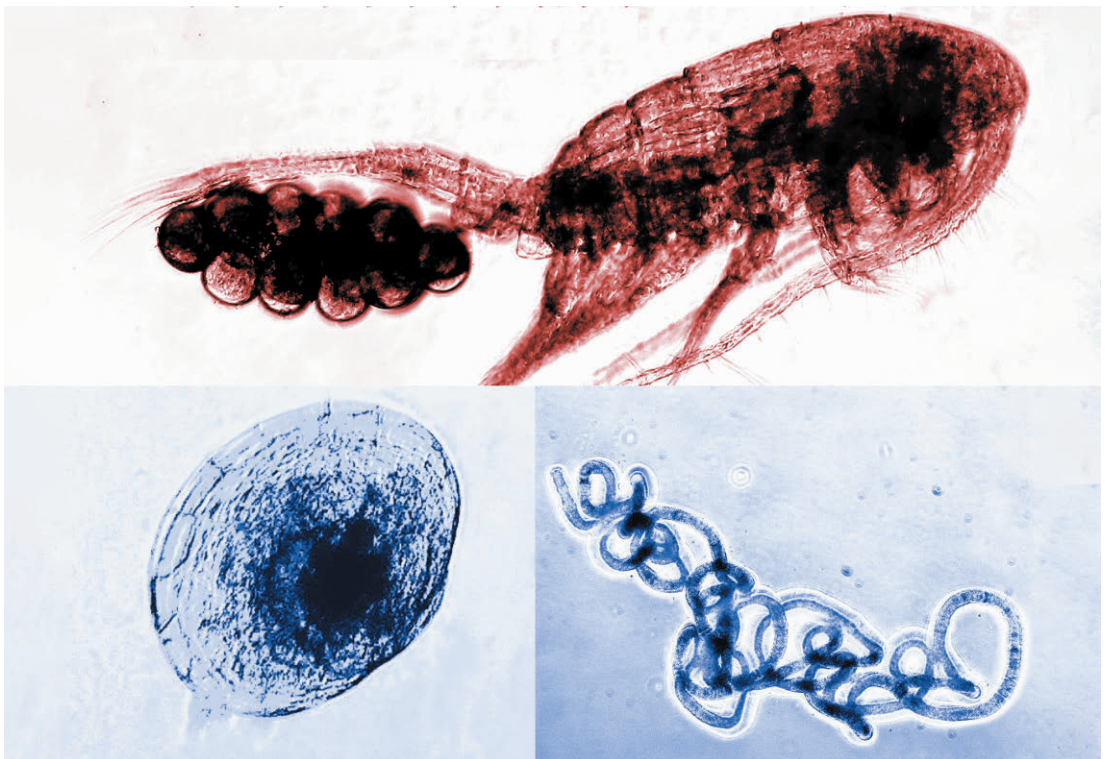Louise Forsblom

Drivers of Plankton Populations in the Baltic Sea

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Abstract

Plankton are at the base of the food chain, and identifying their drivers is important for understanding how climate change will impact populations and communities. The main aim of my thesis was to quantify the effects of environmental drivers on population dynamics of natural phyto- and zooplankton populations (mainly species and genera) using population dynamical modelling of time-series data. However, using time-series data for modelling population dynamics presents multiple challenges as data are never perfect. All data collection and observation processes contain multiple sources of uncertainty and in my thesis, I make an effort to account for such sources, with more detailed consideration of seasonality and wind.

In a case study investigating the spatio-temporal population dynamics of six phytoplankton species, populations displayed a high level of synchrony in their annual biomass dynamics across the northern Baltic Sea, likely caused by the Moran effect. When I further investigated abiotic drivers in the Gulf of Finland, individual auto- and heterotrophic plankton taxa were mainly driven by temperature, salinity and stratification.

Identifying temperature effects on abundance can be challenging, as temperature can also affect seasonal timing of populations. While there were few direct effects of temperature on zooplankton abundances, there were changes in their seasonal occurrence to earlier spring, likely connected to warming.

I also investigated potential biotic interaction between zooplankton and zoobenthos, as zooplankton can have resting eggs in the sediment. The results indicate that biotic interactions were important on annual scale within zoobenthos, but no interactions between zooplankton and zoobenthos were apparent.

Based on the findings in my thesis, many of the identified environmental effects on densities were large in relation to the environmental variability. There is also a need to consider seasonality when investigating plankton populations, as ignoring changes in phenology can lead to noisier estimates or to issues with interpreting temporal patterns.

Keywords: observation error, phenology, plankton, salinity, species interactions, state-space model, stratification, temperature, time-series.

Sammanfattning

Plankton utgör en grundläggande komponent av födovävar, och att identifiera vilka variabler som är viktiga för dem bidrar till vår förståelse av hur klimatförändring kommer att påverka populationer och samhällen. Målet med min avhandling är att undersöka effekterna av miljövariabler på populationsdynamiken hos naturliga populationer av växt-och djurplankton (främst arter och familjer), genom populationsdynamisk modellering av tids-serier. Eftersom inget data är perfekt är användningen av tids-serier för modellering av populationsdynamik sällan utan utmaningar. All datainsamling och alla observationsprocesser innehåller flera källor av osäkerhet och i min avhandling strävar jag till att beakta dessa källor, med en speciell betoning på säsongsbundenhet och vind.

I en fallstudie undersökte jag tids- och rumsvariationen i populationsdynamiken hos sex växtplankton arter. Jag visar att arterna uppvisar synkron biomassdynamik över norra Östersjön, vilket sannolikt är en följd av Moran effekten. Då jag sedan undersökte effekten av abiotiska variabler på årliga biomassan hos auto- och heterotrofa plankton i Finska viken var temperatur, salinitet och skiktning de främsta variablerna.

Att identifiera hur temperatur påverkar abundans kan vara svårt, eftersom temperaturen också kan påverka populationens säsongsberoende. Det fanns få direkta temperatureffekter på abundansen av djurplankton, men deras förekomst har delvis tidigareställts om våren, vilket sannolikt är kopplat till temperaturen.

Jag undersökte också förekomsten av interaktioner mellan djurplankton och bottenfauna, eftersom djurplankton kan ha viloägg i sedimentet. Resultaten visar att interaktioner på årlig skala är viktiga inom bottenfaunan, medan det inte gick att identifiera effekter mellan djurplankton och bottenfauna.

Min avhandling visar att många av de identifierade abiotiska variablerna hade stora effekter på populationens densitet i förhållande till miljöns variation. Det är också viktigt att beakta säsongsberoende då man undersöker plankton, och om det ignoreras kan det leda till brusigare estimat eller försvåra tolkningen av temporala mönster.

Nyckelord: fenologi, mellanarts-interaktioner, observationsfel, plankton, salinitet, skiktning, temperatur, tidsserier, tillstånds-modell.

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III **Forsblom L.**, Lindén A., Lehtiniemi, M., Engström-Öst, J. Drivers of abundance and phenological changes in mesozooplankton. *Manuscript*.

IV **Forsblom L.**, Lindén A., Engström-Öst, J, Lehtiniemi, M., Bonsdorff, E. Identifying biotic and abiotic drivers of benthic and planktonic taxa. *Manuscript*.

Contributions[*]

I Conceived and planned the study: **LF**, AL. Time-series data retrieval and processing: **LF**, SL. Planned the analysis: **LF**, AL. Performed the analysis: **LF**. Prepared the manuscript **LF**, AL, SL.

II Original idea: AL, JE. Planned the study: **LF**, AL, JE and SL. Time-series data retrieval and processing: **LF**, SL, IL. Planned the analysis: **LF**, AL. Performed the analysis: **LF**. Prepared the manuscript **LF**, AL, JE, SL, IL.

III Conceived and planned the study: **LF**, AL, JE, ML. Time-series data retrieval and processing: **LF**, ML. Planned the analysis: **LF**, AL. Performed the analysis: **LF**. Prepared the manuscript **LF**, AL, JE, ML.

IV Original idea: **LF**, EB. Planned the study: **LF**, AL, EB, JE, ML. Field data collection: **LF**, JE, AL. Field sample analysis: **LF**. Planned the statistical analysis: **LF**, AL. Time-series processing and analysis: **LF**. Prepared the manuscript **LF**, AL, EB, JE, ML.

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1 Introduction

1.1 Population dynamics

The dynamics of a species consist of fluctuations in abundances that are determined by the combination of births, deaths, emigration and immigration, all influenced by intrinsic (density) and extrinsic (environment) drivers. Since extrinsic and intrinsic drivers act on the level of the individual, large scale patterns in population fluctuations can be discerned by ignoring individual variation in favour of simplification. The classical Ricker model for population growth can be linearised on the log scale and the population process can be reformulated as a discrete-time Gompertz model (Dennis and Taper 1994; Royama 1981), and to this one can include additional environmental covariates, as

$$x_t = a + bx_{t-1} + uc_t + \omega_t \tag{1}$$

$$\omega_t \sim N(0, q) \tag{2}$$

Here, x_t is the log density at time-step t and is described as a function of the log density at the previous time-step x_{t-1} modified by the density dependence (b). Further, a is the intrinsic rate of population growth, the scalar vector u describes the effect of the environment (c_t), and ω_t is a random variable describing the unexplained variation, with mean 0 and variance q (Equation 1 and 2). Depending on the investigation, the density dependence can be a reflection on the intraspecific competition in the population, or a merely technical reflection of the statistical return tendency of the time-series, affected by a wealth of different processes. In the statistical analysis of a log-transformed time-series of population density x, this stochastic model may be referred to as a first order linear autoregressive model with a covariate (an ARX(1) model). If one is not interested in the average level of the time series, one may subtract the mean from the logged time-series x_t and leave out the intercept term (a) from Equation 1.

In a multi-species system, species can influence each other through competition for resources, predation, facilitation *etc*. This can be achieved by extending Equation 1 and 2 to include multiple species. In Equation 3 and 4 I show a two species example where the matrix **B** describes the inter- and intraspecific interactions. The diagonal of **B** describe the intraspecific density dependence of each species and the off-diagonal elements the interactions of species one on species two and *vice versa* (see Ives et al. 2003 for more details).

