of the time series. This increase is associated with the ecosystem-level regime shift which took place at the end of the 1980s (Arula *et al.*, 2014; ICES, 2014). Thus, the current ecosystem regime is characterized by a still significant, but variable relationship between herring R and the abundance of critical prey, which might not be satisfactory for assessment purposes on a regular basis.

3.5. Data availability, methodological innovations and limitations in results interpretation

When conducting the data analysis for this thesis, special consideration in data preparation was given for any limiting factors, as well as taking advantage of the given data to our best ability. When using long-term time series, it is important to keep in mind when, where and by whom the data/sample has been collected, and whether the method of sample collection and analysis has remained unchanged over time. Studies using long-term data rely mainly on the consistency of the sampling method and sample analysis. For this thesis, the overall sampling strategy and the sample analysis, and the location of sampling sites have remained sufficiently consistent during the nearly 60 years, but some idiosyncrasies were still encountered and were handled in the analyses as explained below.

Paper **I** can be characterized by the most comprehensive analysis of *L. macrurus* to date by covering a longer time scale than any study performed thus far, thereby enabling us to describe the long-term dynamics of this arctic species and better understand its ecology under different ecosystem configurations and different combinations of drivers of change. However, when preparing the observational data, we were challenged by some gaps in the time series. For that reason, only the stations with the highest sampling frequency and continuous time series were used.

Quantification of the impact of NIS through the changed food web interactions of invaded communities by exploiting long-term pre- and post-invasion time series is relatively rare. In paper **II**, special caution was taken to eliminate the effect of confounding factors on changed prey-environment relationships associated with the invasion of *C. pengoi* (for further details, see section 2.2.2. and paper **II**). Also, the frequency of sampling was reduced during the study period, from every second or third day to weekly, from 1993 onwards (**II**). Since the seasonal coverage of sampling remained unchanged, we considered the effect of reduced sampling frequency on the outcomes as low. Nevertheless, when conducting the analysis, we acknowledged this and interpreted the results with care.

When conducting analyses involving comparison of two or more time periods, changed environmental conditions need to be considered too, to eliminate the effect of the likely confounding abiotic factors. In paper **II**, changes in air temperature, and wind speed and strength were considered during the pre-and post-invasion of *C. pengoi*, together with evaluating the actual impact of *C. pengoi* on its prey-environment relationship. Such an approach is generally rare in marine bioinvasion ecology, and the published papers so far fail to consider the potential effect of confounding factors while investigating the food web effects of *C. pengoi*. Moreover, the establishment of *C. pengoi* has likely enhanced intraspecies food competition in the invaded ecosystem where there is evidence on density-dependent regulation of the individual somatic growth of the most dominating zooplanktivorous fish: herring (Raid *et al.*, 2010) as well as three-spined stickleback (*Gasterosteus aculeatus*) and mysid (*Mysis* spp.) (Lehtiniemi and Nordström, 2008; Ojaveer *et al.*, 2017). Due to a lack of relevant data in the study area, we were not able to evaluate the predation effect caused by juvenile coastal fish and pelagic fish.

Among the main strengths of this thesis was the application of different methods to detect the type (i.e. linear or non-linear) and changes in strength and/or direction of these links. An important outcome of this approach is the conclusion that different methods may give either contrasting results or confirm and support one another (**III**). To measure model performance, we additionally applied the out of sample prediction skill. This method provides a more realistic evaluation of models' performance than the adjusted R^2 of the model and is often useful as a performance criterion for time series forecasts. One of the methodological innovations was GWA (**III**), as we failed to find any other study that has used a similar method. This innovative approach on the time series data could be used in further analysis, e.g. to detect the exact time of the "tipping" point in the community.

