

**Long-term population dynamics of key copepods
under climate and food web changes:
The Baltic Sea as a case study**

Dissertation

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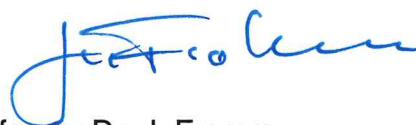
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It is not necessary in any empirical science to keep an elaborate logicomathematical system always apparent, any more than it is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated the machine must be brought out, used, and then put away. (G. Evelyn Hutchinson, 1957)

Table of Content

1	Summary	1
2	Zusammenfassung	3
3	Outline of publications	5
4	General Introduction	7
	Objectives and Modelling Approach.....	12
	References.....	13
5	Habitat heterogeneity influences climate impact on long-term changes in community structure (manuscript 1)	21
	Abstract.....	21
	Introduction.....	22
	Material and Methods.....	25
	Zooplankton data.....	25
	Hydro-climatic and predation data.....	26
	Statistical Analysis.....	27
	Results.....	29
	Discussion.....	34
	References.....	40
	Supporting Information.....	45
6	Life cycle dynamics of a key copepod over long time scales: A complex interplay of internal and external drivers (manuscript 2)	51
	Abstract.....	51
	Introduction.....	52
	Material and Methods.....	54
	The model organism - <i>Pseudocalanus acuspes</i>	54
	Data.....	54
	Abundance of <i>Pseudocalanus acuspes</i>	54
	Hydro-climatic variables.....	54
	Biotic variables.....	55
	Time series modelling and statistical analysis.....	56
	Modelling approach.....	56
	Variable selection.....	57
	Non-additive interactions.....	57
	Results.....	58
	<i>Pseudocalanus acuspes</i> population dynamics.....	58
	Trends in the biotic and abiotic environment.....	59
	Internal density and external environmental effects.....	60
	Non-additive interactions.....	64
	Discussion.....	64
	Internal life cycle dynamics.....	64
	Effects of hydro-climatic drivers.....	65
	Predation effects.....	66

TABLE OF CONTENT

	Non-additive relationships - changes between bottom-up and top-down control.....	67
	Conclusions.....	67
	References.....	69
	Supporting Information.....	75
7	A novel approach to modelling life cycle dynamics of a key marine species under past and future environmental changes (manuscript 3).....	85
	Abstract.....	85
	Introduction.....	86
	Material and Methods.....	88
	Data.....	88
	Zooplankton.....	88
	Environmental data.....	88
	Statistical modelling.....	90
	Model building.....	90
	Model validation.....	93
	Retrospective analysis of environmental effects and their life cycle propagation.....	93
	Projection of potential futures.....	93
	Results and Discussion.....	94
	Performance and robustness of the linked life cycle model.....	94
	Vulnerability of life stages to environmental change.....	95
	Projection of a future shift.....	97
	Identifying the mechanisms and drivers leading to the future shift.....	100
	Conclusion.....	103
	References.....	104
	Supporting Information.....	110
8	Early detection of ecosystem regime shifts: a multiple method evaluation for management application (manuscript 4).....	119
	Abstract.....	119
	Introduction.....	120
	Material and Methods.....	122
	Ecosystem characteristics and data considerations.....	122
	Indicators of critical slowing down.....	122
	Trend analysis.....	123
	Shiftograms.....	123
	Method assessment.....	124
	Results and Discussion.....	124
	Indicators of critical slowing down.....	125
	Trend analysis.....	127
	Shiftograms.....	128
	Conclusions.....	131
	References.....	131
	Supporting Information.....	135
9	Discussion.....	141

Conclusion.....	146
References.....	147
10 Acknowledgments.....	153
11 Annex.....	155
12 Eidesstattliche Versicherung <i>Declaration on oath</i>.....	157

1 Summary

Marine ecosystems provide various kinds of services for human societies, which have to be soundly protected and managed in light of climate fluctuations and changes and increasing human pressure. Profound knowledge of key ecosystem species serves as a basis in ecosystem based management and the advantage of providing detailed information on causal processes and species-environment relationships. Despite the mediating role of zooplankton in trophodynamics, their strong contribution to large-scale community shifts globally observed, and their suitability to identify climate changes and effects, zooplankton is still underappreciated as an indicator for the management of marine ecosystems. In addition, complex time series analysis of single-species dynamics including demographic processes, biotic and abiotic drivers and various types of functional relationships are relatively sparse in zooplankton ecology. The present thesis was therefore designed to study the copepod long-term dynamics the Central Baltic Sea (CBS) using different theoretical perspectives.

The long-term developments of the three major copepods *Acartia* spp., *Temora longicornis*, and *Pseudocalanus acuspes* in the CBS were assessed within the context of the habitat characteristics and their environmental niches. The CBS features a strong vertical and horizontal gradient in temperature and salinity; species are therefore likely to differ stronger in their physiological adaptations (i.e. their fundamental niches) as well as species interactions, which may have implications on the long-term community structure. The comparison of the long-term trends of the three study species and their main drivers, both seasonally and spatially, indicated that effects of climate depended strongly on species-specific habitat utilization. Direct effects of climate changes were more pronounced at the upper water layers, shifting the potential thermal niche of *Acartia* spp. and *T. longicornis* further into the optimal part of their fundamental niche. *Acartia* spp. displayed furthermore significant differences in their spatial distribution, which is probably caused by multiple indirect climate effects. Predation was additionally important as it reduced the size of the realized niche, particularly of *P. acuspes* experiencing the largest vertical overlap with predators.

After the main drivers of the long-term overall population dynamics were identified their contribution to the seasonal life stage abundances of *P. acuspes* in combination with internal density effects were further assessed to improve the understanding of the life cycle dynamics of *P. acuspes*. Within a discrete stage-structured population modelling approach, Generalized Additive Models (GAM) and their threshold formulation (TGAM) were applied to test for changes between bottom-up and top-down trophic regulation under contrasting predation regimes. The integrative analysis revealed a complex interplay of linear density and predation effects and non-linear hydro-climate effects, the latter being stage- and season-specific. In general, younger stages (nauplii, copepodite I-III) were more affected by temperature and the BSI, while older

1 SUMMARY

stages (copepodite IV-V, females) were influenced by salinity, except in winter. Predation had a significant, negative effect on older stages throughout the year and controlled the bottom-up effects (i.e. density and salinity) mainly in summer and autumn on the copepodites IV-V. Based on the findings of this analysis, the major peak in abundances observed for all stages across the seasons in the 1970s/1980s can be better understood as our results suggests a multiplicative effect of various biotic and abiotic conditions.

Based on the empirically derived relationships a single life cycle model was developed to simulate past long-term dynamics by retrospectively changing environmental conditions and project future dynamics under different environmental scenarios.

Results from the simulation indicate that copepodite IV-V in winter and females in spring are the most sensitive stages to direct and indirect effects of salinity and predation. The potential futures of *P. acuspes* were investigated by conducting stochastic projections of the population's response to one climate and a number of fisheries management and eutrophication scenarios. The results show that under a potential climate-induced freshening of the Baltic Sea, salinity may more strongly control the biomass of *P. acuspes* independently of the predation level. The projected salinity drop to levels historically unreported caused a collapse of *P. acuspes* population size in all scenarios. The model output further indicates that density-dependence plays a role but cannot compensate for this collapse.

To detect regime shifts in marine systems such as the one observed in the Baltic Sea in advance for short-term management efforts, a set of early-warning indicator methods based on the Baltic key species *Acartia* spp. and *P. acuspes* were evaluated. Specifically, the practical use of temporal and spatial indicators of critical slowing down, trend analysis and the shiftogram were compared. This comparison revealed different strengths and disadvantages of the various methods, with the shiftogram in combination with the alertogram seeming most promising. However, limitations are given here in the type of transition (e.g. gradual change or a sudden shift), which can influence the degree of detecting the transition sufficiently in advance. Therefore, a multiple approach is eventually suggested to provide a sound scientific basis for evaluating early-warning signals in the management process.

The present study has shown that the multiple internal and external factors strongly interact. To obtain a deeper understanding of the long-term population dynamics we need more complex, integrated analysis approaches. Simulations and future projections based on these detailed knowledge of key zooplankton species can eventually serve as a tool for modern ecosystem-based management of the Baltic Sea.

2 Zusammenfassung

Eines der drängendsten und wichtigsten Probleme weltweit ist die Sicherstellung mariner Ressourcen. Für ein ganzheitliches, Ökosystem-basiertes Management stellt eine wichtige Grundlage die genaue Kenntnis der Schlüsselarten des Ökosystems. Diese Arten können Aufschluss geben über kausale Prozesse wie auch über Interaktionen mit der Umwelt. Obwohl Zooplankton im Energiefluss des Nahrungsnetzes eine vermittelnde Rolle innehat, bei den weltweit beobachteten Strukturveränderungen mariner Gemeinschaften stark beteiligt und gut geeignet ist, Klimaveränderungen und -effekte zu identifizieren, wurde das Zooplankton als Indikator im Management mariner Ökosysteme bisher wenig genutzt. Auch innerhalb der Zooplanktonökologie sind komplexere Zeitserien-Analysen eher die Ausnahme. Die vorliegende Studie versucht daher die Langzeitdynamiken der Haupt-Copepodenarten in der zentralen Ostsee auf Basis verschiedener theoretischer Konzepte der Populationsökologie zu untersuchen.

Zum einen wurde die langzeitliche Entwicklung der 3 dominanten Copepodenarten *Acartia* spp., *Temora longicornis*, and *Pseudocalanus acuspes* in den 3 Becken der zentralen Ostsee im Rahmen ihrer Umweltischen und der Habitateigenschaften untersucht. Die Ostsee weist starke vertikale und horizontale Temperatur- und Salzgradienten auf; vorkommende Arten werden daher größere Unterschiede in ihrer physiologischen Anpassung (sog. fundamentale Nische) wie auch in ihren Interaktionen zu anderen Arten aufweisen. Der saisonale und räumliche Vergleich der Langzeittrends zeigt, dass Klimaeffekte stark von der Arten-spezifischen Habitatausnutzung abhängen. Direkte Effekte waren am stärksten in den obereren Wassertiefen zu beobachten, wobei hier die potenzielle thermale Nische von *Acartia* spp. und *T. longicornis* weiter in den Bereich der fundamentalen Nische gerückt wurde. *Acartia* spp. wies auch signifikante Unterschiede in ihrer räumlichen Verteilung auf, welche durch mehrere indirekte Klimaeffekte vermutlich hervorgerufen wurden. Ein weiterer Faktor war Fraßdruck, der sich allerdings auf die realisierte Nische auswirkte und diese verkleinerte; insbesondere bei *P. acuspes*, welches die größte räumliche Überschneidung mit den Prädatoren aufweist.

Nachdem die Hauptfaktoren der langzeitlichen Populationsdynamik von *P. acuspes* identifiziert waren, wurden ihr Einfluss auf die jahreszeitlichen Abundanzen einzelner Lebensstadien in Kombination mit internen Dichteeffekten untersucht. Im Rahmen eines diskreten, Stadien-strukturierten Populationsmodell-Ansatzes wurden Generalized Additive Models (GAM) und sog. threshold-GAMs (TGAM) angewendet um den Wechsel zwischen einer trophischen "bottom-up" und "top-down" Regulierung unter gegensätzlichen Prädations-Regimes zu untersuchen. Der integrative Ansatz weist auf ein komplexes Zusammenspiel linearer Dichte- und Prädationseffekte mit nicht-linearen, stadien-spezifischen Effekten des Hydro-Klimas hin. Während jüngeren Stadien (Nauplien, Copepodite I-III) mehr vom Klimaindex und der

2 ZUSAMMENFASSUNG

Temperatur beeinflusst sind, sind die älteren Stadien (Copepodite IV-V, Weibchen), mit Ausnahme vom Winter, stärker Salz-abhängig sind. Prädation hatte das gesamte Jahr über einen starken, negativen Effekt auf die älteren Stadien und kontrollierte "bottom-up"-Effekte (Salinität und Dichteeffekte) vor allem im Sommer und Herbst. Anhand der Analyseergebnisse lassen sich die stadien-übergreifend hohen Abundanzen in den 70er und 80er Jahren als Resultat multiplikativer Effekte durch verschiedene biotische und abiotische Bedingungen verstehen.

Basierend auf den empirisch ermittelten Beziehungen wurde ein Lebenszyklus Modell entwickelt um vergangene und zukünftige Langzeit-Dynamiken unter verschiedenen Umweltbedingungen zu simulieren. Anhand dieser Simulationsergebnisse lassen sich die Weibchen im Frühjahr und die Copepodite IV-V im Winter als besonders empfindlich hinsichtlich direkter und indirekter Salz- und Prädationseffekte einstufen. Die möglichen Zukunftsentwicklungen für *P. acuspes* wurden untersucht indem stochastische Projektionen der Populationsdynamiken unter einem Klima und mehreren Fischerei-Management / Eutrophierungs Szenarien vorgenommen wurden. Die Ergebnisse zeigen hier deutlich, dass unter einer potenziellen Klima-induzierten Aussüßung der Ostsee der Salzgehalt eine stärkere kontrollierende Wirkung auf *P. acuspes* haben könnte, unabhängig vom Fraßdruck. Der projizierte Salzgehaltabfall führt in allen Szenarien zu einem Zusammenfall des Gesamtbestandes. Die Modellergebnisse zeigen zusätzlich auf, dass Dichteabhängigkeiten eine Rolle spielen, nicht jedoch den Kollaps kompensieren können.

Um sog. "regime shifts" in marinen System wie den in der Ostsee für entsprechende kurzfristige Managementmaßnahmen rechtzeitig erkennen zu können, wurden verschiedene Frühwarn-Indikatoren mittels Zeitserien der Ostsee-Schlüsselarten *Acartia* spp. und *P. acuspes* evaluiert. Es wurden die praktische Verwendung folgender Methoden verglichen: zeitliche und räumliche Indikatoren des "critical slowing down", die Trendanalyse und das shiftogram. Dieser Vergleich deckt die verschiedenen Stärken und Nachteile auf, wobei das shiftgram in Kombination mit dem alertogram am vielversprechendsten scheint. Jedoch gibt es auch hier Limitationen, die bedingt sind durch die Art des Übergangs (graduell oder abrupt), welcher einen Einfluss auf die Erkennungsstärke dieser Übergangsphase hat. Um eine solide wissenschaftliche Basis der Beurteilung solcher Frühwarnsignale im Managementprozess geben zu können, wird ein Ansatz befürwortet, der auf mehreren Indikatoren basiert.

Die vorliegende Studie hat gezeigt, dass die zahlreichen internen und externen Faktoren sich gegenseitig bedingen. Um ein tieferes Verständnis der Populationsdynamik zu bekommen, sind komplexere Analyse-Ansätze daher erforderlich. Anhand dieser detaillierten Kenntnisse von Zooplankton-Schlüsselarten lassen sich sehr gut Simulationen und Zukunftsprojektionen durchführen, welche einen wichtigen Beitrag für das Management mariner Ökosysteme wie der Ostsee leisten können.

3 Outline of publications

The following overview outlines the four publications included in this thesis and the contribution of each author to the respective manuscript. The overall objectives of this research study were included in the BONUS+ project: Assessment and Modelling of Baltic Ecosystem Response (AMBER).

Manuscript 1

Habitat heterogeneity influences climate impact on long-term changes in community structure

Saskia A. Otto, Juha Flinkman, Georgs Kornilovs, and Christian Möllmann

SAO designed the research, performed the statistical analysis and wrote the manuscript. JF and GK provided the zooplankton data. CM helped with the writing and the design and conduct of the analysis. The manuscript will shortly be submitted to PloS ONE, a peer-reviewed journal.

Manuscript 2

Life cycle dynamics of a key copepod over long time scales: A complex interplay of internal and external drivers

Saskia A. Otto, Marcos Llope, Georgs Kornilovs, and Christian Möllmann

SAO developed the concept of the study, performed the statistical analysis and wrote the manuscript. ML helped with the statistical analysis. GK provided the zooplankton data. CM helped with the writing and the design of the analysis. The manuscript will shortly be submitted to Proceedings of the Royal Society B-Biological Sciences, a peer-reviewed journal.