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix}_t = \begin{bmatrix} b_1 & b_{2,1} \\ b_{1,2} & b_2 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}_{t-1} + \begin{bmatrix} u_{1,trend} & u_{1,env} \\ u_{2,trend} & u_{2,env} \end{bmatrix} \begin{bmatrix} c_{trend} \\ c_{env} \end{bmatrix}_t + \begin{bmatrix} \omega_1 \\ \omega_2 \end{bmatrix}_t \quad (3)$$

$$\omega_t \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} q_1 & q_{1,2} \\ q_{1,2} & q_2 \end{bmatrix} \right) \quad (4)$$

These types of stochastic models, used to investigate interactions between species or populations and the effects of extrinsic variables using multivariate time-series data with lag one, are known as multivariate- or vector autoregressive models (MAR or VAR respectively). They have been extensively applied in analyses of plankton time-series data to investigate interactions and extrinsic drivers, interactions between plankton taxa (Barraquand et al. 2018; Griffiths et al. 2016; Hampton et al. 2006; Hampton and Schindler 2006; Scheef et al. 2013, 2012), and to detect shifts in community interactions (Francis et al. 2012, 2014).

1.2 Plankton as a model system

Plankton consist of a diverse group of organisms unable to swim against currents. Many, however, are capable of limited movement. The main focus of my thesis will be on phyto- and zooplankton.

In a foreseeable future, anthropogenic change is predicted to be the dominant factor modifying global marine food webs, acting by influencing variables such as temperature and salinity, and processes such as acidification (BACC II Author Team 2015; Cloern et al. 2016), by influencing species distributions, species composition, food web functioning and phenology patterns (Beaugrand et al. 2019; Edwards and Richardson 2004; Parmesan and Yohe 2003; Pontavice et al. 2020). Plankton are affected by these anthropogenic changes both directly through effects on their physiology and indirectly through changes in top-down and bottom-up regulations, where *e.g.* an increase in temperature can lead to higher grazing pressure and nutrient availability is influenced by prevailing mixing conditions respectively (Bruno et al. 2015; Sommer and Lewandowska 2011; Winder and Sommer 2012). Elevated temperatures have led to large-scale changes in both phyto- and zooplankton in temperate regions with earlier onset in spring emergence and a size-at-age decrease (Daufresne et al. 2009; Hjerne et al. 2019). In the North Atlantic shifts in species distributions are occurring, where temperate species, such as *Calanus finmarchicus*, are gaining ground and moving northward (Chust et al. 2014). Especially in marginal seas, such as the Baltic Sea,

salinities have locally decreased in part due to increases in freshwater run-off (Meier et al. 2012). The decrease in salinity have in combination with eutrophication and warming contributed to changes in the distribution of plankton and changes in their community composition in the northern Baltic Sea (Hänninen et al. 2003; Kuosa et al. 2017; Mäkinen et al. 2017).

Many plankton taxa are relatively small, fast reproducing and sensitive to their environment, thus considered good indicators of climate change (Andersson et al. 2015; McQuatters-Gollop et al. 2017). Changes in plankton communities and species can have far reaching consequences, as plankton affects biogeochemical cycling and as they constitute the main link between bacteria and fish (Litchman et al. 2015; Tamelander et al. 2017). Their short generation times and rapid response to the environment make plankton excellent candidates for investigating environmental drivers using population dynamical modelling. However, choosing the appropriate spatio-temporal scale for the investigation can prove challenging and requires consideration (*e.g.* Hampton and Schindler 2006; Scheef et al. 2012; Wauchope et al. 2019).

Numerous studies have investigated physiological responses to environmental drivers such as temperature and salinity in both phyto- and zooplankton species using experiments (*e.g.* Diekmann et al. 2012; Kremer et al. 2017; Thomas et al. 2012 and references therein). In natural settings, however, many studies focused on long-term changes use a coarse taxonomical scale. This can be due to many reasons; the question can be about large-scale trends aiming to capture general patterns between environmental variables and plankton or to describe the community composition. Researchers also need to consider quality of the data due to sampling technique or taxonomical resolution (Zingone et al. 2015). However, many taxa can have inherent traits that make the species-level an interesting focus of study and traits can vary also within classes (Litchman and Klausmeier 2008). Some taxa can be toxic and thereby of economic importance for aquaculture and fisheries, while others are excellent quality nutrition to the next trophic level (Litchman and Klausmeier 2008 and references therein). Many cyanobacterial taxa are toxic and the mass-occurrences have been shown to globally increase in frequency, magnitude and length (Huisman et al. 2018). Changes in zooplankton species composition have been linked to declining trends in Baltic herring sizes in the Gulf of Finland, as herring prefers larger marine copepods (Flinkman et al. 1998). If taxa are analysed as larger taxonomical groups, the estimated effects of environmental drivers can be averaged out, particularly if the taxa are inversely affected by the same driver, the effect varies temporally, or if one taxa has a low contribution

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to the biomass or abundance at the chosen scale of investigation (Griffiths et al. 2016). Thus, knowledge of the species and how they affect the functioning of the ecosystem under climate change are needed to make sound management decisions (Andersson et al. 2015; McQuatters-Gollop et al. 2017).

1.3 The detection of environmental drivers

Granger causality

When investigating the effect of both biotic and abiotic variables on population dynamics it is logical to assume that the cause should precede the effect, and to stipulate that a single environmental driver should describe variation in addition to a mere temporal trend. One method for identifying such environmental drivers of population densities is including them as lagged candidate covariates into population models that alone can describe simple trends and autocorrelated temporal structure (see Ives et al. 2003). The approach to identify effects of covariates, by including their lagged effects in autoregressive time-series models is referred to as Granger causality in other contexts (Granger 1969).

Abiotic drivers

The role and detection of abiotic drivers depend on the scale of the investigation (*e.g.* Rantajärvi et al. 1998). Reliably linking covariates to the dynamics of natural populations is essential for understanding the drivers of abundance or biomass, even in cases when a species' ecological requirements and optima are known from experimental studies. To be relevant for population dynamics and to produce a detectable effect, the abiotic driver is required to produce a detectable effect by influencing survival, reproduction or growth (Kremer et al. 2017; Pörtner and Farrell 2008). Additionally, if the fluctuations of the variable are low in nature, or if it varies within the optimal range of the species, it can be irrelevant or undetectable for population dynamics in natural populations (see Pörtner and Farrell 2008; Thomas et al. 2016). The species' tolerance to a physical environmental variable, such as temperature, generally follows a curved pattern where the optimum is reached at the top of the curve at some intermediate environmental values (Eppley 1972). When the variable moves away from the optimum the decrease in fitness is generally steeper above the optimum than below (Diekmann et al. 2012; Eppley 1972; Pörtner and Farrell 2008). As such, the variable

will have the greatest effect on population dynamics in areas where the variable's range also covers suboptimal conditions, where the species' tolerance to the variable has a steep monotonic response.

Biotic drivers

Species can influence each other through biotic interactions and can themselves also be influenced through intraspecific effects. The interaction effects can be negative through processes such as predation or competition for resources, or positive through facilitation. Together both long-term effects of abiotic variables and population- and community level processes explain the functioning of communities (Salo et al. 2019). Properly identifying biotic interactions can be challenging in the presence of environmental effects, especially if the important environmental variables are autocorrelated. Thus, accounting for abiotic effects is required to properly identify biotic interactions (Ripa and Ives 2003, 2007). Phytoplankton have been shown to have different biotic interactions in an open and a coastal area (Griffiths et al. 2016), highlighting the importance of also considering biotic interactions.

1.4 Observation error

To reliably estimate the effect of extrinsic variables and density dependence in population dynamical models, some considerations need to be made if a large amount of observation error is present (Knape 2008), which is suggested to be typical for marine data (Hampton et al. 2013; Scheef et al. 2013). Otherwise, there is a risk that density dependence (b in Equation 1) is biased toward zero, leading to spurious detection of strong density dependence where there is none (*i.e.* when $b = 1$; Knape and de Valpine 2012). In the presence of observation error, also the estimation of extrinsic effects and their uncertainties can be affected, especially when there is strong autocorrelation in the extrinsic variables (Lindén and Knape 2009). Extending the simple AR or MAR model to a multivariate state-space model (SSM) allows us to simultaneously account for both observation and process error (Durbin and Koopman 2012).

The observation process can in itself be influenced by extrinsic variables, such as weather. Prevailing wind conditions can *e.g.* affect the vertical and horizontal distribution of plankton (Kanoshina et al. 2003). Hence, successful analysis of the large-scale dynamics require thorough modelling and consideration of the sampling process.

1.5 Aims

Numerous experimental studies have demonstrated which physical conditions have an impact on plankton populations. Additionally, long-term monitoring data sets investigated through trend analyses and descriptive multivariate analyses have documented changes in plankton populations and communities, which are thought to be linked to changes in environmental conditions (Mäkinen et al. 2017; Suikkanen et al. 2013; Wasmund et al. 2011). However, few studies have used monitoring data to explicitly link plankton population dynamics in the sea to physical conditions using population dynamical models, while aiming for high taxonomical resolution and accounting for a trend *sensu* Granger causality (*cf.* Barraquand et al. 2018). Hence, this thesis is an extension to the existing vast literature on changes in plankton populations and communities. Bridging the gap between patterns in observational data and experiments, each of the four chapters is a step towards understanding what drives natural plankton population dynamics.

I The main aim of my thesis is to quantify the large-scale effects and impacts of key physical variables on the annual variation in phyto- and zooplankton populations in the Baltic Sea. This includes examining the relative contribution of anthropogenic and density-dependent factors in explaining population fluctuations, while applying the logic of Granger causality for identifying effects of extrinsic variables.

II The second aim is to explicitly account for sources of observation error by modelling the observation process, which should ultimately support the aims outlined above by reducing various biases. As some physical processes also affect the small-scale dynamics of the organisms, such as vertical placement or phenology, successful analysis of large-scale dynamics require thorough consideration of the data and modelling of the observation process. The exact definition of observation error in the present work is applied loosely, and the definition is tied to the ecological question, spatio-temporal scale of the investigated system and to the available data. In general, each chapter is an example on how to consider this issue.