As with most investigations of the historical dynamics of populations, the data available for analysis and the documentation for how it was originally sampled and collected, are often incomplete and fragmented. Also, in many cases, the data available have not been collected using consistent or modern data sampling protocols nor with currently used spatio-temporal coverage. To some extent, these data limitations apply to the historical data compiled and analyzed here. For example, while there should be no concerns on the annual-scale consistency in sampling and sample analysis methods, we still lack some information on the amount of data available, together with the details of the exact methods used for calculation of SSB of autumn herring (**II**) and also, calculation of SSB and R for spring herring prior to 1977 (**II, III**). It should also be noted that zooplankton data originate from two sources, both of which are characterized by maintaining similar sample collection and analysis methods over time, but allowing some variability in sampling frequency and sampling locations at the annual level (**I, II, III**).

3.6. Future look

The changing climate along with the direct impact of intensifying human exploitation of the sea continue to shape and implicate marine ecosystems as well as modify existing species-environment relationships and species-specific interactions. While our knowledge is fairly advanced on the effects of several single drivers and the relevant assessment/management frameworks are in place (e.g. EC, 2008), the assessment of cumulative effects and operationalizing of these effects into the decision-making process has started only recently (e.g. Willsteed *et al*., 2017; Stelzenmüller *et al*., 2020). Without any doubt, for future assessments of the species or ecosystem state, the continuation of collecting monitoring data and extending the length of the current time series database is inevitable. This knowledge underpins the scientific advice for management and allows making informed decisions. From the science perspective, new and innovative methodological approaches need to be developed and applied on these long-term data to identify and establish in addition to cumulative effects, for example: i) causal relationships between the state and the driver; and ii) quantifying the effect of change on the impact gradient of a single driver. None of these tasks are straightforward, all of them are extremely important and have very specific requirements and challenges.

Continuous long-term data, as used in the current thesis, is required for detecting causality. Recently, there has been a substantial advancement in methodological development to investigate causality. One of the emerging frameworks is empirical dynamic modeling (EDM), an equation-free numerical tool that can be used to evaluate the complexity of a real-world system that is represented by the time series of a few key variables (Deyle *et al.,* 2016; Chang *et al*., 2017). Different tools of EDM can be used to: i) determine the complexity (dimensionality) of the system; ii) detect and evaluate whether the dynamics of the system are non-linear; iii) determine causal variables, e.g. to test if two variables are interacting directly; iv) make forecasts; and v) track the strength and sign of interaction (Sugihara *et al*., 2012; Chang *et al*., 2017). Some previous research have reported that applying the EDM approach improved e.g. the R-stock forecasts and could be also useful for validating parametric models (Ye *et al*., 2015; Munch *et al*., 2018; Sguotti *et al*., 2020). Applying EDM to continuous time series, such as used in the current study, might help us further advance our understanding of the long-term mechanisms behind the dynamics of the key species in the GoR ecosystem.

CONCLUSIONS

This thesis aimed to investigate non-linear and non-stationary relationships in the Gulf of Riga (Baltic Sea) pelagic ecosystem during almost six decades by applying a suite of analytical methods. The following conclusions can be drawn based on the results obtained.

The most conspicuous and consistent outcome of all analyses was the prevalence of non-linear and non-stationary relationships between the investigated key species and their drivers of change in the pelagic ecosystem of the GoR. Among these relationships, the climate and food web interactions always ended up as significant drivers of the changes. A review of the recent research focused on the long-term changes in the Baltic Sea further corroborated the suggestion that non-linearity and temporal instability are rather a rule than an exception. However, this knowledge is relatively recent (since the end of the 2000s).

Detection and analysis of non-linear and non-stationary relationships presuppose a dedicated analytical approach, which can often mean a combination of simpler but complementary tools. The range of analytical methods used in this study included generalized additive models and two different "moving window" methods. The combined application of these methods enabled to reveal both the non-linear and non-stationary facets of the relationships and unravel the entirety of the processes underlying the long-term changes in the GoR pelagic ecosystem.

Generally, with most investigations of the historical dynamics of populations, the data available for analysis and the documentation for how it was originally sampled and collected, are often incomplete and fragmented. For the time series exploited in this thesis, the overall sampling strategy, the sample analysis, and the location of sampling sites have remained sufficiently consistent during the nearly 60 years. Still, when preparing the observational data, we were challenged by some gaps in the time series. The availability of the continuous time series limited the selection of both sampling stations and parameters considered in the analysis. To be able to permanently advance our understanding of the long-term dynamics of the structure and dynamics of marine ecosystems, continuation of the already existing long-term time series should be prioritized.