Manuscript 3

A novel approach to modelling life cycle dynamics of a key marine species under past and future environmental changes

Saskia A. Otto, Thorsten Blenckner, Georgs Kornilovs, Marcos Llope, Bärbel Müller-Karulis, Susa Niiranen, Maciej T. Tomczak, and Christian Möllmann

SAO conceived the modelling; SAO and CM designed the research and analysed the data. ML provided analytical support. GK, BMK, SN, and MTT provided data and model output. SAO, CM and TB wrote the paper.

| 3 OUTLINE OF PUBLICATION

Manuscript 4

Early detection of ecosystem regime shifts: a multiple method evaluation for management application

Martin Lindegren, Vasilis Dakos, Joachim P. Gröger, Anna Gårdmark, Georgs Kornilovs, Saskia Otto, and Christian Möllmann

ML, VD, AG, and CM designed the research. ML, VD, JG, and SO performed the analysis. SO and GK provided data. All authors took part in the writing. The manuscript has been submitted to PLoS ONE, a peer- reviewed journal.

4 General Introduction

Population ecology started to evolve at the turn of the 20th century with the application of experimental and mathematical models to study individual adaptations, population interactions and community succession (e.g. Forbes 1887, Cowles 1899). In the 1920s, it became a major field of zoological research with strong focus on mathematical approaches to single-species population growth (Pearl & Reed 1920) and two-species interactions (Volterra 1926, Lotka 1932, Gause 1934, Nicholson & Bailey 1935). Since then, contemporary ecological theory has developed around a core of issues, mainly (1) the number and relative abundances of species in a community, (2) the niche theory, (3) spatial and temporal population dynamics of single species and their demography, and (4) multispecies and trophic interactions, (Real & Levin 1991, Turchin 2003). The development of theoretical frameworks involving ecological thresholds and regime shifts is rather new but has become increasingly important in the management of ecosystems (Andersen *et al.* 2009).

In the past 20 years, the focus of the research has generally shifted towards a more integrated ecosystem view. The community with its individual species populations cannot be viewed in isolation from its abiotic environment and vice versa as they are strongly intertwined (Odum 1975). Ecosystems represent this complex and dynamic natural unit of interacting biotic and abiotic components. Within and between these various components large quantities of energy and matter flow in a way that is not yet fully understood. In general, these flows are suggested to be controlled either by primary producers (bottom-up control), by foraging pressure of top-predators (top-down control), by abundant species in intermediate trophic levels controlling the flow up- and down the food web (wasp-waist control) or combinations of these depending on the temporal state of the system (Cury *et al.* 2003, Bakun 2006). Changes in the abundances of species altering the ecosystem structure and functioning are often induced by environmental changes and can appear as a smooth, abrupt or discontinuous shift, the latter leading to an alternative "stable" state (Scheffer *et al.* 2001, Scheffer & Carpenter 2003, Collie *et al.* 2004). The strength of the environmental effect depends on the community's resilience to perturbations, which is determined by the species' ability to adapt to the physical environment and the level of ecological interactions (Holling 1973, Peterson *et al.* 1998). Fishing can similarly induce such changes. In various regions of the Northern Hemisphere major reorganizations were synchronistically observed in the late 1980s and related to large-scale climatic changes, overexploitation of resources or both, e.g. in the North Pacific and Bering Sea (Hare & Mantua 2000), the northeast U.S. continental shelf (Link *et al.* 2002), North Sea (Reid *et al.* 2001), Baltic Sea (Möllmann *et al.* 2009), or the Black Sea (Daskalov *et al.* 2007).

4 GENERAL INTRODUCTION

In view of climatic changes, which are projected to cause further increases in temperature and the occurrence of hot extremes (IPCC 2007), together with growing human pressures (e.g. fishery, shipping traffic, input of nutrients and hazardous substances, introduction of invasive species via the ballast water), ecosystems are severely under pressure. Losses of biodiversity, demographic changes, and simplifications of the food web, to name only a few examples, could be the consequences (Loreau *et al.* 2001, Doney *et al.* 2012). This will have tremendous implications for humans as marine ecosystems provide all different kinds of benefits, beside the more obvious supply of protein sources (Worm *et al.* 2006). These so-called ecosystem services can be of regulatory, socio-economic or cultural value (Millenium Ecosystem Assessment 2005). The importance of the latter for instance has been acknowledged by the New Zealand government, which enacted a law giving the indigenous Maoris exceptional fishing rights. The immediate short-term as well as long-term impacts on several ecosystem services (i.e. fishing industry, recreation, tourism, coastal protection) due to severe ecosystem degradation become especially apparent under catastrophic events such as the oil spill in Guimaras, Philippines, or the Deepwater Horizon oil spill in the Gulf of Mexico (NRC 2012).

Taking effective management decisions to deliver the protection and conservation of these services requires an integrated systems analysis provided by the Ecosystem Approach to Management (EAM) framework (Browman & Stergiou 2004, ICES 2005, Farmer *et al.* 2012). This framework aims to capture the major interactions within an ecosystem, including multiple human impacts. One of its main objectives is the identification of the current ecosystem state and the specification of the "state to be achieved" (ICES 2005). Furthermore, indicators that may describe the ecosystem state, or impacts of human pressures need to be determined. Useful indicator species are often keystone species, which by definition have a proportionally large influence on the community or ecosystem (Power *et al.* 1996), often maintaining its stability (Paine 1966). Although often demonstrated for fish or marine mammals with predation as the major mechanism in the keystone effect, key species are not restricted to higher trophic levels (Power *et al.* 1996). Other interactions such as competition, mutualism or parasitism as well dispersal or habitat modification can be similarly important (Bond 1993). Hence, species of lower trophic levels such as cyanobacteria or endolithic lichens have been suggested as keystone species (Power *et al.* 1996). A key role in the re-organization of marine communities has recently been also attributed to the zooplankton (Alheit *et al.* 2005, Hays *et al.* 2005, Möllmann *et al.* 2009). Zooplankton species play a major role within the food web as they mediate the energy flow between primary producers and secondary and tertiary consumers such as large, commercially important pelagic and demersal fish populations. Because of their high daily fecal pellet production, which is an important food source for microorganisms, they have a great importance in the microbial food web and the biological pump (Richardson 2008, Turner 2002, 2004). Traditionally marine zooplankton is considered as being bottom-up controlled and may serve as suitable indicators of the effect of climate on the ocean, unbiased by anthropogenic

effects at the top of food webs (Hays *et al.* 2005). Their rapid turnover rates and their strong response to temperature changes suggest them being suitable for investigating climate effects on ecosystems (Richardson 2008, Mackas & Beaugrand 2010) and hence a multitude of studies have been published for several areas of the world ocean (e.g. Fromentin & Planque 1996, Conversi *et al.* 2001, Beaugrand 2003, Chiba *et al.* 2006, Turner *et al.* 2006). Within the EAM framework, however, zooplankton has been rather underrepresented and focus set more on species with a direct high economic value such as fish. However, their food web role and suitability to indicate climatic variability and changes suggest great potential in contributing to management and conservation issues.

In the marine environment the zooplankton community is dominated in numbers and biomass by copepods (Miller 2005). With over 10,000 species the taxon Copepoda represents one of the species richest groups within the Crustacea (Westheide & Rieger 1996). They inhabit all aquatic environments, from the hyperbenthic and benthopelagic zones to glacial ponds; but their major habitat is the marine pelagic zone with calanoid copepods being most abundant (Mauchline 1998). Despite their small size (0.5 - 5 mm with few exceptions; Westheide & Rieger 1996) they can present the food source for large predators such as whale sharks (Nelson & Eckert 2007). Copepods have a complex life cycle developing through 11 larval stages (6 nauplii and 5 copepodite stages) to the adult stage with one to 12 generations per year in temperate and high latitude regions (Mauchline 1998). The vital rates of copepods (e.g. growth rate, development times, fecundity, egg hatching rate, etc.) have been intensively studied and related to internal traits such as body size, developmental stage, physiological condition, tolerance to temperature, and feeding activity, which depends for crustaceans on the moulting cycle (Lenz 2000, Kiørboe 2008). Food supply and temperature conditions have been identified as most important external factors for the growth rate (McLaren 1965, Vidal 1980a,b, Davis 1984, Klein Breteler & Gonzalez 1988, Huntley & Lopez 1992, Hirst & Bunker 2003, Liu & Hopcroft 2008, Dutz *et al.* 2010). The empirically established functions of the vital rates are now commonly used in numerical models such as individual bioenergetic and life-history trait models or population models (see Carlotti *et al.* 2000 and references therein).

The investigation of inter-annual dynamics became more and more important in the past two decades. Large-scale monitoring programs like the North Atlantic CPR survey (Batten *et al.* 2003) and the CalCOFI program (Ohman & Venrick 2003) provided the necessary long-term data for this. In these studies long-term variations of zooplankton abundance were related to climatic and hydrological variables rather than to biological processes, with the focus on large-scale, low-frequency climatic drivers. For the North Atlantic and its adjacent seas, the North Atlantic Oscillation (NAO), a decadal mode of variations of atmospheric mass over the North Atlantic, has been identified as a strong force affecting the marine systems at all trophic levels (Ottersen & Stenseth 2001, Blenckner & Hillebrand 2002, Beaugrand 2004, Möllmann *et al.* 2008). Fromentin & Planque (1996) indicated that the abundance of two *Calanus* species in the

4 GENERAL INTRODUCTION

Eastern North Atlantic is directly correlated with the NAO and responses to this climate pattern are species specific. Others demonstrated similar relationships for these or other species in various regions, such as the Gulf of Maine (Conversi *et al.* 2001, Turner *et al.* 2006), the North Sea (Beaugrand 2003), the Baltic Sea (Möllmann *et al.* 2008), or the Barent Sea (Stige *et al.* 2009). Zooplankton species are not directly influenced by supraregional climatic patterns but respond to local environmental conditions (e.g. water temperature, salinity, stratification, flow), which, in turn, can be influenced by regional and large-scale hydroclimatic processes (e.g. changes in slope water circulation, currents such as the Gulf Stream, SST, scalar wind, air pressure, precipitation, large-scale teleconnecting patterns of climate variability) (Roemmich & McGowan 1995, Taylor 1995, Stephens *et al.* 1998, Dippner *et al.* 2001, Greene & Pershing 2000, Möllmann *et al.* 2000, Beare *et al.* 2002, Beaugrand 2003, Molinero *et al.* 2005, Wiafe *et al.* 2008, Gislason *et al.* 2009).

Despite the accumulation of studies on zooplankton time series, complex analysis of single-species dynamics including both, biotic and abiotic drivers on decadal time scales and their implications for the ecosystem are relatively sparse. Most of these studies are based on linear correlation analysis and hence disregard any other shape of relationship. In addition, different life stages may have different environmental niches and vary in their adaptive ability to local climate conditions. Stage-specific differences in thermal tolerance have been demonstrated for instance among eggs, larvae, and pupal of the moth species *Manduca sexta* (Kingsolver *et al.* 2011) or juveniles and adults of the diamondback watersnake (*Nerodia rhombifer*) (Winne & Keck 2005). Yet, stage-specific long-term developments have so far been limited in zooplankton time series analyses.

In the Central Baltic Sea (CBS), i.e. the central basins of the Baltic Sea and our study area (see Fig. 4-1), the study of copepod dynamics is especially challenging as most species live here at their physiological limits. The Baltic Sea in Northern Europe is worldwide one of the greatest brackish water systems, extending over 13 degrees of latitude and thus featuring a strong temperature gradient across the different basins. Due to its semi-enclosed nature with a narrow connection to the North Sea, the Baltic Sea experiences a net positive freshwater balance. In the deep areas of the Central Baltic Sea, this leads to a permanent stratification with a highly saline deepwater (values > 12) being separated from low salinity surface waters (values < 9). Vertical mixing of the water masses is hence restricted by a halocline at about 60-100 m depth. The exchange of deepwater in these areas can only occur by strong pulses of salt water inflow. These so-called “major Baltic inflows” (MBI) (Wyrтки 1954, Fonselius 1969), can change the oceanological regime of the whole water column and improve the living conditions of for example benthic animals by the distribution of oxygenated water. Lack or decreased frequencies of MBIs result in decreased salinity levels due to the shallowing of the halocline and have been generally attributed to changed atmospheric forcing conditions. During the summer months a thermocline develops at a depth of 20-30 m leading to an enhanced vertical habitat differentiation.



Figure 4-1: The Baltic Sea with its catchment area and the region of the Central Baltic Sea.

The main dominating zooplankton species in this region are the euryhaline calanoid copepods *Temora longicornis*, species of the genus *Acartia* (i.e. *Acartia bifilosa*, *A. longicornis*, *A. clausi*), and *Pseudocalanus acuspes*. The latter has been formerly identified as *P. elongatus* or *P. elongatus minutus* but is now recognized as *P. acuspes* singly (Frost 1989, Bucklin *et al.* 2003, Grabbert *et al.* 2010, Holmborn *et al.* 2011). Another important but less abundant calanoid copepod is *Centropages hamatus*. In summer, cladocerans can become additionally abundant with biomass values comparable to *P. acuspes* (Möllmann *et al.* 2000). The pelagic food web in the CBS in terms of species diversity and trophic structure is rather simple. The upper trophic level is represented by the two planktivore clupeids sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) and the piscivore species cod (*Gadus morhua*). Other top predators such as harbour porpoise (*Phocoena phocoena*) or the grey seal (*Halichoerus grypus*) have been abundant until the early 20th century but play now a subordinate role in the CBS (HELCOM 2009). The interactions between the different trophic levels and compartments depend strongly on the temporal horizontal and vertical overlap. For instance, sprat and herring, the main predators of copepods, inhabit the open sea only during certain seasons and life phases (Möllmann & Köster 2002, ICES 2011). Similar to other marine systems, the community in the CBS underwent a great structural re-organization during the late 1980s/early 1990s by shifting from a cod-dominated to a sprat-dominated system (Casini *et al.* 2009, Möllmann *et al.* 2009). On the phytoplankton level, diatom blooms appeared less often while dinoflagellates gained in importance (Wasmund *et al.* 1998, Wasmund & Uhlig 2003). On the zooplankton level, particularly *Acartia* spp. and *T. longicornis* showed an increase whereas *P. acuspes* displayed an overall decrease (Möllmann *et al.* 2000, 2003). This shift appeared rather discontinuously and

4 GENERAL INTRODUCTION

was initiated by climate-induced changes in the hydrography. Fisheries-induced feedback loops further stabilized this shift (Möllmann *et al.* 2009). In this complex interplay of physical forcing and trophic bottom-up and top-down processes, a key role in the food web dynamics has been suggested for *Acartia* spp. as well as *P. acuspes*.

Objectives and Modelling Approach

The aim of this thesis was to investigate the long-term dynamics of the major copepod species in the CBS on different spatial, temporal, and demographic scales and to relate these dynamics to ecosystem changes. The focus in this thesis was laid on the CBS as consistent and large-scale sampling programs over the last 5 decades within this region made it a suitable study area for an inter- and intra-annual analysis.

For this, statistical models were applied on single copepod time series to specifically (i) assess how hydro-climatic changes affect the long-term development of a zooplankton community in a heterogeneous environment (**manuscript 1**), to (ii) investigate stage-specific responses to internal and external forcing and implications to the overall population dynamics (**manuscript 2 and 3**), and (iii) assess within the context of future research the potentials of single-species projections and the practical use of early-detection methods based on copepod time series to forewarn potential ecosystem shifts, both being relevant in conservation and management issues (**manuscript 3 and 4**).

The core of the statistical models applied in this thesis is based on Generalized Additive Model (GAM) techniques (Hastie & Tibshirani 1990, Wood 2006) and their extensions. In ecology, the application of linear regression techniques has a long tradition (Venables & Ripley 2002) but the relationships between biotic and abiotic components are often non-linear (e.g. Ciannelli *et al.* 2004; Stenseth *et al.* 2006; Dingsør *et al.* 2007; Tyler *et al.* 2008; Llope *et al.* 2009). To allow for any curvature in the relationship between two variables, one can include polynomial terms in linear models. However, this technique still makes assumptions on the actual relationship, shows often a poor fit and can lead to numerical stability problems (Wood 2006, Zuur *et al.* 2007). A more flexible approach is the inclusion of spline functions, which are piecewise polynomials over usually a finite range. At the points where the polynomial pieces join, so-called "knots", the spline function is constrained to remain smooth and continuous. At the boundary knots, i.e. the ends of the range, a further constrain is applied to avoid spurious behaviour such as forcing a linear fitted line beyond the smallest and largest X value as in natural cubic regression splines. The problem with spline regression models is that they can be parametrically very expensive and easily lead to over-fitting (Venables & Dichmont 2004). GAMs address this problem by fitting a large number of parameters but compensating for this by adding a penalty term, which reflects the degree of smoothness in the regression, to the log-likelihood and this sum of terms is maximized. The spline functions in GAMs therefore are called penalized splines or smoothing splines. The

appropriate degree of smoothness is estimated from data using cross validation. In summary, GAMs have the advantage to not require an a priori specification of the relationship between the response variable (Y) and the explanatory variable (X). Each Y_i is linked with X_i by a smoothing function instead of a coefficient β as in traditional regression techniques and hence relationships do not have to be linear.