2 Material and Methods

2.1 The Baltic Sea

The Baltic Sea is a semi-enclosed water basin in northern Europe. Due to its brackish water nature and geologically young age, the area has relatively few dominant taxa, and many taxa of marine and freshwater origin exist at the edge of their salinity tolerance (Johannesson and André 2006; Reusch et al. 2018). The chapters of my thesis span three spatial scales located in the northern Baltic Sea (Fig. 1). Chapter I investigates multiple spatial scales, spanning over the largest area including areas from the Gotland Basin in the south to the Bothnian Bay in the north. Chapter II investigates the Gulf of Finland, while chapter III and IV focuses one extensively studied coastal station within that area.
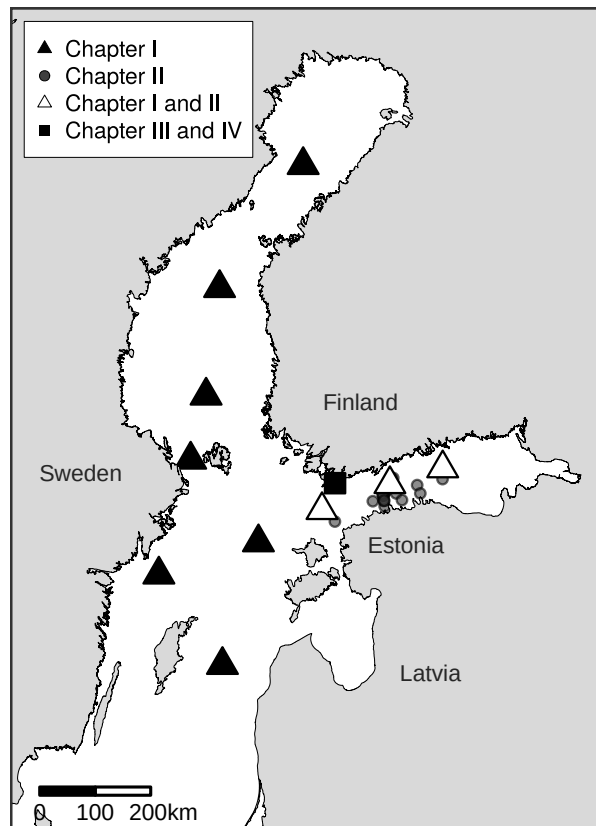

Figure 1: The stations used to gather the plankton and zoobenthic data used in chapters I–IV. The legend shows the stations that were used in each chapter.

The surface salinity in the whole investigated area ranges from ca. 3 to 7.5, while it is ca. 5.6 in the Gulf of Finland (Andersen et al. 2017). All of the basins notoriously suffer from eutrophication (Andersen et al. 2017). Studies have indicated that the salinity has decreased and that the temperature has increased since 1979 for some of the basins (Almén et al. 2017; Suikkanen et al. 2013). Predictions for the Gulf of Finland suggest that annual average temperatures could increase by 2–4°C and that the salinity could decrease by 1–2 by the year 2100 (Meier et al. 2012).

2.2 Brief outline of the chapters

In all chapters, I analyse time-series data and focus on different aspects of planktonic taxa and communities, moving from a simple model system with six phytoplankton taxa (**I**) to a community model with multiple trophic levels, including both cladocerans and copepods and benthic taxa (**IV**). Whereas all approaches in some way account for or explicitly model the observation process, chapters I, II and IV specifically implement uni- or multivariate autoregressive state-space modelling. The outline of the statistical analyses included in each chapter and the temporal scale are summarised in Table 1.

Chapter I considers the spatial scale of phytoplankton populations and compares three spatial scales within the Baltic Sea (the entire investigated area, five sub-basins, and all stations individually) using six model taxa from ten stations. The study also includes different structures of spatial environmental correlation, with three structures considered for the process error covariance matrix (**Q** in equation 3): compound symmetry, autoregressive error structure and no process error correlation (diagonal **Q**). Our main hypothesis was that the intermediate spatial scale would be the most supported alternative, and that synchrony between the populations should decrease with increasing distance between the stations. The thought was that the hydrography and the environmental conditions would be similar within the investigated basins. The plankton biomass data were gathered annually between July and the end of September as part of the national monitoring scheme carried out by the Finnish Environment Institute. The data excludes the spring bloom and captures only part of the seasonal occurrence of the chosen taxa (Fig. 2).

Chapter II focuses on identifying extrinsic drivers of 30 taxa of auto- and heterotrophic plankton and one ciliate species in the Gulf of Finland. The study combines plankton data from two sampling sources (ferrybox and integrated sampling) and creates time-series of annual

log-scaled mean plankton biomasses using an initial day-level observation model. The day-level observation model also accounts for potential biases caused by wind and timing of the sampling. The resulting time-series are further used for estimating the effects of extrinsic variables, applying univariate SSMs. The data for chapter II partially overlaps with that of chapter I, but includes also additional integrated and ferry-box samples provided by the Estonian Marine Institute and the Marine Systems Institute (Tallinn University of Technology). The aim was to investigate which extrinsic variables influenced the taxa, particularly to see if they affected the species and genera the same way within plankton classes. I also wanted to see if the species and genus level results corresponded to the results of previous trend and multivariate analyses in the area using only a subset of the data (see Suikkanen et al. 2013).

Chapters III and IV focus on one coastal station in the Gulf of Finland. Both chapters used the same zooplankton time-series gathered and analysed by Tvärminne Zoological Station (University of Helsinki) and Finnish Environment Institute (described in Viitasalo 1992b). Chapter III uses Generalized Additive Models (GAM) to first model the phenological and between-year patterns of abundance in five groups of zooplankton. The fitted model was further used to calculate annual estimates of the start and end of the season, the length of the season and peak abundances (Fig 2c). Patterns in these derived variables were subsequently investigated. As temperatures have increased in the area, we expected to see a shift towards earlier occurrences of zooplankton as temperatures affect hatching of resting eggs (Katajisto et al. 1998).

Chapter IV used both a zooplanktonic and a zoobenthic time-series. The zooplankton data were the same as in chapter III, but the data were aggregated to only include calanoid copepods and cladocerans (mainly *Bosmina*). The benthic time-series has previously been analysed by Rousi et al. (2013) and Hewitt et al. (2016). The main aim of chapter IV was to contrast different alternatives of benthic-pelagic species interactions while simultaneously accounting for environmental variables. We compared four alternative configurations for the community interactions where alternatives included a) interactions within zoobenthos and by zoobenthos on zooplankton, b) only zoobenthic taxa affecting zooplankton, c) no benthic-pelagic interactions but interactions between zoobenthic taxa allowed and finally d) no interactions. I expected that the benthic species would affect the pelagic zooplankton through predation on their benthic resting eggs (Albertsson and Leonardsson 2001; Viitasalo 2007).

Table 1: Overview of the studies, their temporal scale, the taxa studied, response variables (y), extrinsic variables (x) and statistical methods applied.

Ch.	Taxa	Years	y	Scale	x	Method
I	*Chrysochromulina, Hemiselmis, Plagioselmis prolonga, Pseudopedinella tricostata, Pyramimonas, Teleaulax*	1979–2015	Taxa μL^{-1}	Annual		SSM, AICc
II	24 phytoplankton taxa, 6 heterotrophs and *Mesodinium rubrum*	1993–2016	Taxa μL^{-1}	Intra-annual	Wind	GAMM
			Mean log biomass	Annual	Temp, sal, strat, nutrients, ice	SSM, AICc
III	*Acartia* spp., *Eurytemora affinis, Temora longicornis,* cladocerans and rotifers	1966–2006	Ind. m^{-3}	Annual	temp., sal., strat.	GAM
		1967–2005	Peak abundance (Ind. m^{-3}) and season length, start and end	Intra-annual	Temp, ice	GLS
IV	Cladocerans, copepods, amphipods, polychaetes, *Marenzelleria*, and *Limecola balthica*	1966–2007	Ind m^{-3} and Ind. m^{-2}	Annual	Temp, sal, O_2	SSM, AICc

2.3 State-Space Models

All state-space models were fit using the MARSS package in R by Holmes et al. (2018, 2012). More detailed descriptions on starting values, parametrisation, fitting procedures and model checking can be found in the relevant chapters. The hypotheses in each study were investigated using model selection where candidate models were compared using the Akaike information criterion for small sample size (AICc) (Burnham and Anderson 2002). Model selection was applied for comparison of multiple spatial scales and variance-covariance structure in the process error (I), comparisons of multiple extrinsic variables (II, IV) and a comparison of four hypothesised configurations for the biotic interactions (IV). Models were considered relevant if AICc was at least 2 units smaller, and indicative if AICc was smaller at all compared to the null model in chapter II. In chapters I and IV a difference of 2 AICc was used to distinguish the top model or models.

A density dependent process model, describing two underlying log biomass states is described in the introduction (Equations 3 and 4). Below I link it to an observation model (Equation 5), together with its appurtenant error structure (Equation 6). The observation model (Equation 5 and 6) is written out in Equations 7 and 8 to correspond to a scenario where the two states ($\mathbf{x}_t$) in Equation 3 are described with 2 replicated time-series each.

$$\boldsymbol{y}_t = \boldsymbol{Z}\boldsymbol{x}_t + \boldsymbol{a} + \boldsymbol{v}_t \tag{5}$$

$$\boldsymbol{v}_t \sim N(0, \boldsymbol{R}) \tag{6}$$

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix}_t = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}_t + \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} + \begin{bmatrix} v_1 \\ v_2 \\ v_3 \\ v_4 \end{bmatrix}_t \tag{7}$$

$$v_t \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} r_1 & 0 & 0 & 0 \\ 0 & r_1 & 0 & 0 \\ 0 & 0 & r_2 & 0 \\ 0 & 0 & 0 & r_2 \end{bmatrix} \right) \tag{8}$$

The underlying state variables ($\mathbf{x}_t$) in Equation 3 are linked to the four mean zero standardised log scaled observation time-series ($\mathbf{y}$) by

using the $\mathbf{Z}$ matrix. The 2×4 vector $\mathbf{a}$ can be used to allow for differing intercepts of the $\mathbf{y}$ observational time-series within one state variable or set to 0 if the time-series are true replicates. The observation model also includes its own error structure with zero mean and multivariate normally distributed variance-covariance matrix $\mathbf{R}$ (4×4).