Advanced understanding of the causes and variability of marine ecosystems in time and space are essential for improving assessments and informing management decisions. Long-term time series obtained through monitoring programs along with research efforts to gain deeper insight into mechanistic understanding are the two key components in improving the understanding of ecosystem functioning and overall, move towards ecosystem-based management or marine living resources. The latter is requested by several EU policies and legislative instruments (e.g. Common Fisheries Policy, Marine Strategy Framework Directive). One of the main outcomes of the current thesis is that previous knowledge obtained from the analyses using shorter time series and utilizing simpler and less comprehensive analytical tools does not necessarily hold when extending the length of the time series. While the outcomes of the current thesis might not be explicitly applicable in the management context, they significantly contribute to an improved knowledge base for advancing assessments (biodiversity, non-indigenous species and commercial fish stocks) underpinning the management advice.

One important lesson learned from the analyses in this thesis was that different methods may give either contrasting results or confirm and support one another, and thereby expand the fathomable complexity of the processes. Therefore, it is encouraged to combine several analytical approaches and derive the composite conclusions from even contrasting results. Overall, in this thesis, we excluded data on discontinuous time series, which could be useful for further analysis, but pose a challenge in filling in gaps in data and likely influence the outcome of the results. The following four actions could be proposed for further development based on the results of this thesis: i) identifying causal links between the ecosystem state and the key driver, ii) quantifying the effect of change on the impact gradient of a single driver, iii) including the originally discontinuous time series in developing algorithms for filling in the data gaps, and iv) including the benthic ecosystem.

SUMMARY IN ESTONIAN

Mitte-lineaarsed ja ajas muutuvad seosed Liivi lahe (Läänemeri) pelaagilises ökosüsteemis

Seosed mere ökosüsteemides võivad olla lineaarsed või mitte-lineaarsed ning statsionaarsed või mitte-statsionaarsed (ehk ajas muutuvad nii seose tüüp, suund kui ka tugevus). Mitte-statsionaarsus mere pelaagilistes ökosüsteemides võib avalduda nii ajalisel kui ka ruumilisel skaalal. Mitte-statsionaarsuse põhjusteks võivad olla järkjärgulised muutused ökosüsteemi struktuuris ja funktsioonis ning ka hüppelised muutused, mida nimetatakse režiiminiheteks. Kuigi üldine teadmine sellest, et pikaajalised seosed mere ökosüsteemides on pigem harva stabiilsed ja lineaarsed, kasutatakse tihtipeale jätkuvalt mudeleid, mis ei suuda keerukamaid seoseid tuvastada. See kehtib ka Läänemere kohta, kus mitte-lineaarseid ja ajas muutuvaid suhteid tuvastavate meetodite kasutamine on hoogustunud alles viimasel kümnendil. Selles töös on kasutatud ligi kuuekümne aasta (1958–2018) pikkuseid hüdroklimaatilisi ja bioloogilisi Liivi lahe (Läänemeri) andmeridu, millest mitu on uudsed ja seega ei ole varasemalt analüüsidesse kaasatud. Eesmärk oli uurida Liivi lahe ökosüsteemis olulist rolli täitvate liikide seoseid keskkonna, toidu ja kisklusega, keskendudes muu hulgas ka nende seoste mitte-lineaarsusele ning mitte-statsionaarsusele. Töös uuriti: i) suure järvehormiku (*Limnocalanus macrurus*) pikaajalise varieeruvuse põhjuseid (**I**); ii) invasiivse võõrliigi *Cercopagis pengoi* mõju ta saakloomade arvukusele ning saakloomakeskkonna seoseid enne ja pärast võõrliigi invasiooni (**II**); iii) kohaliku kevadkuduräime (*Clupea harengus membras*) varu/asurkonna täiendi arvukust mõjutavaid tegureid (**III**).