For the stage-specific analysis and the modelling of the life cycle dynamics of *P. acuspes* in **manuscript 2 and 3**, GAMs and their threshold extension are applied within the discrete time model framework. In the analysis of population dynamics, three mathematical frameworks are generally applied (Turchin 2003):

- 1) continuous time models based on ordinary differential equations (ODE),
- 2) continuous time models based on delayed differential equations (DDE), and
- 3) discrete time models based on difference equations

If populations have non-overlapping generations as in the case of *P. acuspes*, discrete time models are a useful tool and easier to apply (Turchin 2003). They are widely adopted in fishery research (e.g. Ricker model, Beverton-Holt model), but in zooplankton ecology numerical models based on differential equations are more common (see Carlotti *et al.* 2000 and references therein). An exception here are discrete population models based on the Leslie matrix (Leslie 1945) or modification of this (Caswell 2001), which explicitly address the population structure (e.g. Davis 1984, Miller & Tande 1993, Twombly *et al.* 2007). However, mainly vital rates such as fecundity or survival, and not abundances as in our approach, are modelled.

In **manuscript 4**, different methods are applied on the copepod time series data to detect trends or structural breakpoints, i.e. trend analysis, shiftograms and temporal and spatial indicators for critical slowing down, and the results compared.

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5 Habitat heterogeneity influences climate impact on long-term changes in community structure

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Abstract

Modeling species abundances and distributions based on the ecological niche concept is increasingly common in terrestrial ecology, but less adopted in the marine realm. This is especially true in zooplankton ecology despite its central role as mediator between primary production and secondary consumers. Here, we investigate how hydro-climatic long-term changes affect the long-term development of a zooplankton community in a heterogeneous environment. We use a unique long-term time series from the Central Baltic Sea, which features distinct habitats due to strong vertical and horizontal gradients in hydrography. Applying statistical modeling techniques to compare long-term population trends and to identify their main drivers, we demonstrate that the direct effect of climate changes was more pronounced at the upper water layers, shifting the potential thermal niche of *Acartia* spp. and *T. longicornis* further into the optimal part of their fundamental niches. *Acartia* spp. displayed furthermore significant differences in their spatial distribution, which is probably caused by multiple indirect climate effects. Predation was additionally important as it reduced the size of the realized niche, particularly of *P. acuspes* experiencing the largest vertical overlap with predators. Our study exemplifies that community structure can be affected by the complexity of the habitat. In heterogeneous environments, coexisting species have more distinct niche separations and, hence, are likely to differ in their temporal responses to environmental changes.

Key words: species distribution over time, potential and realized niche, copepods, *Acartia* spp., *Temora longicornis*, *Pseudocalanus acuspes*, Generalized Additive Models

Introduction

Understanding and predicting species distribution in space and time is an increasingly important issue in ecology, particularly in biodiversity conservation and management as well as climate change research. Modeling approaches linking the physiological requirements of a species to its biogeographical distribution have a long history and date back to the early 19th century (Johnston 1924). Since the first computer-based modeling attempts (Austin 1971) increasing numbers of techniques have emerged, especially in the last 20 years (Mladenoff *et al.* 1995, Zaniwski *et al.* 2002, Hirzel & Le Lay 2008, Reiss *et al.* 2011). These so-called Habitat Suitability Models (HSM), Species Distribution Models (SDM) or Ecological Niche Models (ENM) are based on the Grinnellian / Hutchinson niche concept and try to quantify the realised environmental niche (Guisan & Thuiller 2005), i.e. the portion of niche space occupied by a species in the presence of biotic processes such as competition, predation, and mutualism, but also dispersal and colonization (Pulliam 2000). Most of these studies have set their focus on the spatial dimension of species occurrences. However, less well-studied are the long-term dynamics of the species abundances mediated by temporal habitat dynamics. In general, Hutchinson's niche concept is rather static and ignores temporal changes in environment and population responses (Griesemer 1992).

To acknowledge the important role of climatic changes observed in paleobiology, Jackson & Overpeck (2000) extended the classical niche concept by adding the "potential niche" (PN). In the real world not all environmental combinations are realised at a particular time, or certain combinations do not occur within a region due to spatial heterogeneities (e.g. topography or geology). Consequently, only a subset of the fundamental niche (FN) space, i.e. the n -dimensional hypervolume in environmental space that permits positive population growth (Hutchinson 1957) exists, representing the PN for that time. In this context, the realised niche (RN) can be seen as a subset of the PN, owing to constraints imposed by biotic processes. If conditions of climate or anthropogenic impacts change, shifts within the environmental realizations can be induced and consequently the PN of a species' shape, size and/or position in environmental space changes. Some species may benefit from these changes and increase in abundance if their PN in a given area, i.e., the size of suitable habitat, enlarges. Other species may persist but reduce in numbers if the habitat becomes less suitable. If the changes go beyond the species' environmental tolerance, the population will migrate or undergo local extinctions as niche characteristics are assumed to not evolve fast enough to adapt to environmental changes over short periods of time (Jackson & Weng 1999, Hirzel & Le Lay 2008). Species-specific changes within the community will further lead to changes in biotic interactions, which additionally will contribute to the size of the RN. Hence, with increasing magnitude of environmental changes, species assemblages can show great reorganizations (Foley *et al.* 2003, Hare & Mantua 2000).

The extent of community reorganizations depends further on habitat complexity. Populations for instance, are less disrupted by temporal environmental variability in habitats with spatial heterogeneity as they can provide for instance refugia in which survival of individuals is more likely (Townsend & Hildrew 1994). Similarly, species diversity is known to increase with habitat heterogeneity (MacArthur & Wilson 1967, Cottenie 2005), but effects of temporal changes in habitat heterogeneity have only been recently explored (Munguia *et al.* 2011). Under climate change scenarios for example, individual habitats may respond differentially to temperature increase due to a variable thermal storage capacity of physical or biotic structures. The relative distribution of habitats in an environment and the kind of species occupying these will also influence the long-term development of the whole community. In most habitats, plant communities determine the physical structure of the environment and consequently, have a considerable influence on the distributions of animal species (reviews in Lawton 1983). In the marine pelagic environment, conversely, habitat heterogeneity is created by spatial variability in physical oceanographic parameters such as temperature, salinity and oxygen, but as well through the occurrence of prey and predator populations.

Here, we investigate how hydro-climatic changes affect the long-term development of a zooplankton community in a heterogeneous environment. Our premise is that species in spatially complex habitats strongly differ in their FN and in their species interactions. Consequently they will show different changes in their RN and hence their temporal development under hydro-climatic variability, eventually affecting the community structure (Fig. 5-1a). To investigate this, we use a unique long-term dataset on the zooplankton community of the Central Baltic Sea (CBS), based on five decades of offshore sampling (see Fig. 5-1b). Zooplankton is an especially suitable indicator of the effect of climate change on aquatic ecosystems and long-term changes in marine zooplankton are well studied (Planque & Taylor 1998, Möllmann *et al.* 2000, Mackas & Beaugrand 2010). However, only recently climate induced changes on the ecological niches of zooplankton (i.e. their habitat) have been investigated, but with a focus on potential changes in geographic distribution (Helaouët & Beaugrand 2009, Helaouët *et al.* 2011). The CBS is an especially suitable area for our study since it displays distinct pelagic habitats due to strong hydrographic gradients both in the horizontal (Fig. 5-1c) and the vertical (Fig. 5-1d). The horizontal differentiation is caused by the topography, subdividing the CBS into three major basins. Vertical habitat heterogeneity is induced by the stratification of the water column during most of the productive season into (i) a warm but low saline surface layer, (ii) a cold and low saline intermediate layer, and (iii) a cold and high saline deep layer. The three main zooplankton species in the CBS, the calanoid copepods *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes*, distribute largely according to these hydrographic habitats (Hansen *et al.* 2006), which are differentially susceptible to changes in atmospheric forcing. For example, the surface layer in the CBS is more affected by temperature while the deep layer salinity is set by climatically determined frequency and magnitude of lateral intrusions of water masses originating from the

North Sea (Matthäus & Frank 1992; see SI text on Baltic hydrography). Furthermore, the vulnerability of the zooplankton species to predation is habitat-specific as the dominating planktivore, the small pelagic sprat (*Sprattus sprattus*), feeds mainly in deep and highly saline layers (Möllmann *et al.* 2004), hence is displaying a variable overlap with zooplanktonic prey species (Fig. 5-1d). The population of the main predator sprat has increased drastically during the recent two decades, both due to increased temperature conducive for reproductive success, but also due to the climate- and overfishing-mediated collapse of its main predator (Möllmann *et al.* 2008). It can hence be concluded that the vertical habitat heterogeneity in the CBS may induce strong species-specific responses to climate variability and change. In addition, strong horizontal gradients in temperature and salinity, generally declining in the CBS from west to north-east (Fig. 5-1c), are likely to induce spatial differences in these responses.

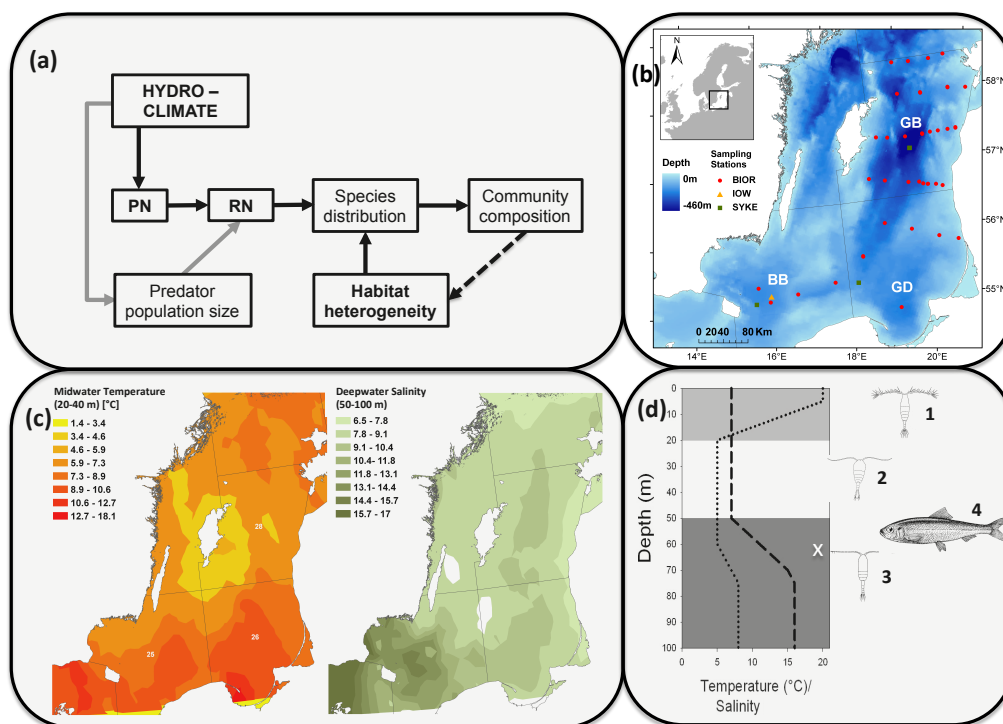


Figure 5-1: Study concept. A flowchart of the theoretical concept is shown in (a) and a map of the central Baltic Sea with its three basins (BB=Bornholm basin, GD=Gdansk Deep, GB=Gotland basin) and the sampling stations of the different datasets in (b). (c) shows a horizontal profile of the hydrology in August (i.e. the gradient in temperature and salinity) based on data for years 2000-2008. (d) presents a schematic vertical profile of the hydrology together with the copepod (1=*Acartia* spp., 2=*T. longicornis*, 3=*P. acuspes*) and predator distribution (4).

To assess the long-term dynamics of the species abundances mediated by temporal habitat dynamics, we here specifically test i) whether our study species display different population trajectories in space and time, and ii) if hydro-climatic and biotic factors differentially affect the long-term development of the individual species' populations. We adopted an inductive approach by first applying statistical modelling techniques to compare species-, basin-, and season-

specific long-term population trends and to identify their main drivers. From these results we then inferred changes in niche space and the role of habitat heterogeneity. The niche concept as defined by Hutchinson (1957) is multidimensional. However, recent studies have demonstrated the importance of temperature, salinity and predation for our study species (Möllmann *et al.* 2000). We therefore focused on the thermohaline PN together with the predation interaction shaping the RN space. To account for further dimensions related to climate changes for which we had no specific time series, we included a local climate index as a proxy for a blend of hydro-climatic conditions other than temperature and salinity. Our study exemplifies that community structure can be affected by the complexity of the habitat. In heterogeneous environments, coexisting species have more distinct niche separations and, hence, are likely to differ in their temporal responses to environmental changes.

Materials and Methods

Zooplankton data

For our study we combined data from three long-term zooplankton monitoring programmes in the Central Baltic Sea (CBS; Fig. 5-1b) covering the last five decades. The most comprehensive programme is conducted by the Latvian Institute of Food Safety, Animal Health and Environment (BIOR) in Riga. Since the late 1950s, quarterly sampling on multiple stations (usually in February, May, August and October) was consistently conducted in the Eastern Gotland Basin, while the Bornholm Basin and Gdansk Deep were sampled irregularly between 1959 and 1991 (Möllmann *et al.* 2000). The sampling gear, a Juday Net (UNESCO 1979), has a mesh size of 160µm and an opening diameter of 0.36m. It is operated vertically and considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be slightly underestimated. Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a maximum depth of 150m.

Further zooplankton monitoring was performed by the Finnish Environment Institute (SYKE) in Helsinki since 1979 in summer (mainly August) at one station per basin. While the sampling was conducted continuously until 2008 in the Gotland Basin, it stopped in 1990 in the Bornholm Basin and the Gdansk deep. In accordance with the Helsinki Commission (HELCOM) monitoring and assessment programme (HELCOM 1988), a WP-2 with a mesh size of 100 µm was hauled vertically. Within the same programme using the same gear, one station in the Bornholm Basin was sampled regularly one to six times per season by various countries. This data was provided by the Leibniz-Institute for Baltic Sea Research (IOW) in Warnemünde, Germany.

In order to construct time series on spring and summer biomass ($\text{mg}\cdot\text{m}^{-3}$) for our study species *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* and the period of 1959 – 2008, we combined data from these monitoring programmes (i.e. from BIOR, SYKE and IOW) into single time series for each basin according to the following procedure:

- First, we calculated for each species and dataset the basin- and season-specific annual mean in biomass by averaging across stations and samplings (within each basin, season and year). All stations within ICES sub-division (SD) 25 were hereby assigned to the Bornholm Basin, stations within SD 26 to the Gdansk Deep, and stations within SD 28-2 to the Eastern Gotland Basin.
- We then combined the dataset-specific time series into a single one by calculating weighted annual means of transformed mean biomass values of each individual time series, which were back-transformed afterwards.
- Eventually, we accounted for gear-specific capture efficiencies and different spatial and temporal resolutions by computing $\log_{10}(Bm+0.001)$ transformed anomalies (see Mackas & Beaugrand, 2010):

$Bm'_{xsb}(y) = \log[Bm_{xsb}(y)] - \log[\overline{Bm}_{xsb}] = \log[Bm_{xsb}(y)/\overline{Bm}_{xsb}]$, where $Bm_{xsb}(y)$ is the mean biomass of species x, in season s and basin b in a particular year y. \overline{Bm}_{xsb} represents the species-, season-, and basin-specific multi-annual mean.

Hydro-climatic and predation data

Main hydrographic variables affecting *Acartia* spp., *T. longicornis* and *P. acuspes* are water temperature and salinity (Vuorinen *et al.* 1998, Möllmann *et al.* 2000, Renz & Hirche 2006, Holste *et al.* 2009). We therefore computed time series of seasonal temperature and salinity values for each basin. To account for the copepods specific habitats, mean values for the observed depth ranges were calculated (Hernroth & Ackefors 1979, Renz & Hirche 2006, Schmidt 2006, Dutz *et al.* 2010), i.e. for *Acartia* spp. and *T. longicornis* in both seasons 0-20 m and 20-40 m, respectively, and for *P. acuspes* in summer 20 – 50 m. In spring *P. acuspes* is observed across a greater vertical range, with younger stages being more in the upper water column and older stages near the halocline. Earlier studies showed a temperature effect on the early copepodit stages while salinity affected late copepodite and adult stages (Möllmann *et al.* 2000, unpublished results). Temperature time series, hence, were calculated for 20-60 m depth and salinity for the halocline region (60-90m in BB/GD and 70-100m in GB). In order to match the timing of the zooplankton sampling, we included only April and May samplings for spring and July and August samplings for summer. Hydrographic data were derived from a database of the International Council for the Exploration of the Sea (ICES; <http://www.ices.dk/ocean/asp/HydChem/HydChem.aspx>).