As the modelling of the observation process and accounting for observation error (v) was one of the main aims of the thesis its handling is described in greater detail in the next section. In all studies, the structure of the observation error was diagonal, assuming no correlation in the errors.

2.4   Observation error

An inherent challenge of state-space modelling is the partitioning between observation and process error variances. Even simple SSMs can suffer from estimation problems (Auger-Méthé et al. 2016), especially as the variance partitioning can be challenging in the absence of replicates (Dennis et al. 2010; Humbert et al. 2009). To accommodate this issue, we apply individual approaches for each chapter, depending on the question and the data (**I**, **II** and **IV**). While the time-series in chapter I was practically unreplicated, and the finest spatial scale considered was station-specific, a few spatial replicates were used to facilitate the partitioning of the process- and observation error (same location and season, different day). The same logic was applied to a larger extent to the zooplankton data in chapter IV by using data from three months and scaling each month using the scaling vector $\mathbf{a}$ to account for phenological change. Here, however, the observation error variances for the two included zooplankton groups were fixed using data from a small field campaign. As the benthic data were replicated, we estimated a separate observation error term for each of the four benthic taxa. In the second chapter, we used a day-level GAM to estimate annual mean log biomass together with standard errors (SE). The squared SE were subsequently included into the final univariate SSM as time-varying observation error variances.

I mainly used the annual scale for all chapters, but as plankton are short-lived and present seasonal succession, I needed to account for intra-annual variability to achieve reasonable annual estimates for further analysis of the extrinsic variables of interest (**II–IV**). To account for the annual succession (phenology pattern), while estimating annual biomass (**II**) or abundance (**III**), as well as cardinal dates (**II** and **III**), I used generalised additive models (GAM) with differing assumptions in both chapters II and III. In chapter II, I assumed that the phenology pat-

terns were constant between years for a given taxon. The main interest was to achieve a reasonable annual estimate for the plankton biomasses and to investigate potential effects of daily wind on the observed plankton biomasses (Fig. 2b). In chapter III, however, the main focus was on cardinal dates such as the start, end and length of the season, subsequently investigating these variables in a second step (Fig. 2c). Thus, variation in the timing of the cardinal dates were of primary interest. In both chapters, the GAM was fitted using a log-link with Tweedie error distribution using the mgcv package in R (Wood 2011, 2017; Wood et al. 2016). In the pure SSM approach of chapter IV, seasonality was accounted for using different intercepts (**a** in Equation 5) for different months of zooplankton data included. The phenology was considered to be a lesser issue in chapter I as the temporal window for the chosen taxa had relatively flat phenology in their late summer biomass (Fig. 2a).
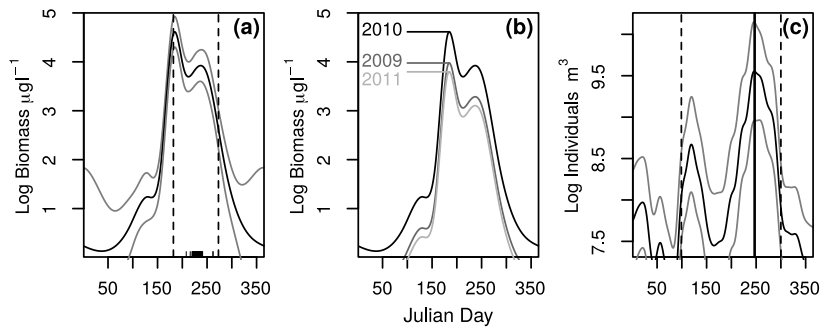

Figure 2: Panel (a) shows the estimated annual phenology (black) together with 95% CI (grey) for *Chrysochromulina* spp. (2010 at station LL7) using the day-level observation model in chapter II. The vertical lines indicate the temporal window used in chapter I for capturing the late summer biomass and the rug indicates the individual observations. The lines in panel (b) correspond to the one in panel (a) but illustrate how variation in annual biomass (years 2009–2011) was modelled accounting for phenology. The horizontal lines illustrate how the time-series of mean biomasses in chapter II were constructed using annual intercepts. Panel (c) illustrates the annual phenology for *Acartia* spp. copepodites for 1998 and the vertical lines from left to right correspond to when the population reached 20% of the peak abundance, the peak abundance and when the population declined below 20% of peak abundance.

2.5 Extrinsic variables

Extrinsic variables were investigated in all chapters, either directly or by interpreting the correlation of the process error. In chapters II and III, the extrinsic variables were included applying the Granger causality principle, *i.e..* the effect preceded the cause. In chapter II, the temperature, salinity and stratification variables included in the annual scale investigation were tailored to the timing of the most rapid population increase 0–59 days prior to the day of the median biomass for each taxon. In the intra-annual model in chapter III the temperature, salinity and stratification considered were from 14 days prior to the sampling event of the zooplankton. In chapter IV, I first used univariate SSMs and model selection to choose the most relevant annually scaled anomalies (from salinity, temperature and oxygen) to include in the full community model.

All model fitting and data processing were done in R (R Core Team 2017). The packages used for the summary and the chapters include: plyr (Hadley Wickham 2011), reshape2 (Hadley Wickham 2007), data.table (Dowle and Srinivasan 2018), gamm4 (Wood and Scheipl 2017), oce (Kelley and Richards 2018) and ggplot2 (Hadley Wickham 2016), zoo (Zeileis and Gabor Grothendieck 2005), nlme (Pinheiro et al. 2018), rgdal (Roger Bivand et al. 2019), optimx (Nash and Varadhan 2011).

3 Results and Discussion

3.1 The spatial scale of plankton population dynamics

The spatial scale, data quality and the ecological scale of the question all affect the interpretation of ecological data. Phytoplankton display synchrony over large geographical distances (Defriez and Reuman 2017), and chapter I shows synchronous patterns of biomasses in six model taxa in the Baltic Sea. When comparing models with multiple spatial structures as well as structures for spatial correlation, the most parsimonious models either included one state for the entire investigated area or multiple states with very high spatial correlation (> 0.92). The spatial correlation structure of the process error (**Q**) varied between compound symmetry and the autoregressive structure, and the alternative without spatial correlation got no support (Fig. 3).

Large scale synchrony can imply that all populations are part of the same panmictic population, or can arise from dispersal between subpopulations. Dispersal between the ten considered populations is not very likely, considering the large spatial extent of the study and small

size of the plankton (Fig. 1). But even isolated sub-populations can be synchronised by correlated environmental forcing, known as the Moran effect (Moran 1953). Large-scale synchrony can arise even if the density dependence is not the same in all sub-populations and there is variation in the local environmental effects (Sæther et al. 2007). The autoregressive coefficient ("*density dependence*") was always judged as uniform across all sub-populations in the most parsimonious model; either the coefficient was equal for all states, or the population was considered as panmictic. Defriez and Reuman (2017) observed global patterns of synchrony in plankton using chlorophyll *a* data, attributed to mixing processes described by temperature. The synchrony observed in their study was higher in the open ocean compared to coastal zones. As the basins included in chapter I are different in many of their physical properties important for plankton, such as salinity and nutrient conditions (Andersen et al. 2017) temperature and the related stratification are likely synchronising variables. The idea of basin level synchrony did not receive conclusive support in any taxa, but the five state option was among the top models, together with the ten and one state option, in *Pseudopedinella tricostata* and *Teleaulax* spp.
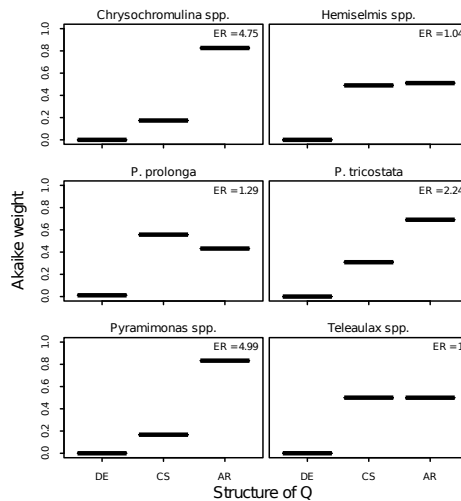

Figure 3: The summed Akaike weights for models with different covariance structure (matrix **Q** in Equation 4) of the process error: DE no spatial correlation, CS compound symmetry, AR autoregressive. The results are based only on the models with five and ten states. The evidence ratios (ER) for the best versus the second best option are displayed in the upper right corners of the panels (Reproduced from chapter I: Forsblom et al. 2019a).

Investigating large scale effects using plankton data from multiple stations could, depending on the ecological question, facilitate analysis, especially in cases where replicates are lacking. In cases with longer time-series, such as for *Chrysochromulina* spp., higher resolution patterns were discernible, and the ten-state model option with high spatial correlation was favoured (Fig. 3). However, if more noise was added to the most parsimonious ten-state model, the one state panmictic model became the most parsimonious one. In line with this finding, I applied the logic of one population in chapter II, using only the Gulf of Finland.

3.2 Extrinsic drivers of plankton population dynamics

Intra-class differences

I detected environmental effects or tendencies in 16 of the 31 investigated plankton taxa in chapter II, and together these taxa represent two thirds of the sampled summer community. Of the observed effects the investigated chrysophytes, *Dinobryon faculiferum* and *Pseudopedinella* spp. had opposite effects of salinity on mean biomass, positive and negative respectively (Fig. 4). Using a subset of the data analyses in chapter II, Suikkanen et al. (2013) have previously shown that chrysophytes have increased in the Gulf of Finland, and that they were negatively correlated with salinity. In their data, *Pseudopedinella* spp. made up the bulk of the biomass of the chrysophytes, and our taxon level study does indeed confirm a negative salinity effect on the biomass of *Pseudopedinella* spp. Aggregating the taxa to chrysophytes thus masks the salinity effects on *D. faculiferum*, as it coincidentally has lower biomass. Other intra-class differences arouse within the cyanophytes, where the temperature effects varied, with positive tendencies on the mean biomass of *Aphanizomenon* spp. and *Woronichinia* spp. and a negative effect of temperature on the mean biomass of *Snowella* spp. (Fig. 4). Additionally, the mean biomasses of both *Snowella* spp. and *Woronichinia* spp. were influenced negatively by stratification. The colonial *Snowella* and *Woronichinia* spp. are known to be more prevalent during turbulent times of the season (Laamanen 1997).