Andmeanalüüsis kasutati variatsioone ning kombinatsioone erinevatest statistilistest meetoditest, et kirjeldada ajas muutuvaid seoseid ja tuvastada põhjuslikke seoseid uuritavate muutujate vahel, näiteks üldistatud aditiivseid mudeleid, ning kahte erinevat „libiseva ajaakna“ meetodit. Neid meetodeid omavahel kombineerides saab tuvastada nii mitte-lineaarseid kui ka mitte-statsionaarseid seoseid ning võrrelda omavahel erinevate meetodite tulemusi (kas toetavad üksteist või mitte).

Liivi lahe pelaagilise ökosüsteemi dünaamikat iseloomustavad lineaarsed ja mitte-lineaarsed ajas muutuvad seosed. Seosed *L. macruruse* arvukuse ja talve karmuse ning põhjakihtide vee temperatuuriga olid mitte-lineaarsed ja ajas muutuvad (**I**). Samuti muutus aja jooksul suure-järvehormiku arvukuse ning Liivi lahe räime kudukarja biomassi suhe. Võrdlusanalüüs, kus uuriti viie saaklooma seoseid kahe keskkonnateguriga (temperatuur ja tormisus) enne ja pärast *C. pengoi* invasiooni (II), tuvastas, et kahekümnest individuaalsest seosest üheksa olid mitte-lineaarsed, ning seose tüüp muutus pärast invasiooni kolmel korral kümnest. Mitte-lineaarseid ja mitte-statsionaarseid seoseid leiti ka Liivi lahe kevadräime täiendi (**III**) ning sellele oluliste tegurite vahel (kevadräime kudukarja biomass, talve karmus ning toit (*Eurytemora affinis* järgud IV–V)).

Pikaajaliste ning katkematute aegridade pikendamine seireprogramme jätkates on väga oluline, et mitte öelda vältimatu eeldus ökosüsteemide uurimiseks. Arusaamine, mis tegelikult on liikidevaheliste suhete või arvukuse varieeruvuse põhjusteks mere ökosüsteemides, on oluline nii keskkonna või liigi seisundi hindamisel kui ka otsuste tegemiseks ökosüsteemide majandamisel, näiteks kalandussektoris. Üks oluline doktoritöö tulemus on see, et pikendades aegridu ning võrreldes neid varem uuritud seostega, kus on kasutatud samade aegridade lühemaid versioone, saame sageli erinevaid tulemusi, ehk seosed muutuvad tihtipeale aegridade pikenedes. Pikaajaliste seireandmete kogumine ning nende perioodiline korduvanalüüs aitab mõista, kuidas ökosüsteem toimib ja reageerib muutuvates oludes, ning ühtlasi nende teadmistega liikuda ka ökosüsteemide põhise haldamise poole, mis on oluline Euroopa Liidu poliitikale ja seadusandlikele kogudele (*Common Fisheries Policy, Marine Strategy Framework Directive*). Kuigi siinse töö tulemused ei ole veel otseselt rakendatavad kalavarude haldamisel, on siin kirjeldatud tulemused tähtsad ning kasutatavad bioloogilise mitmekesisuse, võõrliikide või tööstuslikult oluliste kalavarude seisundi hindamisel ning haldamise nõustamisel.

Töö metoodilise jätku ja edasiarendusena võib näha kindlasti vähemalt järgmisi suundi: i) katsed tuvastada põhjuslikke seoseid oluliste muutujate vahel (nt *Empirical Dynamic Modeling* metoodika abil); ii) uuritud tegurite mõju suuruse hindamine uuritavale liigile muutuvas keskkonnas; iii) lünklike aegridade täitmise metoodika arendamine ja veel rohkemate aegridade kaasamine analüüsidesse; ja iv) põhjaelustiku andmete kaasamine tervikpildi laiendamiseks, kuivõrd seni on olnud sageli tavaks uurida pelagiaali ja põhjaelustikku eraldi ja eri töörühmade poolt.