As indicator for climate variability we used the Baltic Sea Index (BSI), a local climate mode representing the difference of normalized sea level pressure (SLP) anomalies between Oslo in Norway and Szczecin in Poland. Although closely correlated to the NAO (North Atlantic Oscillation Index) and the NAM (Northern Hemisphere Annular Mode), the BSI generally has been better related to local oceanographic processes in the Baltic than remote, large-scale atmospheric patterns over the North Atlantic (Lehmann *et al.* 2002). BSI calculations exist either based on

SLPs obtained from the NCEP (US National Centers for Environmental Prediction) or the SMHI (Swedish Meteorological and Hydrological Institute) database. Both time series differ slightly in their temporal coverage, causing deviations in the overall mean and consequently in the calculated monthly anomalies in overlapping years. In this study, the full time series (1970-2008) of the SMHI based BSI was used, since it is considered to reflect better the local situation (A. Lehmann, GEOMAR, Kiel, Germany, pers. comm.). For missing years 1960 – 1969, the index is based on the NCEP data. Annual winter mean values (Dec-March) were calculated for the BSI, since winter patterns of local and regional wind fields are more pronounced in amplitude and areal coverage (Stenseth *et al.* 2003) and have a strong influence on the hydrographic situation during the seasonal production period in spring (Dippner *et al.* 2000).

Copepods are major prey species for planktivorous fish such as herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea (Möllmann *et al.* 2004). Sprat has been shown to significantly control the population size of *P. acuspes* (Möllmann and Köster 2002) and sprat stock size would be a suitable indicator of predation pressure (Casini *et al.* 2008). However, stock size estimates for sprat are not available prior to 1974 (ICES 2011). Hence, a predation index (PI) was developed using stock size estimates for cod (*Gadus morhua*). Eastern Baltic cod is the major piscivore in the Baltic Sea and its stock size is inversely related to the stock size of sprat (Casini *et al.* 2008, Möllmann *et al.* 2008). We used spawning stock biomass (SSB) estimates for cod from official stock estimates that date back to 1966 (ICES 2011), and extended the time series back to 1960 using estimates by Eero *et al.* (2007). The combined time series was inversed to mimic the predation pressure by planktivorous sprat and standardized to values between 0 and 1 and. The max. value of cod SSB is represented therefore by a PI value of 0 while the min. cod SSB value is indicated by a PI value of 1.

Food-limitation may be an important influence on population dynamics of copepod species. However, studies on the feeding ecology of Baltic copepods in the field are scarce. Investigations using lipid biomarkers showed an opportunistic feeding behaviour of *P. acuspes*, with strong seasonal variability and high importance of ciliates in addition to diatoms, dinoflagellates and cyanobacteria (Peters *et al.* 2006). Unfortunately no reliable estimates of the different food sources were available for our full investigation period. Furthermore earlier studies indicate the stronger importance of hydro-climatic variables as well as predation for the dynamics of *P. acuspes* (Möllmann *et al.* 2008, Casini *et al.* 2009). Hence, we ignored food availability in our analysis.

Statistical Analysis

We used Generalized Additive Modelling (GAM) techniques (Hastie & Tibshirani 1990, Wood 2006) in our study that have the advantage to not require an a priori specification of the relationship between the response variable (Y) and the explanatory variable (X). Each Y_i is linked

with X_i by a smoothing function instead of a coefficient β as in traditional regression techniques and hence relationships do not have to be linear.

For each species we first tested whether the long-term dynamics in spring and summer differed between basins. For this, we compared GAMs in which log-transformed biomass anomalies were either modelled with a single year-smoother for the entire area or alternatively with basin-specific smoothers. To focus only on the major trends and avoid over-parameterisation, we limited the effective degrees of freedom to a maximum of 3. For the comparison of the corresponding models we applied an F-ratio test (Wood 2006). Significant differences (p-values < 0.05) indicated here that the more complex GAMs with basin-specific smoothers were the correct model.

We furthermore used the non-linear regression techniques to identify the role of climate, hydrography and predation pressure on the seasonal long-term trends of each copepod. A first data exploration as well as previous studies revealed linear as well as non-linear relationships particularly between copepods and the abiotic environment. We therefore modelled each spring and summer biomass by smoothing functions of the different environmental variables. By allowing the smoothing functions to differ per basin we tested for basin-specific biomass-environment relationships.

The following model was used for the seasonal model of each species:

$$X_{by}^s = \alpha_b + f_b(BSI_y) + g_b(T_{by}^s) + i_b(S_{by}^s) + j_b(PI_y) + \varepsilon_{by}^s$$

where X_{by}^s is the season-specific (index s) log-transformed biomass anomaly of species X in basin b and year y. f_b , g_b , i_b , and j_b are basin-specific thin plate regression spline functions describing the effect of the locale climate index BSI, temperature (T), salinity (S), and predation (PI) respectively. α_b is the intercept at basin b and ε the random noise term assumed to be normally distributed with zero mean and finite variance. To avoid over-smoothing, which is likely to occur with small data sets (<50) (Zuur *et al.* 2009), we let the effective degrees of freedom be restricted to a maximum of 4. The optimal amount of smoothing was estimated each time using the cross-validation method (Wood 2006). In deciding which smoothing term to include in the final model, we applied a backward stepwise selection approach. Initially, we started with a full model that included a basin effect and basin-specific smoothers for all four covariates. As selection criterion we used the Akaike's Information Criterion (AIC), a measure of the goodness of fit of a model, which takes also the number of parameters into account by imposing a penalty term for increasing the number of parameters. The underlying statistical assumptions were then tested through residual diagnostics of the optimal model. The residuals of the final models showed no evidences of non-normality, heterogeneity or autocorrelation. Except for the alternative spring model of *Acartia* spp., which indicated temporal dependencies of the residuals. To account for this autocorrelation, we extended the GAM to a Generalized Additive Mixed

Model (GAMM) by including a correlation structure in the model. This extension allows the model a more complex stochastic structure and implies that the single elements of the response variable are not independent anymore (Wood 2006). We hereby tested various structures and chose the one performing best based on the AIC (Zuur *et al.* 2009). The analyses were performed using the package 'mgcv' (with version R2.10) (Wood 2006) within the 'R' statistical and programming environment (R Development Core Team 2009).

Results

To understand how climatic variability and change affect the zooplankton level within marine, open sea habitats over long time-scales, we examined first the long-term development of the major copepod species *Acartia* spp., *Temora longicornis*, and *Pseudocalanus acuspes* in the Central Baltic Sea (CBS). The comparison revealed species-specific long-term trends that varied between seasons (Fig. 5-2). The overall trend in *Acartia* spp. biomass was positive in all areas, particularly in spring and in the Gdansk Deep (GD), and linear between the mid-1970s and 1990. Non-linearity arose either from a delayed biomass increase as seen in the Gotland Basin (GB) in spring and the GD in summer, or by a saturation at high biomass values at the end of the study period in summer (GD) or in both seasons in the Bornholm Basin (BB). Similar to *Acartia* spp., *T. longicornis* displayed a strong increase in spring biomass. The rise in population size was continuous in the BB and rather step-wise in the more eastern GD and GB as was the overall trend. No significant trends were observed for *T. longicornis* in summer. Contrary to the other two calanoids, *P. acuspes* displayed in almost all basins an increasing trend until the late 1970s and a decreasing trend thereafter. This trend is most pronounced in summer where biomass started to increase again during the 2000s. Only in GD in spring we find a generally continuous trend.

As a first step in our statistical analysis we tested for differences in the temporal development of copepod species biomass between the three basins of the CBS. We compared Generalized Additive Models (GAMs) with a single year-smoother for the entire CBS with those having basin-specific smoothers. We found only the long-term spring and summer dynamics of *Acartia* spp. to significantly differ between the three sub-areas (Tab. 5-1). In contrast, *T. longicornis* and *P. acuspes* displayed statistically homogenous trends in all sub-areas.

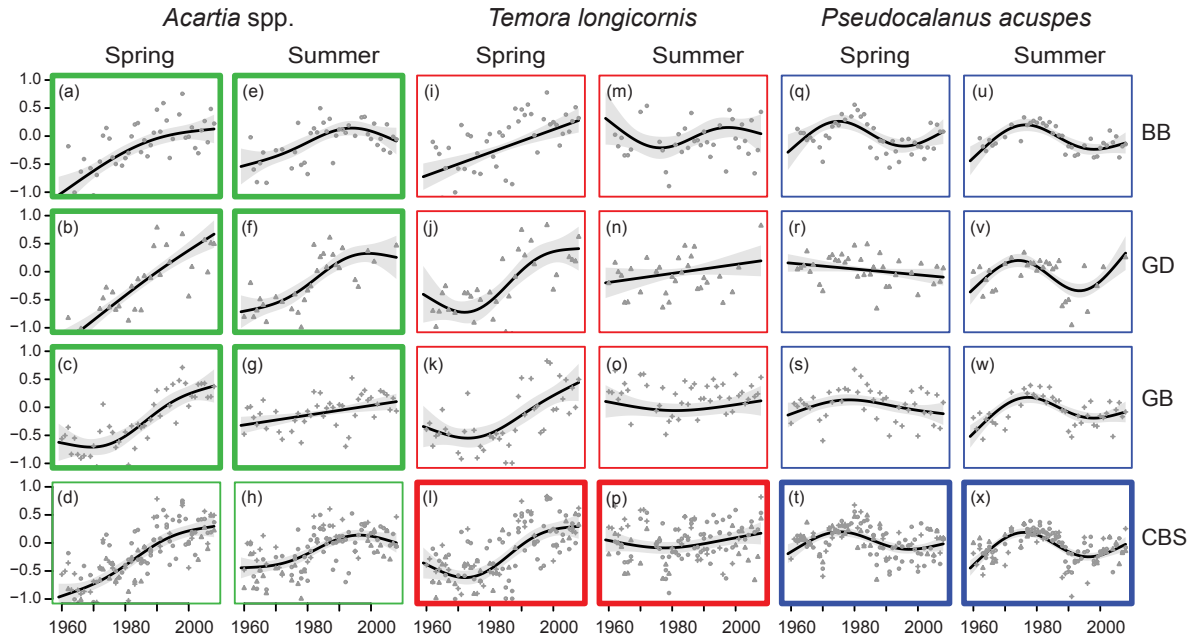


Figure 5-2: Observed and predicted long-term trends. Spring and summer biomass anomalies of *Acartia* spp. (a-h, green boxes), *T. longicornis* (i-p, red boxes), and *P. acuspes* (q-x, blue boxes) are presented for the Bornholm Basin (BB), the Gdansk Deep (GD), the Gotland Basin (GB), and all three basins together (CBS). Open circles (BB), triangles (GD) or crosses (GB) represent the observed values in each basin, while the continuous lines indicate the predicted trends from the Generalized Additive Models (GAM) based on basin-specific smoothers or on a single smoother for the entire CBS region. The shaded areas indicate the pointwise 95% CI. Trends from GAMs showing a better performance, i.e. a lower AIC, are indicated in bold boxes.

Table 5-1: Summary of the F-ratio tests. Comparison of models with a single year-smoother for the entire CBS and basin-specific smoothers using the F-ratio tests for each species and season. The residual deviance and the residual degrees of freedom (df) are given for each model together with the reduction in deviance and the change in df's, the F-statistic and its probability value. P-values < 0.05 indicate the more complex GAM with basin-specific smoothers to be correct and are indicated in bold.

Species-Season	Model	Resid.	Df Resid.	Dev.	Df Dev.	F	P-value
<i>Acartia</i> spp. - Spring	f(Year)	121.35	16.15				
	f (Year):basin	118.06	14.04	3.29	2.11	5.40	0.001
<i>Acartia</i> spp. - Summer	f (Year)	112.16	9.40				
	f (Year):basin	108.72	8.06	3.45	1.33	5.21	0.001
<i>T. longicornis</i> - Spring	f (Year)	121.13	19.54				
	f (Year):basin	117.78	19.14	3.35	0.40	0.73	0.6
<i>T. longicornis</i> - Summer	f (Year)	112.94	17.02				
	f (Year):basin	109.61	16.41	3.32	0.61	1.23	0.3
<i>P. acuspes</i> - Spring	f (Year)	121.08	7.24				
	f (Year):basin	117.72	7.16	3.36	0.09	0.42	0.8
<i>P. acuspes</i> - Summer	f (Year)	112.03	4.87				
	f (Year):basin	106.21	4.35	5.81	0.52	2.19	0.1

Next we used GAMs to test for the effects of important external driving variables on the biomass of these main CBS copepod species (Tab. 5-2). Candidate environmental drivers were selected based on prior knowledge (see Tab. 5-S1 in Supporting Information SI). First of all we found differences in the average biomass level between basins as indicated by a basin effect on the intercept. Biomass of *Acartia* spp. as well as *T. longicornis* in spring was higher in the more western BB and did not significantly differ between the GD and GB. In summer, we observed in contrast the highest biomass of *T. longicornis* and *P. acuspes* in the GB. The effects of external variables on the long-term dynamics were only partly basin-specific and differed between species and seasons (see below).

The most parsimonious and best-fitted models for *Acartia* spp. in spring and summer explained 62% and 30% of the total variance, respectively (Tab. 5-2). The climate index (Baltic Sea Index – BSI) explained most of the annual variation in biomass. Spring BSI effects were positively linear, but of basin-specific strength (Fig. 5-3). In contrast, the effect on summer biomass was spatially consistent and non-linear with a stronger positive influence during periods with negative BSI anomalies. Temperature was a significant predictor of *Acartia* spp. biomass only in spring, but similar to the BSI of basin-specific strength. While the effect of temperature was weakly positive for BB, it was highly significant and non-linear in the GD with an overall negative trend. Further significant predictors for *Acartia* spp. were salinity and predation, having uniform effects across basins. The salinity effect was in both seasons close to negatively linear as was the predation effect in summer. In contrast, the *Acartia* spp. response to predation in spring was highly non-linear, being positive at the highest predation levels. As this is ecologically difficult to explain and rather points towards a spurious relationship, we conducted an alternative model selection excluding predation. This resulted in significant autocorrelation, which we accounted for by including an exponential correlation structure. The selected alternative model contained only BSI as significant driver, but had less explanatory power than the model including predation (Tab. 5-S2, Fig. 5-S1 in SI).

In our statistical analyses for *T. longicornis*, external environmental drivers had no basin-specific effects (Tab. 5-2). The most parsimonious and best-fitted spring model included, similarly to *Acartia* spp., a significant, albeit ecologically difficult to explain predation effect (Fig. 5-4). We hence again applied an alternative model selection without predation, which resulted in a model where most of the variance was explained by the positive linear effects of temperature and BSI. Increasing salinity had additionally a strong, though negative influence. Differences between the models with and without predation were only minor, explaining 62% and 56% of the total variation. The finally selected summer model for *T. longicornis* retained only the BSI as significant predictor. Similar to *Acartia* spp. in summer, the relationship was mainly positive during phases of negative BSI anomalies but explained alone only 5% of the fluctuations. Most of the variance in the summer model was explained by the basin effect only.

Table 5-2: Generalized Additive Model (GAM) results for the three copepods in spring and summer.

The intercept, individual significances of the parametric basin term, estimated degrees of freedom (edf), significance (P-value), and explained deviance of the various smoothing effects are presented together with the adjusted R^2 . If basin had an effect on the average biomass anomaly (i.e. the intercept), the intercept for the Bornholm Basin was used as a baseline while estimates of the Gdansk Deep and Gotland Basin are corrections on this. Note that for the *Acartia* spp. spring model the BSI and temperature smoother are presented for each basin separately but explained deviance is given for all three combined. The covariate that explains most is indicated in bold.