Future changes in plankton biomass in the Gulf of Finland

The variability in annual salinity, temperature and stratification experienced by the plankton taxa during 0–59 days before reaching median biomass was relatively low. As salinity has been projected to decrease by 1–2 units and temperature to increase by 2–3°C (Meier et al. 2012), the
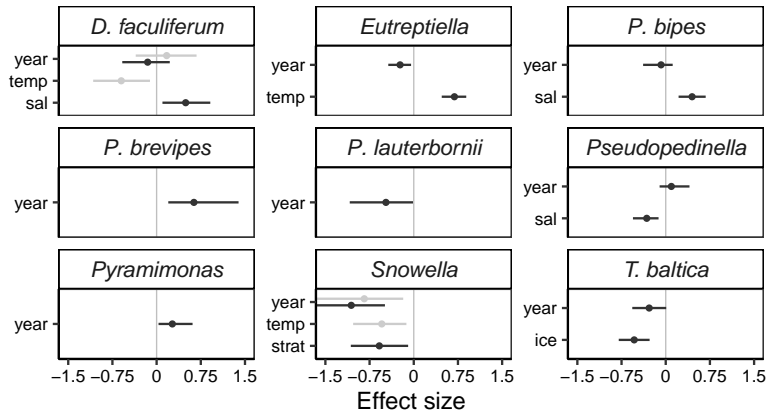
Figure 4: Estimated parameter effects of the z-scored environmental co-variates on the annual mean biomasses in the most parsimonious models (black). Competing models are shown in grey. The error bars indicate 95% confidence intervals. Covariates: temp = temperature, sal = salinity, strat = stratification index, ice = number of days with ice cover. All models also include a partial temporal trend (year) (Reproduced from chapter II: Forsblom et al. 2019b).

changes for individual species can thus be substantial. These changes are beyond the variability observed in chapter II and would correspond to approximately a 3.9–7.8 SD decrease in salinity and a 2.3–3.4 SD rise in temperature. In the light of the point estimate effects for the chrys-ophyte *D. faculiferum* and the dinophyte *Protoperidinium bipes*, the predicted salinity decrease would correspond to ca. 84–98% decrease in mean biomass. The expected increase in temperature would similarly be beneficial for taxa, such as euglenophyte *Eutreptiella* spp. (Fig. 4).

There was also an indication of an ongoing temporal shift in the community possibly linked to salinity. The effects were not always significant, but all taxa with a positive effect of salinity on mean biomass also had negative partial trends, while the opposite was true for taxa with positive effects of salinity. Studies in the Bothnian Bay and Bothnian Sea areas have linked community changes in plankton to salinity (Kuosa et al. 2017), while Olli et al. (2011) showed that temporal change, instead of salinity, better explained changes in community composition in the northern Baltic.
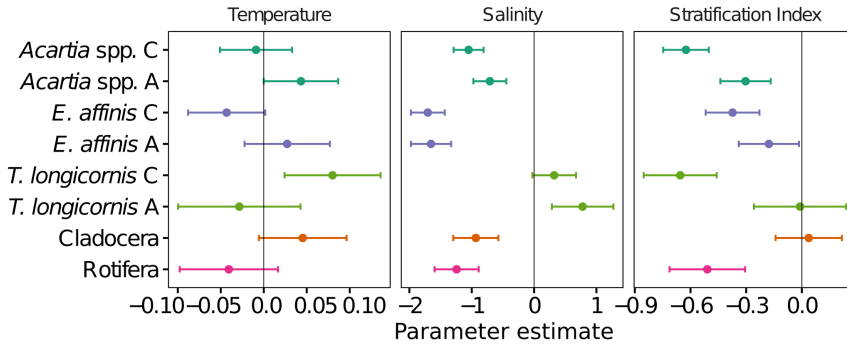
Figure 5: The effects of the environmental covariates on the intra-annual zooplankton abundance estimates using GAM. The bars are 95% confidence intervals.

Accounting for extrinsic effects in annual abundance estimates for zooplankton

All salinity effects on abundance observed in zooplankton, both in chapter III and IV were negative, with the exception of *Temora longicornis* (III) that is known to prefer higher salinities (Holste et al. 2009; Hänninen et al. 2003) (Fig. 5). The salinity preferences of the zooplankton taxa in the area using the first part of the time-series (> 1984) have been previously investigated in great detail by Viitasalo (1992b) and Viitasalo et al. (1994, 1995). The studies highlight the importance of hydrographical conditions in structuring the population and suggest that some of the observed dynamics can be due to movements of the water layers (Viitasalo et al. 1995). Zooplankton are generally known to form horizontal patches and to migrate vertically, experiencing a wide range of physiochemical variables diurnally (Almén et al. 2014; Folt and Burns 1999), and the present study only focuses on the upper 25 meters of the water column. Thus, the effects of salinity in the abundance model likely also reflects advection. The main aim of the abundance model, however, was to account for the environmental variables to achieve reliable estimates of the abundance as the main interest lay with investigating the phenology of the taxa investigated in the subsequent step.

Distinguishing temperature effects on zooplankton abundances (**III**) also proved difficult and it seems the temperature effects were confounded by the seasonality pattern also included in the GAM. In addition, previous studies have indicated that both salinity and temperature effects vary during the season in a non-linear fashion (Klais et al. 2017;

Viitasalo et al. 1994), thus leading to a risk that potential effects are averaged out. When I investigated the annual temperature effect on the abundance of copepods with a narrower temporal window from June to August (**IV**), the most parsimonious model included a positive effect of temperature on abundance.

Accounting for wind effects on the observation process

In the same manner as zooplankton, also the horizontal and vertical distribution of phytoplankton can be influenced by physical forcing. Many phytoplankton taxa are known to aggregate in specific layers of the water column especially during low mixing (Klausmeier and Litchman 2001). For example, *Nodularia spumigena* aggregates at the surface during calm conditions and can prove difficult to sample representatively (Kanoshina et al. 2003). Mixing of the surface water can thus potentially affect the sampled abundance by dispersing aggregates in the water column. There were 16 detected effects of mean daily wind speed on the mean biomass of the investigated plankton taxa in the day-level observation model (**II**). There was no apparent common pattern in which taxa were affected related to taxonomic rank, size or mobility. Whereas wind indeed can affect plankton population dynamics on a short timescale, *e.g.* by influencing nutrient availability (Rantajärvi et al. 1998), the day-level effects in this study were viewed as noise as the main goal was the abundance dynamics on annual scale.

Density dependence, or perhaps not?

The classical interpretation of density dependence assumes it reflects intraspecific competition within a population (Royama 1992). The results in chapter I and II suggest density dependent dynamics in most of the taxa, and previous studies have indeed identified density dependence in plankton (Barraquand et al. 2018; Ohman and Hirche 2001). However, as our temporal scale spans a year it is implausible that this reflects anything else than a statistical property of the time-series. It is more plausible that the density dependence detected for the benthic taxa (**IV**) reflect real intraspecific competition (**IV**). Some of the investigated taxa can be long lived, such as *Limecola balthica* that can reach an age of 30 years (Segerstråle 1960). The benthic community in the area is dependent on sedimenting resources derived from primary production that can be limiting (Ehrnsten et al. 2019). Species additionally compete for space and studies have shown that the species settling first after disturbance can be the main factor affecting subsequent dynamics

(Eriksson Wiklund and Andersson 2014).

Biotic interactions

The most parsimonious model for the biotic interaction included only the interactions within the benthic taxa and no biotic interactions between zoobenthos and zooplankton (the matrix **B** Equation 3). These biotic interactions had a one-year lag, which likely was not ideal, especially for zooplankton. Cladocerans in lakes have been shown to contribute to the resting egg standing stock mostly at the end of summer when the environment becomes less favourable (Chen and Folt 1996). In the investigated area zooplankton nauplii emergence and hatching experiments suggest that the hatching number peaks in warm water in autumn (Katajisto et al. 1998), and field data suggest that resting eggs in the sediment contribute to copepod recruitment in spring (Viitasalo 1992a). Thus, how well potential predation on eggs is reflected in the summer abundances the following year can be discussed.

Whereas no direct interactions were observed between zooplankton and zoobenthos, the unexplained process error variance can give clues of intra-annual correlations. The process error correlation between the investigated taxa were positive between cladocerans and copepods and within the benthos (with few exceptions), whereas the interactions between pelagic and benthic taxa were generally negative (Table 2). This can imply that the taxa are correlated due to similar environments within the pelagic and the benthic systems. The negative correlation between zooplankton and zoobenthos could indicate that zooplankters influence the resource availability of zoobenthos by consuming the primary production before it has reached the sediment (Tamelander et al. 2017). The highest negative correlations are between copepods and amphipods, and *Monoporeia affinis*, in particular, is known to rely on newly sedimented material (Eriksson Wiklund and Andersson 2014), and the influx of organic matter from the pelagic zone has likely been finite in the area in recent years (Ehrnsten et al. 2019). However, as all correlations except for the one between copepods and cladocerans were weak, this is speculation.

Table 2: The correlation matrix for the most parsimonious model without benthic-pelagic interaction (**IV**). The correlation matrix is calculated using the variance-covariance matrix in the process error (q parameters in Equation 4).