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PUBLICATIONS

CURRICULUM VITAE

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Education

2017–…	University of Tartu, Doctoral studies in Zoology and Hydrobiology
2015–2017	Estonian Nautical School Tartu department, Inland Waterways Boatmaster
2014–2016	University of Tartu, Ecology and Biodiversity Conservation, Master of Science
2011–2014	University of Tartu, Ecology and Biodiversity Conservation, Bachelor of Science
2005–2011	Tallinn Secondary School of Science

Professional career

2021–...	University of Tartu Pärnu College, analyst
2016–2018	Tartu Nature House, environmental information specialist
2017–2018	Tartu Nature House, project manager (founded by Environmental Investment Center)

Research interests

Ecology, marine ecology, zooplankton ecology, analysis of time-series data, statistical modeling.

Scientific publications

Behrens, J. W., Ryberg, M. P., **Einberg, H**. Eschbaum, R., Florin, A.-B., Grygiel, W., Hermann, J. P., Huwer, B., Hüssy, K., Knospina, E., Nõomaa, K., Oesterwind, D., Polte, P., Smoliński, S., Ustups, D., van Deurs, M., and Ojaveer, H. 2021. Seasonal depth distribution and thermal experience of the non-indigenous round goby *Neogobius melanostomus* in the Baltic Sea: implications to key trophic relations. Biological Invasions. https://doi.org/10.1007/s10530-021-02662-w

Ojaveer, H., Klais-Peets, R., **Einberg, H.**, and Rubene, G. 2021. Spawning stock biomass modulation of environment – recruitment relationship in a marginal spring spawning herring (*Clupea harengus membras*) population. Canadian Journal of Fisheries and Aquatic Sciences, 78(12): 1805–1815.

Ojaveer, H., Kotta, J., Outinen, O., **Einberg, H**., Zaiko, A., and Lehtiniemi, M. 2021. Meta-analysis on the ecological impacts of widely spread non-indigenous species in the Baltic Sea. Science of the Total Environment, 786:147375. https://doi.org/10.1016/j.scitotenv.2021.147375.

Einberg, H., Klais-Peets, R., Põllumäe, A., and Ojaveer, H. 2020. Taxon-specific response to the invasion of a pelagic invertebrate predator, revealed by comparison of pre- and post-invasion time series. Journal of Plankton Research, 42(6): 714–726.

Einberg, **H.**, Klais, R., Rubene, G., Kornilovs, G., Putnis, I., and Ojaveer, H. 2019. Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea. ICES Journal of Marine Science, 76(7): 2427–2436.

Scholarships

DoRa Plus T1.1 travelling scholarship, Archimedes Foundation (2018)

Conference presentations

Oral presentation "Taxon-specific response to the invasion of a pelagic invertebrate predator, revealed by comparison of pre- and post-invasion time series", BO-ZO PhD Student Conference, 22 January 2021, Tartu (online), Estonia.

Poster presentation "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Baltic Sea Science Congress, 19–23 August 2019, Stockholm, Sweden.

Poster presentation "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Baltic Earth Workshop on Multiple Drivers Conference, 26–27 November 2018, Tallinn, Estonia.

Poster presentation "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Oceans Past VII Conference, 22–26 October 2018, Bremerhaven, Germany.

Membership in organizations:

Member of Tartu Students' Nature Conservation Circle

Additional coursework and improvement skills

Technical University of Denmark (DTU Aqua) research vessel R/V DANA monitoring cruise, bottom trawling and plankton sampling with BONGO net, 11.–27. March and 7.–15. November 2019, Baltic Sea, Denmark.

Sugihara Lab, University of California San Diego, Scripps Institution of Oceanography. 20th of May to 2th of June, guest student, Empirical Dynamic Modeling (EDM), La Jolla, San Diego, California, USA.

OTGA/DOALOS Training Course: Conduct of Marine Scientific Research (MSR) under the United Nations Convention on the Law of the Sea (UNCLOS), 6.–10. May 2019, Ostend, Belgium. Oral presentation "Marine scientific research in Estonia".

International School of Marine Conservation Science, summer school. 21.–30. June 2018, Slovenia, Italy and Croatia.