<i>Acartia</i> spp.							
Spring				Summer			
R^2 - adj. = 0.621				R^2 - adj. = 0.299			
	Estimate	P-value		Estimate	P-value		
Intercept (BB)	-0.111	0.057		Intercept (BB)	0.049	0.049	
GD	-0.25	0.004		GD	-0.168	0.031	
GB	-0.19	0.039		GB	-0.324	0.001	
Covariate	edf	P-value	expl. dev.	Covariate	edf	P-value	expl. dev.
BSI : BB	1	0.003		BSI	2.745	<0.001	13.0%
BSI : GD	1	<0.001	39.3%	S	1	<0.001	7.24%
BSI : GB	1	0.001		PI	1.567	<0.001	7.21%
T : BB	1	0.049					
T : GD	3.78	<0.001	22.2%				
T : GB	1	0.779					
S	1.76	0.005	15.3%				
PI	3.25	0.002	19.5%				
<i>Temora longicornis</i>							
Spring				Summer			
R^2 - adj. = 0.556				R^2 - adj. = 0.192			
	Estimate	P-value		Estimate	P-value		
Intercept (BB)	0.001	0.991		Intercept (BB)	-0.095	0.056	
GD	-0.271	0.001		GD	0.024	0.749	
GB	-0.359	<0.001		GB	0.292	<0.001	
Covariate	edf	P-value	expl. dev.	Covariate	edf	P-value	expl. dev.
BSI	1	0.008	30.3%	BSI	1.88	0.043	5.02%
T	1	0.002	36.3%				
S	1.99	<0.001	19.6%				
<i>Pseudocalanus acuspes</i>							
Spring				Summer			
R^2 - adj. = 0.275				R^2 - adj. = 0.496			
	Estimate	P-value		Estimate	P-value		
Intercept	0.02	0.323		Intercept (BB)	-0.166	<0.001	
				GD	0.105	0.091	
				GB	0.2	0.003	
Covariate	edf	P-value	expl. dev.	Covariate	edf	P-value	expl. dev.
BSI	1	0.017	8.54%	BSI	3.891	<0.001	16.5%
T	2.04	0.01	8.18%	S	1	<0.001	23.1%
PI	1	<0.001	22.1%	PI	1.03	<0.001	40.4%

Basins: BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin

Covariates: BSI=Baltic Sea Index, T=Temperature, S=Salinity, PI=Predation Index

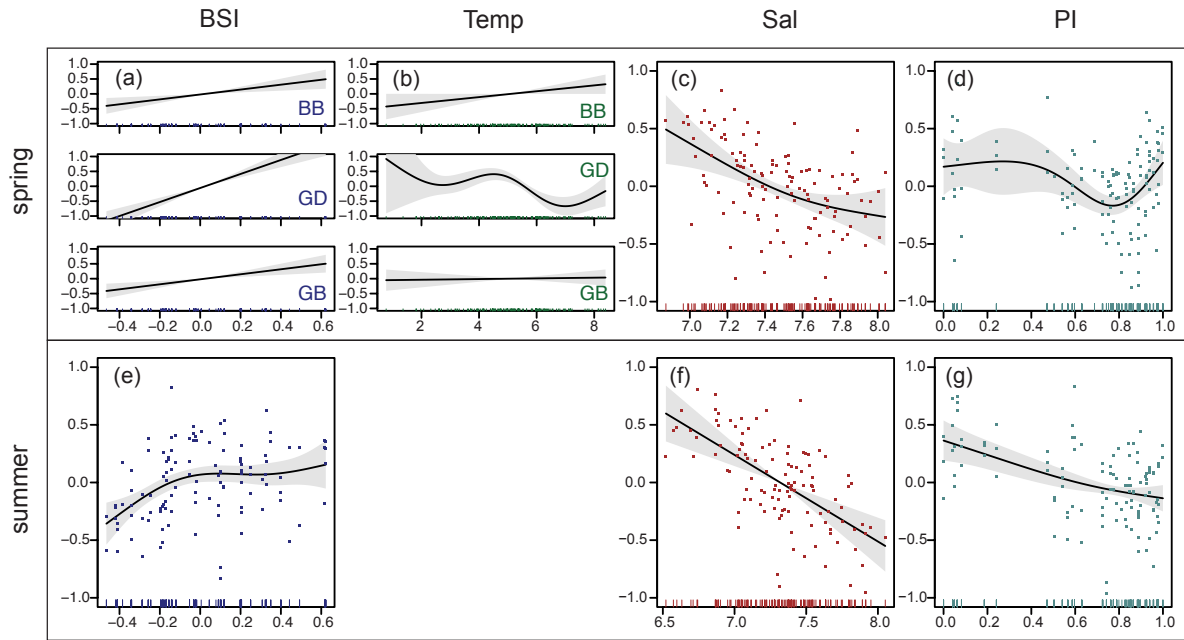


Figure 5-3: Statistical model results of *Acartia* spp. Partial plots from the final spring (upper row) and summer (lower row) GAM models showing the effect of significant covariates. The effects of the BSI (a,e), temperature (b), salinity (c,f), and PI (d,g) are presented for each basin separately or together depending on the significance and model performance. Values on the y-axis indicate the effect that the term on the x-axis has on the biomass anomaly. The solid lines indicate the smoothed (non-) parametric trend, shaded areas indicate the pointwise 95% CI. The rug along the x-axis indicates the location of the observations.

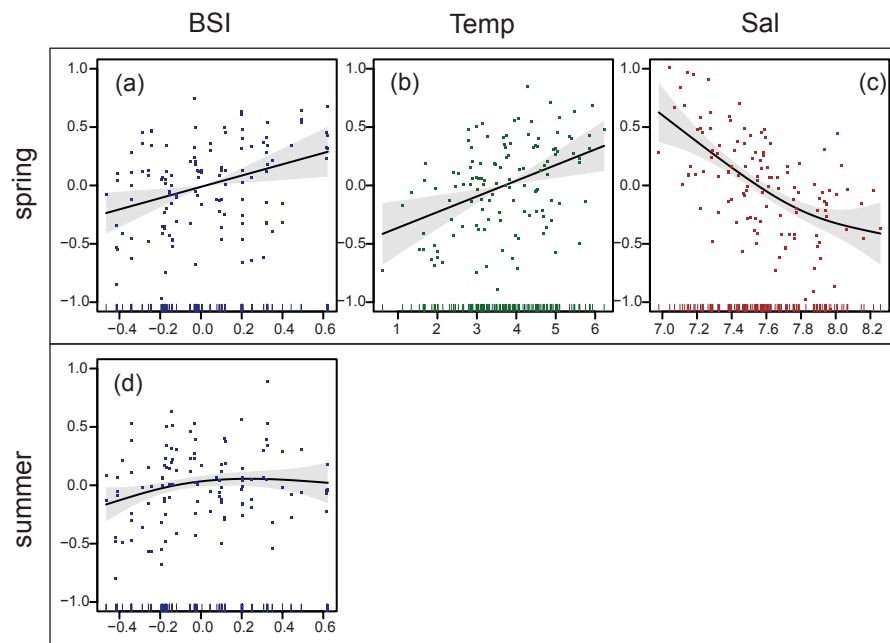


Figure 5-4: Statistical model results of *T. longicornis*. Partial plots from the final spring (upper row) and summer (lower row) GAM models showing the effect of significant covariates. The effects of the BSI (a,d), temperature (b), and salinity (c) are presented for all three basins together. For further details see Fig. 5-3.

Modelling long-term dynamics of *P. acuspes* revealed significant effects of BSI, temperature, and predation in the final spring model (explaining 28% of the total variance), whereas in the summer model temperature was the only insignificant variable (the summer model explained 50% of the total variance) (Tab. 5-2). Overall *P. acuspes* showed no basin-specific responses to these drivers (Fig. 5-5). The most important driver was in general the predation pressure with a negative effect explaining 22% and 40% in spring and summer biomass, respectively. Temperature had a generally positive and slightly non-linear effect in spring while salinity had an overall positive effect in summer. The BSI showed a clear negative linear effect in spring, while in summer a highly non-linear effect was observed with two difficult to explain maxima. However, excluding this predictor would reduce the explanatory power of the model only by a few percent but would cause a strong impairment of the residual variance. We therefore kept the BSI in the final summer model.

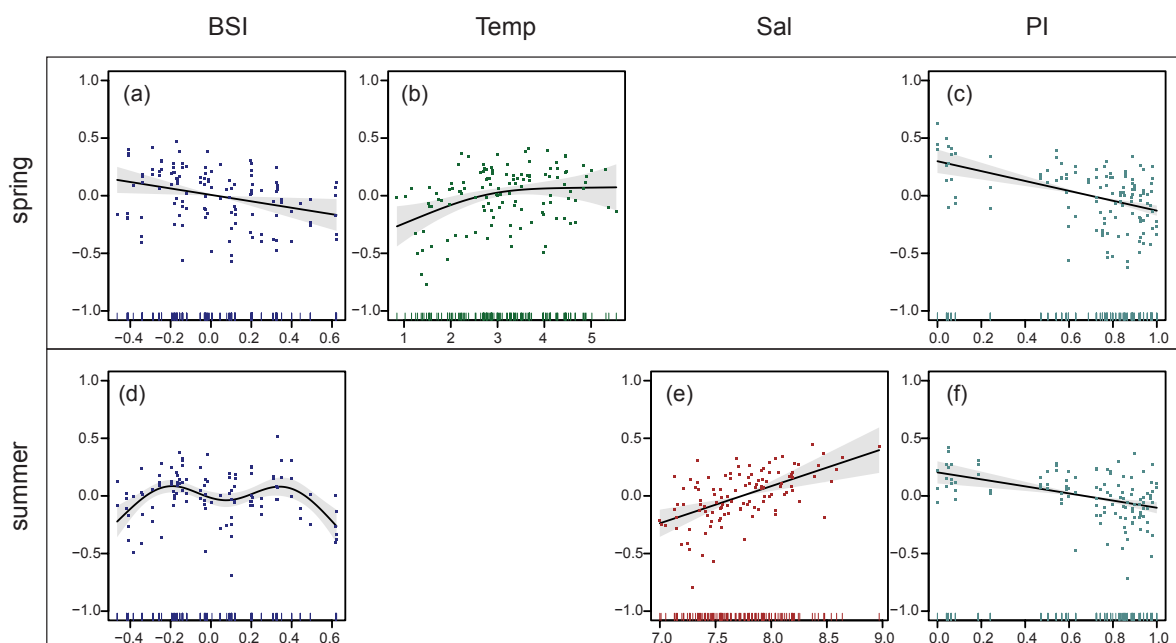


Figure 5-5: Statistical model results of *P. acuspes*. Partial plots from the final spring (upper row) and summer (lower row) GAM models showing the effect of significant covariates. The effects of the BSI (a,d), temperature (b), salinity (e), and PI (c,f) are presented for all three basins together. For further details see Fig. 5-3.

Discussion

Using a unique long-term data set of marine zooplankton we demonstrated that the effect of climate variability and change on the dominant Baltic zooplankton species depends strongly on species-specific habitat utilization. Our three study species, the calanoid copepods *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes*, utilize to a large degree vertically separated water layers, characterized by different abiotic and biotic conditions. Since these water layers are differentially affected by climatic changes, significant predictor variables in our statistical

modelling exercise were as well species-specific. Generally, *Acartia* spp. inhabiting surface water was mainly affected in spring by atmospheric conditions, while *P. acuspes* due to its deeper habitat was mainly influenced in summer by variability in salinity and fish predation. Biomass of *T. longicornis* inhabiting the mid-water was consequently determined by both atmospheric conditions and mid-water temperature.

In the CBS, *Acartia* spp. is the most surface-orientated species and hence more directly exposed to warming effects than our other study species (Hansen *et al.* 2006). Consequently most of the temporal variability in biomass was explained by the climate index BSI and temperature, agreeing with laboratory experiments that show high temperatures to increase reproductive success (Holste & Peck 2006). Previous studies could also demonstrate the importance of sea surface temperature (SST) on the long-term spring dynamics of *Acartia* spp. (Dippner *et al.* 2000, Möllmann *et al.* 2000). However, in our study *Acartia* spp. showed a stronger response to the local climatic winter conditions, indicating that other factors related to the BSI are of importance. Winter patterns of local and regional wind fields are known to have a strong influence on phytoplankton dynamics and the onset of the spring bloom (Wasmund & Uhlig 2003). After mild winters for instance the water column remains stratified, which prevents the deepwater mixing and upward nutrient transport necessary particularly for diatoms (Harrison *et al.* 1986). The recent shift of the spring bloom to earlier periods observed in the Baltic Sea (Trzosinska & Lysiak-Pastuszek 1996, Wasmund & Uhlig 2003) has been related to decreased mixing due to increases in winter SST. Phytoplankton production is known to be an important driver for *Acartia* spp. (Möllmann *et al.* 2008), having a stronger effect on egg production than temperature (Koski & Kuosa 1999, Dzierzbicka-Glowacka *et al.* 2010). Due to a lack of long-term data we here could not test for the additional effect of phytoplankton on copepod dynamics directly, but assuming BSI and SST to reflect to some degree phytoplankton production changes.

We found climate to affect *Acartia* spp. strongest in spring, which is in agreement with earlier studies that show that climate impact is strongest in the beginning of the production season affecting phenology and overall biomass levels (Dippner *et al.* 2000, Möllmann *et al.* 2000, Möllmann *et al.* 2008). Our results suggest that long-term spring dynamics are translated to summer but dampened by predation pressure. Adult sprat usually feed mainly in the deep-water layer, hence not overlapping with *Acartia* spp. (Möllmann *et al.* 2004). But in summer, sprat larvae feed at the surface, particularly on *Acartia* spp. copepodites (Voss *et al.* 2003, Voss *et al.* 2007) and the amount of food consumed by sprat larvae can account for a relatively high proportion of the total sprat consumption (Arrhenius & Hansson 1993). Earlier studies did not find a significant predation effect (Kornilovs *et al.* 2001, Möllmann *et al.* 2008), which may be due to the fact that our dataset compared to earlier studies now includes the period of peak sprat population size. In contrast to earlier studies on *Acartia* spp. long-term dynamics (Möllmann *et al.* 2000) but in agreement with laboratory experiments (Holste & Peck 2006), we found a significantly negative effect of salinity. This may again be a result of the longer period covered by

our updated dataset, including now constantly decreasing surface salinities (see Fig. 5-S2, 5-S3), probably now being critical to reproductive success of *Acartia* spp. (Holste & Peck 2006).

Population dynamics of *T. longicornis* in the Baltic Sea have been recently shown to depend on the prevailing temperature conditions as well as on the spring bloom timing and post-bloom food availability (Dutz *et al.* 2010). This is in line with our findings for the long-term dynamics, where temperature and the BSI (as an indicator for phytoplankton dynamics) explained most of the variance. While the phytoplankton bloom triggers the onset of egg production by females, higher temperatures shorten the development time, increase the number of larger copepodite stages, and in consequence also the total spring biomass (Dutz *et al.* 2010). As *T. longicornis* shows also a stronger positive response in egg production rate to temperature increases than *Acartia* spp. (Holste & Peck 2006), temperature explained most of the long-term variation of *T. longicornis* in our spring model. The positive temperature effect on the long-term spring dynamics has been already recognized in previous studies (Dippner *et al.* 2000, Möllmann *et al.* 2000), whereas the relevance of primary production dynamics has only recently been observed (Dutz *et al.* 2010), which points towards the need to include phytoplankton as a driving variable in long-term studies on zooplankton dynamics.

We only found a positive response of *T. longicornis* to the environmental changes in spring. It was suggested that the observed increase in biomass in the last two decades (Alheit *et al.* 2005, Möllmann *et al.* 2009) was not a numerical population response but rather reflects an earlier onset of population development (Dutz *et al.* 2010). Comparing the spring with the summer trends supports this hypothesis as no long-term increase in biomass was translated from spring to summer as observed for *Acartia* spp. or *P. acuspes*. Our dataset however is lacking the temporal resolution to identify this potential phenological change. On the other hand, as climatic conditions in the recent past seem to be generally in favour for *T. longicornis*, there must have been strong factors controlling its production leading to the different summer dynamics. One possible explanation could be food limitation in early summer, which limits the copepod development and body growth (Dutz *et al.* 2010) and reduces the rate of egg production as seen for the southern Gulf of St. Lawrence (Maps *et al.* 2005). Since *T. longicornis* inhabits mainly the water layer below the thermocline, individuals depend strongly on sinking materials whereas *Acartia* spp. can feed directly on the phytoplankton at the surface. Yet another reason could be the increase of predation pressure on this species by sprat (Möllmann & Köster 2002), which counterbalanced the simultaneous increase in population biomass of *T. longicornis*, hence keeping the inter-annual summer dynamics rather constant and obscuring any detectable effect in the statistical model. We also obtained, similarly to *Acartia* spp., a negative effect of increasing salinities in the final spring model, which is not in agreement with laboratory results (Holste *et al.* 2009) and previous field studies (Vuorinen *et al.* 1998, Möllmann *et al.* 2000). As euryhaline species *T. longicornis* can tolerate a wide range of salinity concentrations but usually prefers

salinities > 8 (Holste *et al.* 2009). The importance of salinity for Baltic *T. longicornis* hence needs further investigation.