	L. balthica	Poly.	Marenz.	Amphi.	Cope.	Clado.
L. balthica	1	0.166	0.306	0.091	-0.114	-0.359
Polychaeta	0.166	1	0.255	0.431	-0.320	-0.050
Marenzelleria	0.306	0.255	1	0.160	0.167	-0.115
Amphipoda	0.091	0.431	0.160	1	-0.419	-0.140
Copepoda	-0.114	-0.320	0.167	-0.419	1	0.690
Cladocera	-0.359	-0.050	-0.115	-0.140	0.690	1

Variability in biotic interactions

It is important to remember that biotic interactions are not static through time and can be subjected to change. Species interactions have been suggested to vary due to environmental variables, such as periods of high or low temperature and periods of high and low nutrient availability, as well as due to changes in species composition or succession patterns (Francis et al. 2012, 2014). A change in the species' phenology can lead to shifts in the strength of interaction as a result of increased mismatch between species (Cushing 1990). Interactions can also occur in abrupt non-linear ways leading to shifted communities (Beaugrand et al. 2019). The interactions discussed and presented here are average interactions spanning 1966 to 2007. Introduction of new species can also lead to changes in interactions and in the early 1990s the study area was colonised by *Marenzelleria* spp. (Kauppi et al. 2015), and specifically *M. arctia* is thought to occur at the investigated station (Kauppi et al. 2018). The taxon is considered to have invaded a free niche, and not competing for resources with other native taxa (Karlson et al. 2015). *M. arctia* is suggested to be a welcome invader as it enhances oxygen conditions in the sediment through bioturbation (Norkko et al. 2011). Changes in biotic interactions over the investigated time are thus likely, and cannot be ruled out; however, due to data limitations this was not within the scope of chapter IV.

3.3 Phenology

Phenology changes in mesozooplankton

Many data sets lack observations from the winter months in temperate regions. Sampling is generally more challenging in winter and a

common view has been that the winter resets the community especially in regions with ice-cover (see Hampton and Schindler 2006). This is a simplification and with climate warming there have been signs of increasing activity during winter and improved wintertime survival in marine environments (Schlüter et al. 2010). On the other hand, warming can also lead to increased respiration and negatively influence oxygen availability (Panigrahi et al. 2013). Chapter III investigated the start of the season for five taxa of zooplankton and demonstrates that *Acartia* spp. copepodites became earlier in spring. The phenomenon of earlier occurrence has been demonstrated widely in zooplankton (Mackas et al. 2012 and references therein), as well as in other organisms in both aquatic and terrestrial systems such as plants, birds and insects (Edwards and Richardson 2004; Parmesan and Yohe 2003; Thackeray et al. 2016). Increased zooplankton grazing is seen in phytoplankton as a decrease in the sizes of individuals and a decrease in large sized species (Sommer and Lewandowska 2011). As warming can increase the densities of overwintering zooplankton this can also influence the phytoplankton community composition (Sommer and Lewandowska 2011). In the investigated area recruitment in spring occurs both from resting eggs and from overwintering individuals (Katajisto et al. 1998).

In recent years autumns have become warmer and we expected the warm conditions to extend the seasonal occurrences of the investigated zooplankton groups by enabling more generations. Contrary to our expectations, the season did not become longer over the whole investigated period, with the exception of adult *T. longicornis*. The end was negatively correlated with temperature in *T. longicornis* copepodites and positively in cladocerans. It has been previously shown that high temperatures can influence the resting egg production in autumn for cladocerans (Chen and Folt 1996). The peak abundances of adult *T. longicornis* also declined over the investigated period. The observed shift in occurrence and abundance can potentially affect other trophic levels, as copepods in the area are an important food source for planktivorous fish and mysid shrimps (Flinkman et al. 1998). Mysid shrimps shift to feed on zooplankton when they reach a certain size (Viherluoto et al. 2000), thus changed timing of zooplankton peaks could affect their predator-prey dynamics.

Accounting for phenology in the observation model

Warming has not only influenced the emergence of zooplankton, but also influenced the spring bloom and phenology of phytoplankton species (Edwards and Richardson 2004; Hjerne et al. 2019; Scharfe and Wilt-
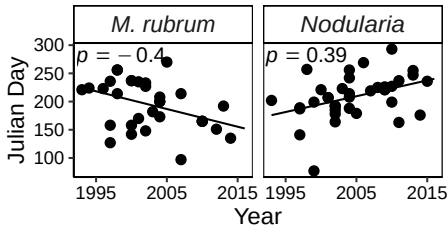
Figure 6: The most extreme outliers (> 2 SD) from the day-level observation model (filled circles). Line shows the regression of Julian Day against year with the pearson correlation p.

shire 2019). I did not explicitly investigate and account for changes in timing of the annual biomass estimate in chapter II, but I did notice that a phenology shift might have taken place based on patterns in the residual diagnostics. An analysis of the most extreme positive residuals revealed that, eight out of 31 investigated taxa showed a negative correlation between Julian day and year (two taxa shown in Fig. 6). Hence, in the beginning of the time-series outliers occurred more often late in the season, and *vice versa*, suggesting earlier phenology. In contrast, the correlations for *Nodularia* spp. were positive, suggesting a shift to later timing of the peak. This is important to consider for monitoring if the investigated period is short and coincides with a period of high variability in timing, *e.g.* during times of rapid increase during the spring bloom.

4 Conclusions and future perspectives

The interpretation is tied to the scale of investigation (**I–IV**), whether it is the spatial scale, or species level investigated. In my thesis I primarily investigate drivers of plankton population dynamics using annual timescale. While the coarse scale leaves something to be desired, it was possible to quantify some extrinsic drivers influencing annual biomasses of phytoplankton and heterotrophs in the Gulf of Finland (**II**), changes in seasonality of zooplankton (**III**), as well as the interactions (or lack thereof) between zooplankton and zoobenthos (**IV**).

Especially when investigated on large spatial scale, phytoplankton populations from the northern Baltic Sea display high levels of synchrony and spatially correlated process error structure. A likely driver of these synchronous patterns spanning a large spatial scale and partially isolated populations is the Moran effect (**I**). Going further to investigate specific drivers in the Gulf of Finland population, the abiotic drivers with most numerous effects detected were temperature, salinity and stratification. These estimated environmental effects on the biomass in chapter II are substantial in relation to the variability of the drivers. In

light of projected future changes in the area, potential effects can thus be large. Knowing what happens to individual species and not only classes of plankton is important as phytoplankton traits can differ and also affect biogeochemical cycling (Litchman et al. 2015).

Identifying direct temperature effects proved challenging, as the succession patterns of many taxa overlap with the seasonal change in temperature. There were especially few temperature effects on zooplankton abundance in chapter III, while copepod abundances seem to be positively influenced on annual scale when the temporal window was restricted to three months (**IV**). All zooplankton taxa in the area were influenced by salinity, however, all the observed environmental effects were not necessarily direct effects influencing survival, growth or reproduction, but might also reflect physical forcing. In chapter II, I explicitly accounted for wind effects and in chapter III some of the environmental effects are likely attributable to advection. The observation model was crucial for handling phenology (**II–IV**) and for enabling flexible modelling of the standardised biomass and abundance units using the Tweedie distribution (**II**, **III**).

Changes in phenology were apparent or implied in both chapters II and III, and a noteworthy issue is how this can influence the interpretations of long-term trends. Many taxa have complicated seasonal patterns with multiple peaks making inter-annual comparisons more challenging (Scharfe and Wiltshire 2019). Thus, in the best case, changes in phenology only add noise to the investigation (**II**), but if the investigated temporal window is small it is possible to miss partial or entire abundance peaks. In that case, changes in temporal patterns in species densities can in the worst case only be a reflection of the changed timing. While there was an indication of phenology shifts also in phytoplankton (**II**), this needs to be explicitly confirmed and further investigated.

The final chapter on community interactions left some open questions and future opportunities of study, especially concerning the biotic interactions within the benthic community and potential temporal shifts in interactions. Studies on pelagic communities have shown that interactions are variable in time and space (Francis et al. 2012; Griffiths et al. 2016), and to fully understand the functioning of communities this needs to be considered.

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References

Albertsson, J. and Leonardsson, K. (2001). Deposit-feeding amphipods (*Monoporeia affnis*) reduce the recruitment of copepod nauplii from benthic resting eggs in the northern Baltic Sea. *Marine Biology*, 138:793–801.

Almén, A.-K., Glippa, O., Pettersson, H., Alenius, P., and Engström-Öst, J. (2017). Changes in wintertime pH and hydrography of the Gulf of Finland (baltic sea) with focus on depth layers. *Environmental Monitoring and Assessment*, 189(4).

Almén, A.-K., Vehmaa, A., Brutemark, A., and Engström-Öst, J. (2014). Coping with climate change? Copepods experience drastic variations in their physicochemical environment on a diurnal basis. *Journal of Experimental Marine Biology and Ecology*, 460:120–128.

Andersen, J. H., Carstensen, J., Conley, D. J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B. G., Josefson, A. B., Norkko, A., Villnäs, A., and Murray, C. (2017). Long-term temporal and spatial trends in eutrophication status of the Baltic Sea: Eutrophication in the Baltic Sea. *Biological Reviews*, 92(1):135–149.

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K.,

Legrand, C., Figueroa, D., Paczkowska, J., Lindehoff, E., Tysklind, M., and Elmgren, R. (2015). Projected future climate change and Baltic Sea ecosystem management. *AMBIO*, 44(S3):345–356.

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., and Mills Flemming, J. (2016). State-space models' dirty little secrets: even simple linear Gaussian models can have estimation problems. *Scientific Reports*, 6(1).

BACC II Author Team (2015). *Second Assessment of Climate Change for the Baltic Sea Basin.* Springer-Verlag, New York.

Barraquand, F., Picoche, C., Maurer, D., Carassou, L., and Auby, I. (2018). Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127(12):1834–1852.

Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., Kirby, R. R., Greene, C. H., Goberville, E., Otto, S. A., Reid, P. C., Stemmann, L., and Edwards, M. (2019). Prediction of unprecedented biological shifts in the global ocean. *Nature Climate Change*, 9(3):237–243.

Bruno, J. F., Carr, L. A., and O'Connor, M. I. (2015). Exploring the role of temperature in the ocean through metabolic scaling. *Ecology*, 96(12):3126–3140.

Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Sringer, New York, 2 edition.

Chen, C. Y. and Folt, C. L. (1996). Consequences of fall warming for zooplankton over wintering success. *Limnology and Oceanography*, 41(5):1077–1086.

Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., and Irigoien, X. (2014). Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES Journal of Marine Science*, 71(2):241–253.

Cloern, J. E., Abreu, P. C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J. O. R., Kahru, M., Sherwood, E. T., Xu, J., and Yin, K. (2016). Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. *Global Change Biology*, 22(2):513–529.

Cushing, D. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In *Advances in Marine Biology*, volume 26, pages 249–293. Elsevier.

Daufresne, M., Lengfellner, K., and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31):12788–12793.

Defriez, E. J. and Reuman, D. C. (2017). A global geography of synchrony for marine phytoplankton. *Global Ecology and Biogeography*, 26(8):867–877.

Dennis, B., Ponciano, J. M., and Taper, M. L. (2010). Replicated sampling increases efficiency in monitoring biological populations. *Ecology*, 91(2):610–620.

Dennis, B. and Taper, M. L. (1994). Density dependence in time series observations of natural populations: Estimation and testing. *Ecological Monographs*, 64(2):205–224.

Diekmann, A. B. S., Clemmesen, C., St. John, M. A., Paulsen, M., and Peck, M. A. (2012). Environmental cues and constraints affecting the seasonality of dominant calanoid copepods in brackish, coastal waters: a case study of *acartia*, *temora* and *eurytemora* species in the south-west Baltic. *Marine Biology*, 159(11):2399–2414.

Dowle, M. and Srinivasan, A. (2018). data.table: Extension of

'data.frame'. *R package version 1.11.4.*

Durbin, J. and Koopman, S. J. (2012). *Time series analysis by state space methods*. Oxford university press.

Edwards, M. and Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430(7002):881–884.

Ehrnsten, E., Norkko, A., Timmermann, K., and Gustafsson, B. G. (2019). Benthic-pelagic coupling in coastal seas – Modelling macrofaunal biomass and carbon processing in response to organic matter supply. *Journal of Marine Systems*, 196:36–47.

Eppley, R. W. (1972). Temperature and phytoplankton growth in the sea. *Fishery Bulletin*, 70:1063–1085.

Eriksson Wiklund, A.-K. and Andersson, A. (2014). Benthic competition and population dynamics of *Monoporeia affinis* and *Marenzelleria* sp. in the northern baltic sea. *Estuarine, Coastal and Shelf Science*, 144:46–53.

Flinkman, J., Aro, E., Vuorinen, I., and Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s:top-down and bottom-up processes at work. *Marine Ecology Progress Series*, 165:127–136.

Folt, C. L. and Burns, C. W. (1999). Biological drivers of zooplankton patchiness. *Trends in Ecology & Evolution*, 14(8):300–305.

Francis, T. B., Scheuerell, M. D., Brodeur, R. D., Levin, P. S., Ruzicka, J. J., Tolimieri, N., and Peterson, W. T. (2012). Climate shifts the interaction web of a marine plankton community. *Global Change Biology*, 18(8):2498–2508.

Francis, T. B., Wolkovich, E. M., Scheuerell, M. D., Katz, S. L., Holmes, E. E., and Hampton, S. E. (2014). Shifting regimes and changing interactions in the lake Washington, U.S.A., plankton community from 1962–1994. *PLoS ONE*, 9(10):e110363.

Granger, C. W. J. (1969). Investigating causal relations by econometric models and cross-spectral methods. *Econometrica*, 37:424–438.

Griffiths, J. R., Hajdu, S., Downing, A. S., Hjerne, O., Larsson, U., and Winder, M. (2016). Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*, 125(8):1134–1143.

Hadley Wickham (2007). Reshaping Data with the reshape Package. *Journal of Statistical Software*, 21(12):1–20.

Hadley Wickham (2011). The Split-Apply-Combine Strategy

for Data Analysis. *Journal of Statistical Software*, 40(1):1–29.

Hadley Wickham (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.

Hampton, S. E., Holmes, E. E., Scheef, L. P., Scheuerell, M. D., Katz, S. L., Pendleton, D. E., and Ward, E. J. (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, 94(12):2663–2669.

Hampton, S. E., Scheuerell, M. D., and Schindler, D. E. (2006). Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography*, 51(5):2042–2051.

Hampton, S. E. and Schindler, D. E. (2006). Empirical evaluation of observation scale effects in community time series. *Oikos*, 113(3):424–439.

Hewitt, J. E., Norkko, J., Kauppi, L., Villnäs, A., and Norkko, A. (2016). Species and functional trait turnover in response to broad-scale change and an invasive species. *Ecosphere*, 7(3).

Hjerne, O., Hajdu, S., Larsson, U., Downing, A. S., and Winder, M. (2019). Climate driven changes in timing, composition and magnitude of the Baltic Sea phytoplankton spring bloom. *Frontiers in Marine Science*, 6:482.

Holmes, E., Ward, E., and Scheuerell, M. (2018). Analysis of multivariate time-series using the marss package version 3.4. *NOAA Fisheries, Northwest Fisheries Science Center*.

Holmes, E. E., Ward, E. J., and Wills, K. (2012). MARSS: multivariate autoregressive state-space models for analyzing time-series data. *The R Journal*, 4:11–19.

Holste, L., St. John, M. A., and Peck, M. A. (2009). The effects of temperature and salinity on reproductive success of *Temora longicornis* in the Baltic Sea: a copepod coping with a tough situation. *Marine Biology*, 156(4):527–540.

Huisman, J., Codd, G. A., Paerl, H. W., Ibelings, B. W., Verspagen, J. M. H., and Visser, P. M. (2018). Cyanobacterial blooms. *Nature Reviews Microbiology*, 16(8):471–483.

Humbert, J.-Y., Scott Mills, L., Horne, J. S., and Dennis, B. (2009). A better way to estimate population trends. *Oikos*, 118(12):1940–1946.

Hänninen, J., Vuorinen, I., and Kornilovs, G. (2003). Atlantic climatic factors control decadal dynamics of a baltic sea cope-

pod *temora longicornis. Ecography*, 26(5):672–678.

Ives, A. R., Dennis, B., Cottingham, K. L., and Carpenter, S. R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, 73(2):301–330.

Johannesson, K. and André, C. (2006). Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology*, 15(8):2013–2029.

Kanoshina, I., Lips, U., and Leppänen, J.-M. (2003). The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (baltic sea). *Harmful Algae*, 2(1):29–41.

Karlson, A. M. L., Gorokhova, E., and Elmgren, R. (2015). Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. *Scientific Reports*, 5(9715).

Katajisto, T., Viitasalo, M., and Koski, M. (1998). Seasonal occurrence and hatching of calanoid eggs in sediments of the northern baltic sea. *Marine Ecology Progress Series*, 163:133–143.

Kauppi, L., Norkko, A., and Norkko, J. (2015). Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biological Invasions*, 17(7):2055–2074.

Kauppi, L., Norkko, A., and Norkko, J. (2018). Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats. *Journal of Sea Research*, 131:46–60.

Kelley, D. and Richards, C. (2018). oce: Analysis of Oceanographic Data. *R package version 0.9-23*.

Klais, R., Otto, S. A., Teder, M., Simm, M., and Ojaveer, H. (2017). Winter–spring climate effects on small-sized copepods in the coastal Baltic Sea. *ICES Journal of Marine Science*, 74(7):1855–1864.

Klausmeier, C. A. and Litchman, E. (2001). Algal games: The vertical distribution of phytoplankton in poorly mixed water columns. *Limnology and Oceanography*, 46(8):1998–2007.

Knape, J. (2008). Estimability of density dependence in models of time series data. *Ecology*, 89(11):2994–3000.

Knape, J. and de Valpine, P. (2012). Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance?: Density de-

pendence in the GPDD. *Ecology Letters*, 15(1):17–23.

Kremer, C. T., Thomas, M. K., and Litchman, E. (2017). Temperature- and size-scaling of phytoplankton population growth rates: Reconciling the Eppley curve and the metabolic theory of ecology. *Limnology and Oceanography*, 62(4):1658–1670.

Kuosa, H., Fleming-Lehtinen, V., Lehtinen, S., Lehtiniemi, M., Nygård, H., Raateoja, M., Raitaniemi, J., Tuimala, J., Uusitalo, L., and Suikkanen, S. (2017). A retrospective view of the development of the Gulf of Bothnia ecosystem. *Journal of Marine Systems*, 167:78–92.

Laamanen, M. J. (1997). Environmental factors affecting the occurrence of different morphological forms of cyanoprokaryotes in the northern Baltic Sea. *Journal of Plankton Research*, 19(10):1385–1403.

Lindén, A. and Knape, J. (2009). Estimating environmental effects on population dynamics: consequences of observation error. *Oikos*, 118(5):675–680.

Litchman, E., de Tezanos Pinto, P., Edwards, K. F., Klausmeier, C. A., Kremer, C. T., and Thomas, M. K. (2015). Global biogeochemical impacts of phytoplankton: a trait-based perspective. *Journal of Ecology*, 103(6):1384–1396.

Litchman, E. and Klausmeier, C. A. (2008). Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution, and Systematics*, 3:615–639.

Mackas, D., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M., Batten, S., Richardson, A., Johnson, C., Head, E., Conversi, A., and Peluso, T. (2012). Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Progress in Oceanography*, 97-100:31–62.

McQuatters-Gollop, A., Johns, D. G., Bresnan, E., Skinner, J., Rombouts, I., Stern, R., Aubert, A., Johansen, M., Bedford, J., and Knights, A. (2017). From microscope to management: The critical value of plankton taxonomy to marine policy and biodiversity conservation. *Marine Policy*, 83:1–10.