ELULOOKIRJELDUS

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Haridus:

2017–…	Tartu Ülikool, doktoriõpe, zooloogia ja hüdrobioloogia, Eesti Mereinstituut
2015–2017	Eesti Merekooli Tartu filiaal, siseveelaeva laevajuht
2014–2016	Tartu Ülikool, ökoloogia ja elustiku kaitse, magistriõpe (MSc)
2011–2014	Tartu Ülikool, ökoloogia ja elustiku kaitse, bakalaureus (BSc)
2005–2011	Tallinna Reaalkool

Teenistuskäik

2021– …	Tartu Ülikooli Pärnu kolledž, analüütik
2016–2018	Tartu Loodusmaja, keskkonnainfo spetsialist
2017–2018	Tartu Loodusmaja, projektijuht

Peamised uurimisvaldkonnad

Ökoloogia, merebioloogia ja ökoloogia, planktoloogia, pikaajaliste aegridade analüüs.

Teadusartiklid:

Behrens, J. W., Ryberg, M. P., **Einberg, H**. Eschbaum, R., Florin, A.-B., Grygiel, W., Hermann, J. P., Huwer, B., Hüssy, K., Knospina, E., Nõomaa, K., Oesterwind, D., Polte, P., Smoliński, S., Ustups, D., van Deurs, M., and Ojaveer, H. 2021. Seasonal depth distribution and thermal experience of the non-indigenous round goby *Neogobius melanostomus* in the Baltic Sea: implications to key trophic relations. Biological Invasions. https://doi.org/10.1007/s10530-021-02662-w

Ojaveer, H., Klais-Peets, R., **Einberg, H**., and Rubene, G. 2021. Spawning stock biomass modulation of environment – recruitment relationship in a marginal spring spawning herring (*Clupea harengus membras*) population. Canadian Journal of Fisheries and Aquatic Sciences, 78(12): 1805–1815.

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Einberg, H., Klais-Peets, R., Põllumäe, A., and Ojaveer, H. 2020. Taxon-specific response to the invasion of a pelagic invertebrate predator, revealed by comparison of pre- and post-invasion time series. Journal of Plankton Research, 42(6): 714–726.

Einberg, H., Klais, R., Rubene, G., Kornilovs, G., Putnis, I., and Ojaveer, H. 2019. Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea. ICES Journal of Marine Science, 76(7), 2427–2436.

Uurimistoetused ja stipendiumid

DoRa Pluss T1.1 doktorantide õpirände toetus, Archimedes (2018)

Konverentsiettekanded

Suuline ettekanne: "Taxon-specific response to the invasion of a pelagic invertebrate predator, revealed by comparison of pre- and post-invasion time series", BO-ZO osakondade doktorantide konverents, 22. jaanuar 2021, Tartu (veebipõhine), Eesti.

Stendi ettekanne: "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Baltic Sea Science Congress, 19–23. august 2019, Stockholm, Rootsi.

Stendi ettekanne: "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Baltic Earth Workshop on Multiple Drivers Conference, 26–27. november 2018, Tallinn, Eesti.

Stendi ettekanne: "Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in the relation to environmental variability in the Baltic Sea", Oceans Past VII Conference, 22–26. oktoober 2018, Bremerhaven, Saksamaa.

Organisatsioonidesse kuulumine:

Tartu Üliõpilaste Looduskaitseringi liige

Erialane täiendamine

Technical University of Denmark (DTU Aqua) uurimislaeva R/V DANA serie, planktoni proovide kogumine BONGO võrk ning kalaseire põhjatraaliga, 11.–27. märts ja 7–15. november 2019, Läänemeri, Taani.

Sugihara Lab, University of California San Diego, Scripps Institution of Oceanography. 20. mai kuni 2. Juuni 2019, külalistudeng, Empirical Dynamic Modeling (EDM). La Jolla, San Diego, California, USA.

OTGA/DOALOS Training Course: Conduct of Marine Scientific Research (MSR) under the United Nations Convention on the Law of the Sea (UNCLOS), 6.–10. mai 2019, Oostende, Belgia. Ettekanne "Marine scientific research in Estonia".

Suvekool "International School of Marine Conservation Science", 21.–30. juuni 2018, Sloveenia, Itaalia ja Horvaatia.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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