In contrast to *Acartia* spp., later developmental stages and adults of *P. acuspes* are directly exposed to fish predation in the deepwater (Möllmann *et al.* 2004) supporting our statistical result of predation as the main driver of its long-term dynamics. *P. acuspes* showed also a positive response to increases in deepwater salinity in summer. This in accordance to earlier studies claiming this marine, glacial relict species prefers high salinities particularly for reproduction (Ojaveer *et al.* 1998, Möllmann *et al.* 2000, Renz & Hirche 2006). However, in our final spring model salinity showed no significant effect on the total biomass. An alternative modelling study based on stage-specific abundances confirmed a negative salinity relationship for later developmental and adult stages (unpublished results). The salinity dependence is relaxed in earlier developmental stages, leading to an ontogenetic vertical distribution (Hansen *et al.* 2006, Renz & Hirche 2006). As nauplii and young copepodite stages account for two-third of the total biomass in spring, the peak reproduction season, salinity in our model played only a minor role in the long-term dynamics of the total biomass. In summer, though, late copepodite stages are highly abundant and account for most of the total biomass, which explains why we identified a significant salinity effect for this season.

Although *P. acuspes* is a cold-water species with temperature preferences e.g. in the Chukchi Sea below < 3 °C (Hopcroft & Kosobokova 2010), we found a positive temperature effect in spring that levelled off around 4 °C. Temperature has generally a positive effect on growth rates and development times of copepods (Vidal 1980, Hirst & Bunker 2003, Liu & Hopcroft 2008). It is, therefore, likely that the overall effect we found was mainly related to the dynamics of the younger stages as growth rates become less temperature-dependent with increasing age (Vidal 1980, Dzierzbicka-Glowacka 2004). This is in line with findings of our stage-specific modelling study (unpublished results), in which temperature affected only the copepodit stages 1-3 with highest abundances between 4 to 6 °C. Previous long-term studies in the Baltic Sea, in contrast, could not find significant relationships between *P. acuspes* total biomass and temperature (Dippner *et al.* 2000, Möllmann *et al.* 2000). These studies, however, covered only a shorter time period, not including the warm years in the last decade.

We also found a negative, albeit weak linear effect of the BSI on *P. acuspes* in spring and a strong non-linear effect in summer. As lower salinities have been related to positive BSI anomalies and *vice versa* (Möllmann *et al.* 2003), the BSI effect in spring could indirectly reflect the positive influence of deepwater salinity. However there is a lack of correlation between BSI and salinity in the BB, the latter showing a different trend than in the GD and the GB (see Fig. 5-S3). In our stage-specific modelling study (unpublished results), we found a weak non-linear and mainly negative BSI effect on the nauplii stages, which inhabit the upper water layer. Hence, the overall negative effect of higher temperatures observed in this study, might be driven by nauplii dynamics. A potential explanation could be that during periods with negative BSI anomalies (Fig.

5-S4), *Acartia* spp. was less abundant and therefore competition for food less intensive. The highly non-linear relationship is however difficult to interpret ecologically and has to be left unexplained.

The underlying assumption of our study was the role of habitat heterogeneity in the species-specific response to environmental changes due to differences in their physiological adaptations (i.e. their fundamental niches – FN) and species interactions (Fig. 5-1a). This is supported by our findings for the three major zooplankton species, which show clear differences in long-term trends and their main drivers. As other, less dominating zooplankton species, which we have not tested for, are also probable to vary in their response to hydro-climatic changes zooplankton assemblages are likely to undergo temporal changes. In spring however, differences between *Acartia* spp. and *T. longicornis* abundances were only minor. Both species showed a strong response to the surrounding temperature conditions, which only differed to a minor degree between the surface (inhabited by *Acartia* spp.) and the mid-water (*T. longicornis*) (Fig. 5-S2). They further show highest egg production rates under laboratory conditions at similar temperatures, i.e. 13-18 °C for *Acartia* spp. and 17 °C for *T. longicornis* (Koski & Kuosa 1999, Holste *et al.* 2009), suggesting a great overlap in their thermal FN. As the water temperature in the CBS in spring ranged only from 1 to 8 °C in the upper 40 m over the investigated time period (Fig. 5-S2), their thermal potential niches (PN) might not have been fully within the optimal part of their FN and a further increase in biomass under higher temperatures is even likely. This could be particularly the case for *T. longicornis* as this species responds stronger to temperature changes than *Acartia* spp. (Holste & Peck 2006).

The role of biotic interactions becomes particularly apparent in the long-term dynamic of *P. acuspes*. The fact that we identified predation as the most important factor suggests that mainly the realised niche (RN) space changed over time, which by definition represents the FN including biotic interactions such as predation or competition (Hutchinson 1957). Originally the RN space was perceived as a subset of the FN space, or PN, limited by e.g. competitive exclusion. But recently other mechanisms influencing the RN have been included, which could also increase this niche space such as dispersal (Holt 1985, Pulliam 2000). In the case of the marine copepods *Calanus finmarchicus*, Helaouët & Beaugrand (2009) observed a strong coupling of the realized and the fundamental thermal niche with rather similar niche widths. Dispersal was here suggested to be limited due to hydrodynamical barriers. But for Baltic Sea copepods, the realized niche is smaller owing to the strong fish predation. Particularly when the vertical overlap is high as in the case of *P. acuspes*.

In addition to the importance of vertical habitat heterogeneity for our study species, we investigated the effect of spatial thermohaline variability on intra-specific population trends. As this has not been strongly investigated in the realm of marine, pelagic systems we compared long-term dynamics of populations of our study species that live in different basins of the CBS. We found that the importance of horizontal habitat heterogeneity strongly interact with vertical

habitat heterogeneity. Although the CBS features a horizontal gradient in temperature and salinity, we did not observe basin-specific changes in biomass of *T. longicornis* or *P. acuspes*, which were strongly influenced by temperature and salinity respectively. A possible explanation is the temporal consistency of these gradients, as indicated by common long-term trends (Fig. 5-S3). The lack of basin-specific responses indicates that differences in both hydrographic parameters seem to be not strong enough to cause populations of both species to follow different trajectories as response to size differences in the potential thermohaline niche space. In contrast, populations of *Acartia* spp. showed long-term trends specific to their vertical habitat, coupled with basin-specific, spatial responses to changes in the BSI and temperature. While BSI and the surface temperature in spring were not basin-specific, long-term trends of phytoplankton groups varied spatially (Wasmund & Uhlig 2003, Wasmund *et al.* 2011), suggesting effects to be rather indirect via the phytoplankton dynamics. Regional differences in the coupling of water flow and heat exchange, indicated by e.g. basin-specific correlations between BSI and SST (Hinrichsen *et al.* 2007), can lead in combination with differences in nutrient loadings and salinity concentrations to different developments of phytoplankton taxa (Wasmund *et al.* 2011).

To address the importance of habitat complexity for intra-specific population variability, we had to merge data sets from different monitoring programmes. The robustness of our model results and the consistency of long-term trends between basins within each species indicate that the application of log-transformed anomalies is an appropriate tool when merging different datasets (Mackas & Beaugrand 2010). Despite the fact that sampling methods were different between the three datasets, we did not identify any bias of varying capture efficiencies when incorporating the IOW and SYKE dataset into the BIOR time series. On the contrary, merging the different time series enabled us to use this unique spatially resolved dataset covering a period of five decades. It further allowed us to increase the sample size and hence the statistical robustness of our statistical models. The focus on the thermohaline potential niche and predation affecting the realised niche space together with a local climate index as a blend of further, yet undefined variables of the n-dimensional hypervolume, demonstrated to be adequate in explaining long-term dynamics of main copepods during their main reproduction period. An important field of future research are potential mechanisms how phytoplankton changes affect Baltic zooplankton populations. Eventually, a further source of uncertainty is embedded in our predation index. However, our results support earlier studies that show significant top-down control to occur in the Baltic ecosystem (Möllmann & Köster 2002, Casini *et al.* 2008), which give us confidence in our approach.

The concept of the environmental niche has and continues to show that it can be a powerful tool in understanding broad patterns of species abundance, distribution and diversity (MacArthur 1958, Chase & Leibold 2003, Hirzel & Le Lay 2008). Nevertheless, niche modelling in the marine realm have been rather under-utilized relative to terrestrial applications, particularly in zooplankton ecology (Robinson *et al.* 2011). But considering their important role as mediator in

the food web, knowledge of potential responses of single species and communities to changes in climate or fishery is especially needed in ecosystem management. Linking physiology, environmental niches and the spatial or temporal distribution can be a useful approach as indicated by this and other recent studies (Helaouët & Beaugrand 2009, Helaouët *et al.* 2011). Our study exemplifies that community structure can be affected by the complexity of the habitat. In heterogeneous environments, coexisting species have more distinct niche separations and, hence, are likely to differ in their temporal responses to environmental changes.

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Supporting Information

SI text

Hydrography of the Baltic Sea

The Baltic Sea is a semi-enclosed, brackish water system in a temperate region comprising of several basins separated by sills. Due to its semi-enclosed nature with only a narrow connection to the North Sea, the Baltic Sea experiences a net positive freshwater balance. In the deep basins of the Central Baltic Sea, our study area, this leads to a permanent stratification with a highly saline deepwater (< 12) being separated from low salinity surface waters (< 9). Vertical mixing of the water masses is hence restricted by a halocline at about 60-100m depth. The exchange of deepwater in these basins can only occur by strong pulses of salt water inflow. These so-called “major Baltic inflows” (MBI) (Wyrтки 1954, Fonselius 1969), which occurred more frequently until the 80s, can change the oceanological regime of the whole water column and improve the living condition by the distribution of oxygenated water. Lack or decreased frequencies of MBIs result in decreased salinity levels due to the shallowing of the halocline and have been generally attributed to changed atmospheric forcing conditions. During the summer months a thermocline develops at a depth of 20-30 m leading to an enhanced vertical habitat differentiation.

Supporting references

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Supporting tables and figures

Table 5-S1: List of environmental variables used as covariates in the GAM analyses. Modelled species for which the variables were included as covariates in the initial model are given together with the definition and data source/type of the variable. (A=*Acartia* spp., T=*T. longicornis*, and P=*P. acuspes* (P))

Variable	Species	Definition	Data Source/Type
BSI	A, T, P	Baltic Sea Index; mean value of winter months Dec-March. BSI calculations exist either based on sea level pressure values obtained from the NCEP (US National Centers for Environmental Prediction) or the SMHI (Swedish Meteorological and Hydrological Institute) data bank. Both time series differ slightly in their temporal coverage, causing deviations in the overall mean and consequently in the calculated monthly anomalies in overlapping years. In this study, the full time series (1970-2008) of the SMHI based BSI was used, since it is considered to better reflect the local situation (A. Lehmann, IFM-GEOMAR, pers. comm.) For the missing years 1960 – 1969, the index is based on NCEP data.	IFM-GEOMAR
Surface S	A	mean salinity in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 0-20m	bottle data from ICES database
Midwater S	T	mean salinity in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 20-40m	bottle data from ICES database
(Mid- to) Deepwater S	P	mean salinity in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 30-50m in summer and the halocline region in spring (i.e. 60-90m in the BB, GD and 70-100m in the GB)	bottle data from ICES database
Surface T	A	mean temperature in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 0-20m	bottle data from ICES database
Midwater T	T	mean temperature in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 20-40m	bottle data from ICES database
(Mid- to) Deepwater T	P	mean temperature in spring (Apr-May) and summer (Jul-Aug); averaged for each basin (i.e. BB, GD, and GB) and the species-specific depth layer of 20-60m	bottle data from ICES database
PI		predation index based on Eastern Baltic cod spawning stock biomass (SSB); to mimic the predation pressure by planktivorous sprat we used inversely scaled values between 0 and 1. For this, we calculated the ratio between the difference of the annual SSB to the time series maximum and the overall min./max. range	VPA estimate

Basins: BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin

Table 5-S2: Generalized Additive Mixed Model (GAMM) result of the alternative spring model of *Acartia* spp.. Excluding predation in the initial model resulted in a final model with only BSI as covariate but significant autocorrelation. To account for in the temporal dependencies of the residuals we included an exponential correlation structure into the model. The estimate of the intercept, the estimated degrees of freedom (edf) of the covariate, and the significance (P-value) are presented together with the R^2 .

	Estimate	P-value
Intercept	- 0.253	0.188
Covariate	edf	P-value
BSI	1	0.008
$R^2 = 0.291$		

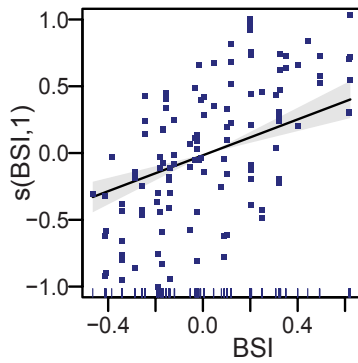


Figure 5-S1: Partial plot from the BSI effect in the alternative spring model of *Acartia* spp. Values on the y-axis indicate the effect that the BSI has on the biomass anomaly. The number in parentheses on the y-axis indicates the estimated degrees of freedom. The solid line indicates the smoothed (non-) parametric trend, shaded areas indicate the pointwise 95% CI. The rug along the x-axis indicates the location of the observations.

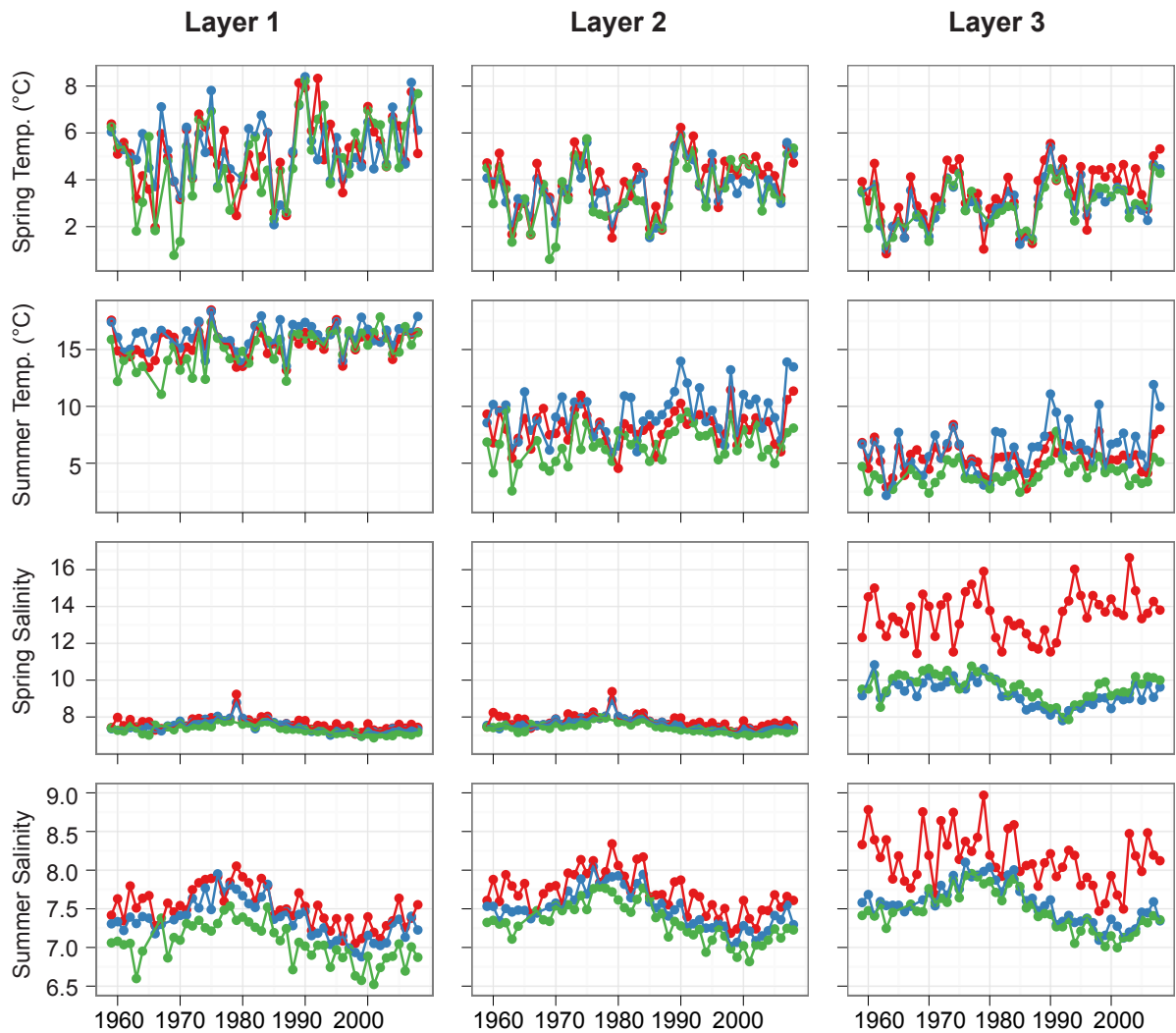


Figure 5-S2: Basin-specific time series of hydrography. The time series of the spring (first row) and summer (second row) temperature, together with the spring (third row) and summer (fourth row) salinity are given for each basin (red=Bornholm Basin BB, blue=Gdansk Deep GD, green=Gotland Basin GB). Layer 1 represents in both seasons the water depth 0-20 m (inhabited mainly by *Acartia* spp.) and layer 2 the water depth 20-40 m (inhabited mainly by *T. longicornis*). Layer 3 (corresponding to the main habitat of *P. acuspes*) represents in summer the water depth 30-50 m. In spring, the water depth of the temperature time series is 20-60m, whereas layer 3 for salinity represents the halocline region (60-90m in BB/GD and 70-100m in GB).