Meier, H. E. M., Andersson, H. C., Arheimer, B., Blenckner, T., Chubarenko, B., Donnelly, C., Eilola, K., Gustafsson, B. G., Hansson, A., Havenhand, J., Höglund, A., Kuznetsov, I., MacKenzie, B. R., Müller-Karulis, B., Neumann, T., Niiranen, S., Piwowarczyk, J., Raudsepp, U., Reckermann, M., Ruoho-Airola, T., Savchuk, O. P., Schenk, F., Schimanke, S., Väli, G., Weslawski, J.-M., and

Zorita, E. (2012). Comparing reconstructed past variations and future projections of the Baltic Sea ecosystem—first results from multi-model ensemble simulations. *Environmental Research Letters*, 7(3):034005.

Moran, P. A. (1953). The statistical analysis of the canadian lynx cycle. *Australian Journal of Zoology*, 1(3):291–298.

Mäkinen, K., Vuorinen, I., and Hänninen, J. (2017). Climate-induced hydrography change favours small-bodied zooplankton in a coastal ecosystem. *Hydrobiologia*, 792(1):83–96.

Nash, J. C. and Varadhan, R. (2011). Unifying Optimization Algorithms to Aid Software System Users: optimx for R. *Journal of Statistical Software*, 43(9):1–14.

Norkko, J., Reed, D. C., Timmermann, K., Norkko, A., Gustafsson, B. G., Bonsdorff, E., Slomp, C. P., Carstensen, J., and Conley, D. J. (2011). A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology*, 18(2):422–434.

Ohman, M. D. and Hirche, H.-J. (2001). Density-dependent mortality in an oceanic copepod population. *Nature*, 412(6847):638–641.

Olli, K., Klais, R., Tamminen, T., Ptacnik, R., and Andersen, T. (2011). Long term changes in the Baltic Sea phytoplankton community. *Boreal Environment Research*, 16:3–14.

Panigrahi, S., Nydahl, A., Anton, P., and Wikner, J. (2013). Strong seasonal effect of moderate experimental warming on plankton respiration in a temperate estuarine plankton community. *Estuarine, Coastal and Shelf Science*, 135:269–279.

Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918):37–42.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and (2018), R. C. T. (2018). nlme: Linear and Nonlinear Mixed Effects Models. *R package version 3.1-137*.

Pontavice, H., Gascuel, D., Reygondeau, G., Maureaud, A., and Cheung, W. W. L. (2020). Climate change undermines the global functioning of marine food webs. *Global Change Biology*.

Pörtner, H. O. and Farrell, A. P. (2008). Physiology and Climate Change. *Science*, 322:4.

R Core Team (2017). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna Austria*.

Rantajärvi, E., Olsonen, R., Hällfors, S., Leppänen, J.-M.,

and Raateoja, M. (1998). Effect of sampling frequency on detection of natural variability in phytoplankton: unattended high-frequency measurements on board ferries in the Baltic Sea. *ICES Journal of Marine Science*, 55(4):697–704.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., Hasler, B., Hinsby, K., Hyytiäinen, K., Johannesson, K., Jomaa, S., Jormalainen, V., Kuosa, H., Kurland, S., Laikre, L., MacKenzie, B. R., Margonski, P., Melzner, F., Oesterwind, D., Ojaveer, H., Refsgaard, J. C., Sandström, A., Schwarz, G., Tonderski, K., Winder, M., and Zandersen, M. (2018). The Baltic Sea as a time machine for the future coastal ocean. *Science Advances*, 4:eaar8195.

Ripa, J. and Ives, A. R. (2003). Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology*, 64(3):369–384.

Ripa, J. and Ives, A. R. (2007). Interaction assessments in correlated and autocorrelated environments. In *The impact of environmental variability on ecological systems.*, pages 111–131. Springer, Dordrecht.

Roger Bivand, Tim Keitt, and Barry Rowlingson (2019). rgdal: Bindings for the 'Geospatial'

Data Abstraction Library. *R package version 1.4-4.*

Rousi, H., Laine, A. O., Peltonen, H., Kangas, P., Andersin, A.-B., Rissanen, J., Sandberg-Kilpi, E., and Bonsdorff, E. (2013). Long-term changes in coastal zoobenthos in the northern Baltic Sea: the role of abiotic environmental factors. *ICES Journal of Marine Science*, 70(2):440–451.

Royama, T. (1981). Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecological Monographs*, 51(4):473–493.

Royama, T. (1992). *Analytical population dynamics*. Springer Science & Business Media.

Salo, T., Mattila, J., and Eklöf, J. (2019). Long-term warming affects ecosystem functioning through species turnover and intraspecific trait variation. *Oikos*.

Scharfe, M. and Wiltshire, K. H. (2019). Modeling of intra-annual abundance distributions: Constancy and variation in the phenology of marine phytoplankton species over five decades at Helgoland Roads (North sea). *Ecological Modelling*, 404:46–60.

Scheef, L. P., Hampton, S. E., and Izmest'eva, L. R. (2013). Inferring plankton community structure from marine and

freshwater long-term data using multivariate autoregressive models: Freshwater and marine data MAR models. *Limnology and Oceanography: Methods*, 11(9):475–484.

Scheef, L. P., Pendleton, D. E., Hampton, S. E., Katz, S. L., Holmes, E. E., Scheuerell, M. D., and Johns, D. G. (2012). Assessing marine plankton community structure from long-term monitoring data with multivariate autoregressive (MAR) models: a comparison of fixed station versus spatially distributed sampling data: Point versus spatial data MAR models. *Limnology and Oceanography: Methods*, 10(1):54–64.

Schlüter, M. H., Merico, A., Reginatto, M., Boersma, M., Wiltshire, K. H., and Greve, W. (2010). Phenological shifts of three interacting zooplankton groups in relation to climate change. *Global Change Biology*, 16:3144–3153.

Segerstråle, S. (1960). Investigations on Baltic populations of the bivalve *Macoma Baltica* (L): part 1; introduction; studies on recruitment and its relation to depth in Finnsih coastal waters during the period 1922-1959; age and growth. *Societas scientiarum Fennica*.

Sommer, U. and Lewandowska, A. (2011). Climate change and the phytoplankton spring bloom:

warming and overwintering zooplankton have similar effects on phytoplankton. *Global Change Biology*, 17(1):154–162.

Suikkanen, S., Pulina, S., Engström-Öst, J., Lehtiniemi, M., Lehtinen, S., and Brutemark, A. (2013). Climate change and eutrophication induced shifts in northern summer plankton communities. *PLoS ONE*, 8(6):e66475.

Sæther, B.-E., Engen, S., Grøtan, V., Fiedler, W., Matthysen, E., Visser, M. E., Wright, J., Møller, A. P., Adriaensen, F., Van Balen, H., Balmer, D., Mainwaring, M. C., Mccleery, R. H., Pampus, M., and Winkel, W. (2007). The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. *Journal of Animal Ecology*, 76(2):315–325.

Tamelander, T., Spilling, K., and Winder, M. (2017). Organic matter export to the seafloor in the baltic sea: Drivers of change and future projections. *Ambio*, 46(8):842–851.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., Elliott, J. M., Hall,

S. J. G., Harrington, R., Pearce-Higgins, J. W., Høye, T. T., Kruuk, L. E. B., Pemberton, J. M., Sparks, T. H., Thompson, P. M., White, I., Winfield, I. J., and Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611):241–245.

Thomas, M. K., Kremer, C. T., Klausmeier, C. A., and Litchman, E. (2012). A global pattern of thermal adaptation in marine phytoplankton. *Science*, 338(6110):1085–1088.

Thomas, M. K., Kremer, C. T., and Litchman, E. (2016). Environment and evolutionary history determine the global biogeography of phytoplankton temperature traits: Phytoplankton temperature trait biogeography. *Global Ecology and Biogeography*, 25(1):75–86.

Viherluoto, M., Kuosa, H., Flinkman, J., and Viitasalo, M. (2000). Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Marine Biology*, 136(3):553–559.

Viitasalo, M. (1992a). Calanoid resting eggs in the Baltic Sea: implications for the population dynamics of *Acartia bifilosa* (Copepoda). *Marine Biology*, 114(3):397–405.

Viitasalo, M. (1992b). Mesozooplankton of the Gulf of Finland and northern baltic Proper a review of monitoring data. *Ophelia*, 35(2):147–168.

Viitasalo, M., Katajisto, T., and Vuorinen, I. (1994). Seasonal dynamics of *Acartia bifilosa* and *Eurytemora affinis* (Copepoda: Calanoida) in relation to abiotic factors in the northern baltic sea. *Hydrobiologia*, 292/293:415–422.

Viitasalo, M., Vuorinen, I., and Saesmaa, S. (1995). Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research*, 17(10):1857–1878.

Viitasalo, S. (2007). Effects of bioturbation by three macrozoobenthic species and predation by necto-benthic mysids on cladoceran benthic eggs. *Marine Ecology Progress Series*, 336:131–140.

Wasmund, N., Tuimala, J., Suikkanen, S., Vandepitte, L., and Kraberg, A. (2011). Long-term trends in phytoplankton composition in the western and central Baltic Sea. *Journal of Marine Systems*, 87(2):145–159.

Wauchope, H. S., Amano, T., Sutherland, W. J., and Johnston, A. (2019). When can we trust population trends? A method for quantifying the effects of sampling interval and duration. *Methods in Ecology and Evolution*, 10(12):2067–2078.

Winder, M. and Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, 698(1):5–16.

Wood, S. and Scheipl, F. (2017). gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. *R package version 0.2-5*.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(1):3–36.

Wood, S. N. (2017). *Generalized additive models: an introduction with R.* Chapman and Hall/CRC.

Wood, S. N., Pya, N., and Säfken, B. (2016). Smoothing parameter and model selection for general smooth models. *Journal of the American Statistical Association*, 111(516):1548–1563.

Zeileis, A. and Gabor Grothendieck (2005). zoo: S3 Infrastructure for Regular and Irregular Time Series. *Journal of Statistical Software*, 14(6):1–27.

Zingone, A., Harrison, P. J., Kraberg, A., Lehtinen, S., McQuatters-Gollop, A., O'Brien, T., Sun, J., and Jakobsen, H. H. (2015). Increasing the quality, comparability and accessibility of phytoplankton species composition time-series data. *Estuarine, Coastal and Shelf Science*, 162:151–160.