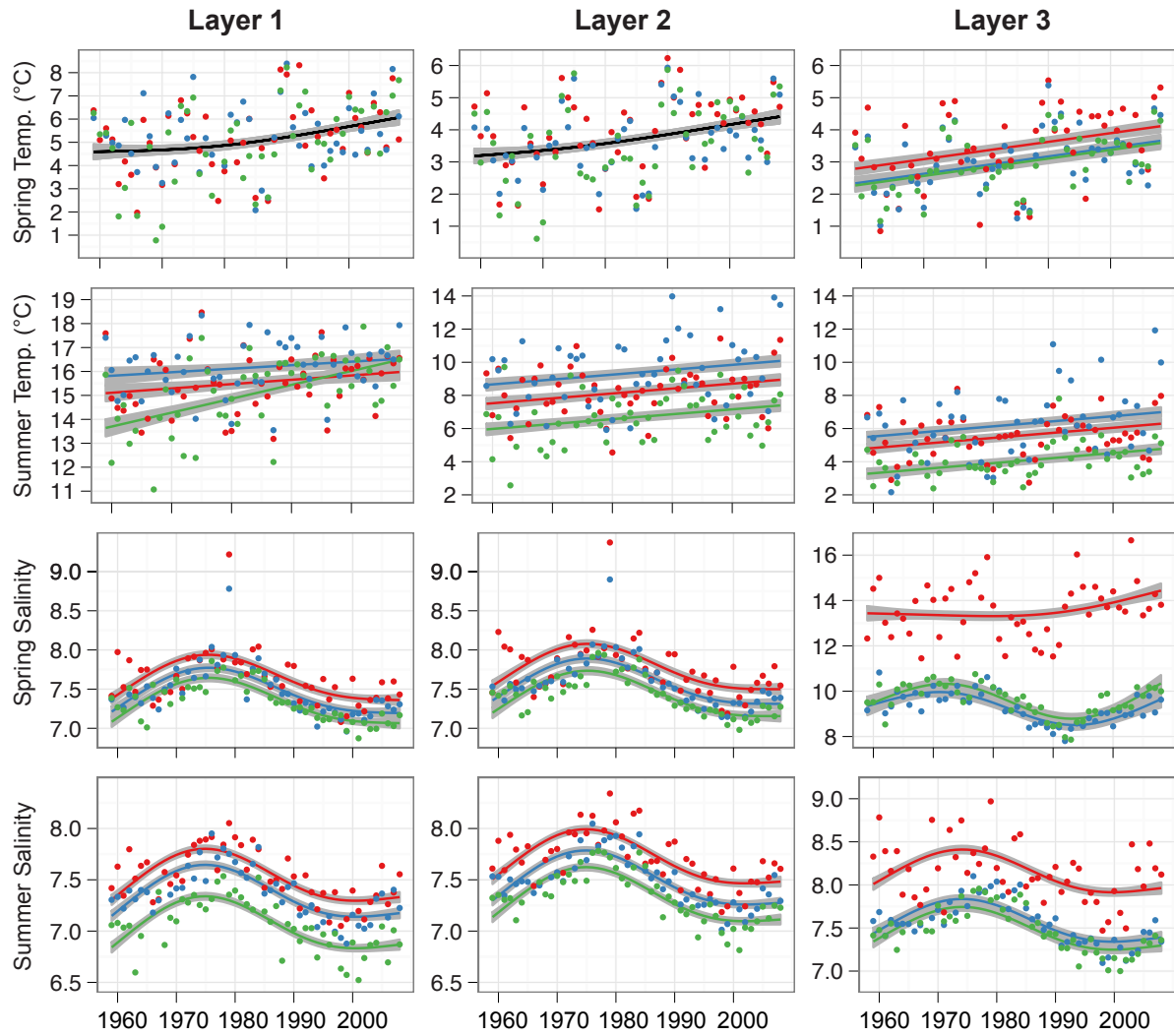


Figure 5-S3: Main trends of the hydrography within the Central Baltic Sea (CBS). The main trend of the spring (first row) and summer (second row) temperature, together with the spring (third row) and summer (fourth row) salinity are given for each basin (red=Bornholm Basin BB, blue=Gdansk Deep GD, green=Gotland Basin GB) or the entire CBS region if trends and overall values were basin-unspecific (black line). The coloured points represent the observed values in each basin, while the continuous lines indicate the predicted trends from Generalized Additive Models (GAM). The grey shaded areas indicate the associated standard errors. Layer 1 represents in both seasons the water depth 0-20 m (inhabited mainly by *Acartia* spp.) and layer 2 the water depth 20-40 m (inhabited mainly by *T. longicornis*). Layer 3 (corresponding to the main habitat of *P. acuspes*) represents in summer the water depth 30-50 m. In spring, the water depth of the temperature time series is 20-60m, whereas layer 3 for salinity represents the halocline region (60-90m in BB/GD and 70-100m in GB).

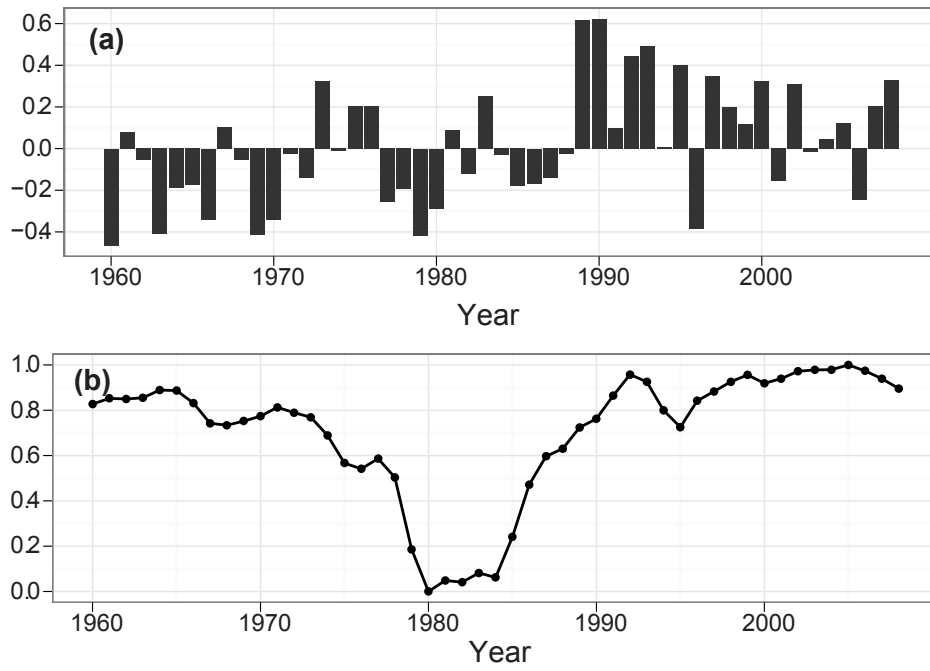


Figure 5-S4: Time series of BSI and PI. (a) shows the winter anomalies of the Baltic Sea Index (BSI) (Dec-March) and (b) the predation index (PI) based on the cod spawning stock biomass. Both, BSI and PI have dimensionless units.

6 Life cycle dynamics of a key copepod over long time scales: A complex interplay of internal and external drivers

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Abstract

In light of the increasing impacts of climate change and anthropogenic pressures on aquatic and terrestrial animal populations, there is an emerging need of understanding the complex life cycle dynamics of key species and their response to external factors. External physical and biological drivers can have linear, non-linear and non-additive effects on population sizes, which vary in species with complex life cycles between the various life-history stages. To fully understand the long-term dynamics of animal populations it is hence crucial to consider stage-specific effects of external drivers and how these propagate through the life cycle. Here we provide a novel, integrative study on long-term population dynamics of the ecologically important zooplankton species *Pseudocalanus acuspes* in the Baltic Sea, explicitly considering linear, non-linear and non-additive life cycle, climate and food web effects. Our study is based on a unique data set of seasonal stage-specific abundance covering almost five decades of sampling. We here show the importance of linear density effects for the life cycle dynamics as well as their interaction with season- and stage specific non-linear effects of hydro-climatic drivers. Our results furthermore add to the increasing knowledge on the importance of variability in top-down and bottom-up control for regulating long-term population dynamics.

Key words: climate change, life cycle dynamics, copepod, linear and non-linear effects, non-additive effects, generalized additive modelling

Introduction

Population dynamics of animal populations are emergent properties of a complex set of interacting internal and external factors during a species' life cycle. External physical and biological drivers can have linear or non-linear effects on population sizes hereby (Ellis & Post 2004, Yen *et al.* 2004), and the various driving variables frequently interact at particular spatial or temporal scales (Bjørnstad & Grenfell 2001). Hence, long-term studies on several terrestrial and aquatic species demonstrate interactions between internal non-linear processes and various exogenous factors such as food, climate, temperature, precipitation or wind speed (Arcese & Smith 1988, Higgins *et al.* 1997, Grenfell *et al.* 1998, Stenseth *et al.* 1999, Jacobson *et al.* 2004). Interestingly, the interactions between driving variables are often characterized as non-additive, i.e. the effect of one variable can change under contrasting states of another variable, and are best represented by statistical threshold models (Ciannelli *et al.* 2004, Dingsør *et al.* 2007, Llope *et al.* 2011, Stenseth *et al.* 2004).

In species with complex life cycles, such as marine zooplankton, the various life-history stages usually vary in size and shape, and therefore also in their ability to acquire resources and their response to environmental conditions (Frank & Leggett 1994, Boggs 2009, Hart & Bychek 2011, Kingsolver *et al.* 2011). Vital rates (e.g. mortality, fecundity and growth) can be stage-specific, and consequently biotic and abiotic bottom-up effects are likely to differ among them. Furthermore, morphological differences between life-history stages may lead to a variable vulnerability to top-down predation pressure (Brooks & Dodson 1965, Pennington *et al.* 1986, Möllmann & Köster 2002). The effects of external drivers on a specific life stage may eventually propagate through the life cycle and indirectly affect a subsequent life stage (Benton *et al.* 2006). To fully understand the long-term population dynamics of animal populations it is hence crucial to consider the various external drivers affecting each life-history stage and how stage-specific effects propagate through the life cycle, a task frequently hindered by limited or even lacking highly resolved long-term data series.

Marine zooplankton species usually have complex life cycles with up to 12 different life-history stages (Mauchline 1998). These organisms are of vast ecological importance due to their role in mediating ocean primary production to secondary and tertiary consumers such as large, commercially important pelagic and demersal fish populations. Copepods are in numbers and biomass the dominating zooplankton group and play a major role in the flow of matter and energy in pelagic food webs (Miller 2005). Traditionally marine zooplankton is considered as being bottom-up controlled and may serve as suitable indicators of the effect of climate on the ocean, unbiased by anthropogenic effects at the top of food webs (Hays *et al.* 2005). Consequently, a multitude of studies has been published that relate long-term zooplankton dynamics to hydro-climatic variables (e.g. Taylor 1995, Fromentin & Planque 1996, Beare *et al.* 2002, Beaugrand 2003, Möllmann *et al.* 2000, Molinero *et al.* 2005, Stenseth *et al.* 2006, Wiafe

et al. 2008, Gislason *et al.* 2009). However, recently trophic cascading has been shown for many marine ecosystems such as the Eastern Scotian Shelf (Frank *et al.* 2005), the Black Sea (Daskalov *et al.* 2007) and the Baltic Sea (Casini *et al.* 2008, Möllmann *et al.* 2008). Trophic cascading can involve a change in trophodynamic control frequently induced by overfishing (Frank *et al.* 2007, Strong & Frank 2010), although oscillations in control can also be induced by climate variability and change (Hunt *et al.* 2002, Litzow & Ciannelli 2007). Trophic cascade studies show that planktonic trophic levels can be changed by food web effects and especially that marine zooplankton can be top-down controlled by planktivores (Baum & Worm 2009). Hence, a few recent studies on long-term changes in zooplankton included predation effects and especially tested for non-additive dynamics by modelling changes between bottom-up and top-down controls (Stige *et al.* 2009, Llope *et al.* 2011). However, these studies consider the effects on zooplankton communities, lacking the investigation of stage-specific responses of individual species.

For the Baltic Sea, Casini *et al.* (2009) demonstrated that zooplankton and especially the calanoid copepod *Pseudocalanus acuspes* changed from a state controlled by hydro-climatic variables to a top-down regulation by planktivorous fish populations. The genus *Pseudocalanus* spp. is one of the dominant zooplanktonic animals in the world oceans (Corkett & McLaren 1978, Kane 1993, Richter 1995, Nielsen & Andersen 2002) and in the Baltic *P. acuspes* is key to ecosystem functioning. The copepod is important food for mesopredators, mainly planktivorous fish such as sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) (Möllmann *et al.* 2003, Möllmann *et al.* 2004), but also provides food for early-life history stages of the Baltic top-predator cod (*Gadus morhua*) influencing its recruitment success (Hinrichsen *et al.* 2002, Köster *et al.* 2005, Möllmann *et al.* 2008).

Here we provide a novel integrative study on long-term population dynamics of the ecologically important zooplankton species *P. acuspes* in the Baltic Sea, explicitly considering linear, non-linear and non-additive life cycle, climate and food web effects. Based on a unique data set of seasonal stage-specific abundance covering almost five decades of sampling (1960 – 2008, 1408 samples), we statistically model (i) density effects on subsequent life-history stages within the annual life cycle and (ii) the effect of exogenous bottom-up (i.e. hydro-climatic) and top-down (i.e. predation) variables that determine population abundances. We furthermore (iii) investigate the functional form of the derived statistical models (i.e. linear or non-linear) and (iv) test for changes from bottom-up to top-down trophic regulation under contrasting predation regimes. For each season, we modelled stage specific abundances using Generalized Additive Modelling (GAM) and its respective threshold formulation (TGAM; Ciannelli *et al.* 2004), hence allowing not only for non-linear relationships but also for non-additive interactions. We here show the importance of linear density effects for the life cycle dynamics as well as their interaction with season- and stage specific non-linear effects of hydro-climatic drivers. Our results add further to

the increasing knowledge on the importance of variability in top-down and bottom-up control for regulating long-term population dynamics.

Material and Methods

The model organism – *Pseudocalanus acuspes*

We investigated the long-term population dynamics of *Pseudocalanus acuspes* in the Baltic Sea (see Fig. 6-S1c in supporting information (SI)). Calanoid copepods such as *P. acuspes* have complex life cycles developing through 11 larval stages (6 nauplii and 5 copepodite stages) to the adult stage. In contrast to other *Pseudocalanus* spp. congeners, the life cycle of Baltic *P. acuspes* is characterized by an annual generation with a reproductive peak in spring, usually around May (Renz & Hirche 2006). Although a small fraction of the egg-carrying population is able to reproduce year round (Renz *et al.* 2007), a stable progression of the stage structure is observed (Fig. 6-1a). This life cycle characteristic of *P. acuspes* allowed us to model density effects by following successive stages over subsequent seasons.

Data

Abundance of *Pseudocalanus acuspes*

Abundance ($N \cdot m^{-3}$) data for *P. acuspes* are derived from a database of a zooplankton monitoring programme of the Institute of Food Safety, Animal Health and Environment (BIOR) in Riga, Latvia. Sampling is conducted seasonally since the 1960s, usually in February, May, August and October, with a variable number of stations in the Eastern Gotland Basin (Möllmann *et al.* 2000; see Fig. 6-S1a,b and Tab. 6-S1 in SI). The sampling gear, a Juday Net (Unesco 1979), has a mesh size of 160 μm and an opening diameter of 0.36 m. It is operated vertically and considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be slightly underestimated. Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a maximum depth of 150 m. During analysis, abundance of nauplii (N), copepodites I – III (in the following termed C13), copepodites IV – V (in the following termed C45) as well as adult females (F) were enumerated. For our analysis, stage-specific abundance data were averaged across stations and season (i.e. yearly quarters) and covered the period 1960 – 2008.

Hydro-climatic variables

We used a set of hydro-climatic variables in modelling stage-specific abundance of *P. acuspes*, which we here consider as bottom-up controls on the copepod. Main hydrographic variables affecting *P. acuspes* are water temperature and salinity (Möllmann *et al.* 2000). Stage-specific temperature time series were computed for specific depth ranges accounting for the ontogenetic vertical distribution of the copepod and related environmental adaptations and preferences

(Hansen *et al.* 2006, Renz & Hirche 2006). Salinity time series were only calculated for a deepwater layer (70-100 m depth), since earlier studies showed an effect of salinity only on late copepodite and adult stages residing in this part of the water column (Möllmann *et al.* 2000). In order to match the timing of the zooplankton sampling, seasonal temperature and salinity time series were constructed for February/March (winter), April/May (spring), July/August (summer), and October/November (autumn) data. Hydrographic data were derived from the International Council of the Exploration of the Sea (ICES; <http://www.ices.dk>) as well as from BIOR.

As an indicator for atmospheric variability we used the Baltic Sea Index (BSI) (see also Tab. 6-S2 in SI). The BSI is a local climate mode representing the difference of normalized sea level pressure (SLP) anomalies between Oslo in Norway and Szczecin in Poland and is correlated to the NAO (North Atlantic Oscillation Index) and the NAM (Northern Hemisphere Annular Mode). Oceanographic processes in the Baltic have generally been better related to local atmospheric conditions (Lehmann *et al.* 2002, Möllmann *et al.* 2003). Annual winter mean values (Dec-March) were calculated for the BSI, since winter patterns of local and regional wind fields are more pronounced in amplitude and areal coverage (Dippner *et al.* 2000, Stenseth *et al.* 2003) and have a strong influence on the hydrographic situation in spring (Dippner *et al.* 2000), the period most important for reproductive success of *P. acuspes*.

Biotic variables

In addition to physical variables we modelled biological effects on our model species. Older stages of *P. acuspes* represent one of the major prey species for the planktivorous fish species herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Möllmann *et al.* 2004). Sprat has been shown to significantly control the population size of *P. acuspes* (Möllmann and Köster 2002) and sprat stock size would be a suitable indicator of predation pressure. However, stock size estimates from stock assessments for sprat are not available prior to 1974 (ICES 2011). Hence, a predation index (PI) was developed using stock size estimates for cod (*Gadus morhua*). Eastern Baltic cod is the major piscivore in the Baltic Sea and its stock size is inversely related to the stock size of sprat (Casini *et al.* 2008, Möllmann *et al.* 2008). We used spawning stock biomass (SSB) estimates for cod from official stock estimates that date back to 1966 (ICES 2011), and extended the time series back to 1960 using estimates by Eero *et al.* (2007). The combined time series was inversed to mimic the predation pressure by planktivorous sprat and scaled to values between 0 and 1 (see Tab. 6-S2 in SI).

Food-limitation may be an important bottom-up influence on population dynamics of a zooplankton species such as *P. acuspes*. Studies on the feeding ecology of *P. acuspes* are however scarce. Investigations using lipid biomarkers showed an opportunistic feeding behaviour, with strong seasonal variability and high importance of ciliates in addition to diatoms, dinoflagellates and cyanobacteria (Peters *et al.* 2006). Unfortunately no reliable estimates of the different food sources of *P. acuspes* were available for our investigation period. Earlier studies indicated also the stronger importance of hydro-climatic variables as well as predation for the

dynamics of *P. acuspes* (Möllmann *et al.* 2008, Casini *et al.* 2009). Hence, we did not include food availability in our analysis, rather considering that bottom-up hydro-climatic variables implicitly represent food availability as well.

Time series modelling and statistical analysis

Modelling approach

We used non-linear regression techniques to capture the seasonal population dynamics of *P. acuspes* and to disentangle the roles of life cycle effects (i.e. density effects between successive life stages within and between seasons) relative to extrinsic processes (i.e. hydro-climate and predation).

A first data exploration as well as previous studies (e.g. Ciannelli *et al.* 2004, Stenseth *et al.* 2006, Dingsør *et al.* 2007, Tyler *et al.* 2008, Llope *et al.* 2009) revealed non-linear relationships, in particular between abundance and environmental variables. We therefore used the more flexible Generalized Additive Modelling (GAM) technique (Hastie & Tibshirani 1990, Wood 2006), which have the advantage to not require an a priori specification of the relationship between the response variable (Y) and the explanatory variable (X). Each Y_i is linked with X_i by a smoothing function instead of a coefficient β as in traditional regression techniques.

The following model was used for the seasonal abundance of each life-history stage:

$$X_{sy} = \alpha + \sum_i f_i(\mathbf{D}^i) + \sum_j g_j(\mathbf{I}_y^j) + \varepsilon_{sy}$$

where X_{sy} is the natural logarithm ($\ln(X+1)$) of the abundance of a particular life stage group (i.e. N, C13, C45, and F) of *P. acuspes* during a particular season s in year y . \mathbf{D}^i represents a vector of density effects, i.e. $\ln(X+1)$ -transformed population abundances of different stage groups in the same or previous season of year y or $y-1$. Hydro-climatic and predation variables of the same year y (and in the case of temperature/salinity also the same season) are summarized in the row vector \mathbf{I}_y^j . The superscripts i and j identify the single components of both vectors. α is the intercept and ε_{sy} random noise term assumed to be normally distributed with zero mean and finite variance. f_i and g_j are thin plate regression spline functions describing the effect of internal and external processes respectively.

Stage group abundances were only modelled for seasons, in which they dominated the total abundance or played a major ecological role (e.g. reproducing females in spring). The $\ln(X+1)$ – transformation was applied to all seasonal stage abundance data of *P. acuspes* to reduce intrinsic mean-variance relationships. This transformation was favoured over the inclusion of variance structures as in Generalized Additive Mixed Models (GAMMs) due to very strong variability in the plankton data (probably caused by patchiness and differences in sampling intensity and strategy). It is important to note that in our statistical analysis we could not test for

density-dependence as regulatory mechanism to control population growth, as we did not model the growth or survival rate. Further, log-transforming the stage abundances might have masked any possible pattern of regulatory mechanism. We will, therefore, term the dependence between subsequent stage abundances simply as density effect in this study.

Variable selection

In deciding which term to include in the final model, we applied a backward stepwise selection approach. Initially, we started with a full model (Tab. 6-S3 in SI) that always included as density effect a minimum of two stage abundances. Because of the low temporal resolution of the sampling design and the fact that some stages are primarily dominant during one season (e.g. nauplii in spring) we not only included abundances of preceding stages or reproducing females from the previous season but also from the same season. Further covariates were temperature, salinity and the BSI. The PI was only included when modelling abundances of C45 and F as these are significantly consumed by predators (Möllmann *et al.* 2004). The least significant variables (p -value > 0.05) were individually removed until the generalized cross-validation (GCV) criterion of the model was minimized (Wood 2000). The GCV criterion is a proxy for the out-of-sample predictive performance of the model and is related to the Akaike's Information Criterion (AIC; Wood 2006). The optimal amount of smoothing was estimated each time with the cross-validation method (Wood 2006). To avoid over-smoothing, which is likely to occur with small data sets (<50) (Zuur *et al.* 2009), we let the effective degrees of freedom (edf) be restricted to a maximum of 4. Optimal models including parameters with smoothers of one degree of freedom (linear relationship) were refitted in which these variables were added as linear terms. The underlying statistical assumptions were then tested through graphical residual analysis of the optimal model. Normality of residuals was assessed by plotting theoretical versus sample quantiles (Q-Q-plot), homogeneity of variance was evaluated by plotting residuals versus fitted values and temporal independence was verified plotting the autocorrelation function. The validation procedure showed that these assumptions were reasonably met (see for the residual diagnostics Fig. 6-S2 in SI). For data and outlier handling see SI text.

Non-additive interactions

After identifying the main population dynamics and drivers we tested for changes in the internal population control processes and changes in bottom-up vs. top-down control as a function of predation pressure. We applied a non-additive threshold formulation (TGAM) using the PI as a threshold variable and applied it to the density variables that were significant or showed a potential relationship in the initial GAM analyses (see Tab. 6-S3 in SI) as well as to the hydro-climatic variables and the PI itself. TGAMs are useful if changes in the response to external driving variables are rather discrete (see Ciannelli *et al.* 2004 for a detailed account of TGAMs). They are composed of two additive formulations in which the relationship between modelled

stage-group abundance and each explanatory variable can have different shapes in years above and below a level r of the threshold variable:

$$X_{sy} = \begin{cases} \alpha_1 + \sum_i f_{1,i}(\mathbf{D}^i) + \sum_j g_{1,j}(\mathbf{I}_y^j) + \varepsilon_{sy} & \text{if PI} \leq r \\ \alpha_2 + \sum_i f_{2,i}(\mathbf{D}^i) + \sum_j g_{2,j}(\mathbf{I}_y^j) + \varepsilon_{sy} & \text{otherwise} \end{cases}$$

r is here the predation threshold (reflecting the cod SSB) across which the functions of the density-dependent and –independent variables switch from $f_{1,i}$ to $f_{2,i}$ and $g_{1,j}$ to $g_{2,j}$ respectively with possible changes in the intercept (from α_1 to α_2). The threshold is estimated from the data and chosen by minimizing the GCV score over an interval defined by the 10 and 90 percentiles of the PI (Ciannelli *et al.* 2004). The effective degrees of freedom were here restricted to a maximum of 3 to avoid over-smoothing and high model complexities. In order to determine the best modelling approach and compare GAM and TGAM models, we used as criterion the “genuine” cross-validated squared prediction error (gCV), which has the advantage to account for the parameters defining the threshold.

All analyses were performed using the package ‘mgcv’ (with version R2.10) (Wood 2006) and the ‘tgam’ library (with version R2.5) (created by K.-S. Chan for version R2.5 and based on the mgcv library) within the ‘R’ statistical and programming environment (R Development Core Team 2009).

Results

***Pseudocalanus acuspes* population dynamics**

The life cycle of *P. acuspes* is characterized by a reproduction period in spring when overall abundance peaked and female (F), nauplii (N) and early copepodites (C13) dominated the population (Fig. 6-1a). During summer and autumn N developed through C13 to late copepodites (C45). The latter eventually constituted the overwintering stock together with the developing adult male (M) and F population. Long-term trends of the seasonally dominant stage groups displayed a major peak during the 1970s, starting a few years earlier for N and C13 (Fig. 6-1b-e). Some stages showed also a second but minor peak (i.e. C45 in winter and F and N in spring) or an increasing trend (i.e. C13 in summer and autumn) in the last decade. The levels of abundance prior to the major peak were higher for N in spring and for late copepodites in autumn, whereas for the latter we observed the opposite in winter. Early copepodites in summer and autumn were similarly more abundant in the recent period.

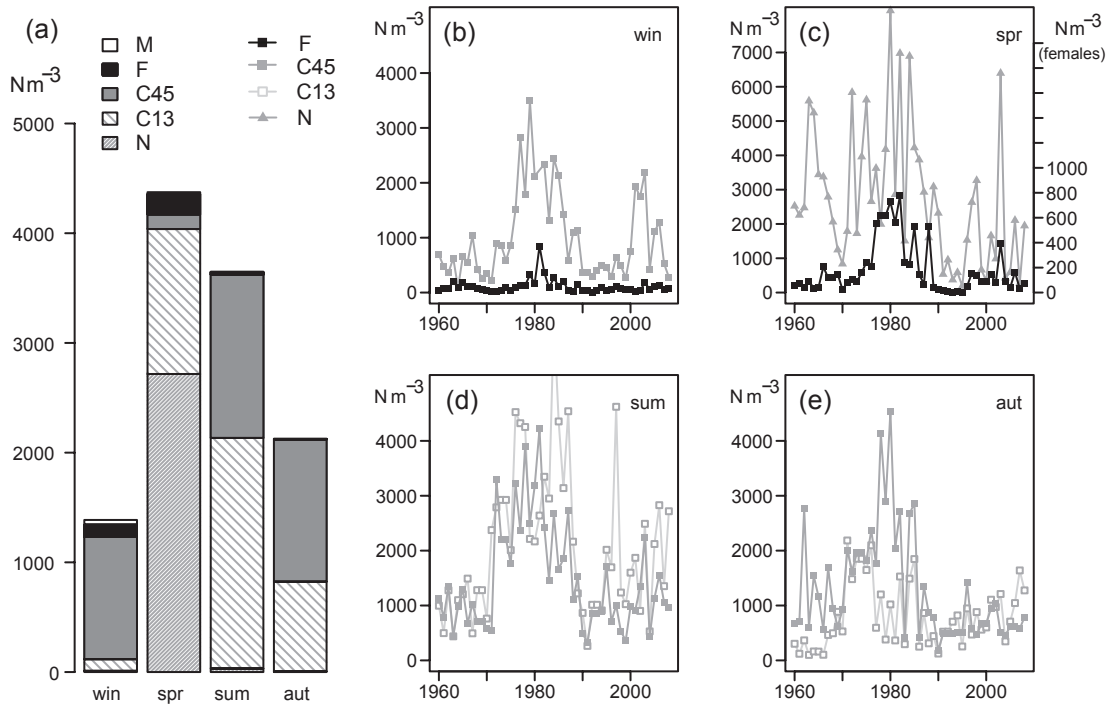


Figure 6-1: Seasonal stage distribution and inter-annual stage dynamics of *Pseudocalanus acuspes* with (a) the distribution of absolute stage abundances in each season identifying spring as the main reproductive season with a peak of females and nauplii and the successive accumulation of late copepodite stages thereafter, and (b)-(e) long-term dynamics of the two to three most abundant stage-groups in each season (win = winter, spr = spring, sum = summer, aut = autumn).

Trends in the biotic and abiotic environment

Atmospheric conditions over the Baltic Sea were characterized by a shift of the BSI from a negative to a positive phase with highest anomalies in 1988/1989 and a slightly decreasing trend thereafter (Fig. 6-2a). Across all depth strata temperature showed no seasonal long-term trend but rather fluctuations that followed the BSI dynamics (Fig. 6-2b). In spring and summer, we found a pronounced temperature increase in the late 1980s/early 1990s. Deepwater salinity varied only slightly between seasons and showed a decreasing trend until the early 1990s, increasing thereafter (Fig. 6-2c). We found two periods of strong predation pressure on *P. acuspes* (Fig. 6-2d). The first period lasted until the mid 1970s, the second starting in the late 1980s. Between these periods predation pressure was low with minimum values between 1980 and 1984.

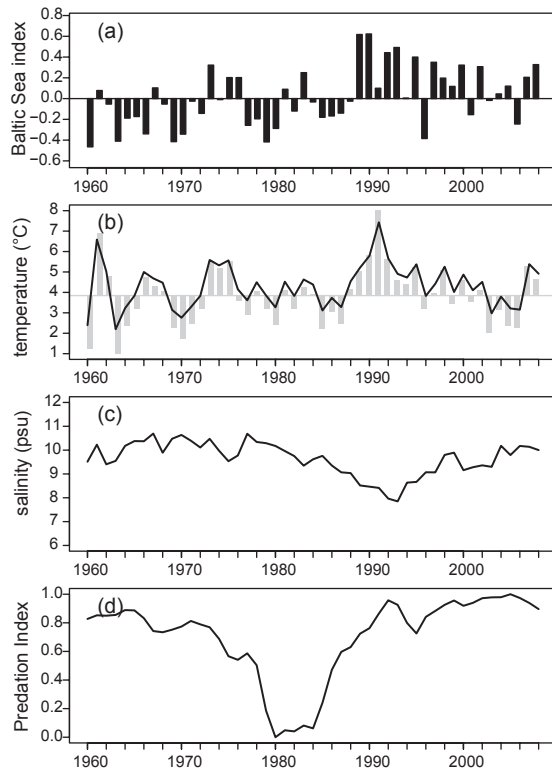


Figure 6-2: Time series of the hydroclimatic variables and the predation index (PI) showing significant effects in the statistical models: Winter anomalies of the Baltic Sea Index (BSI) (a), mean summer temperature for the depth range 20-60 m (b), the spring salinity averaged across the deepwater layer (70-100 m) (c), as well as the PI (d). Both, BSI and PI have dimensionless units.

Internal density and external environmental effects

We first statistically modelled the long-term abundance of seasonally dominant stage groups of *P. acuspes* as a function of preceding stage specific abundances (i.e. density effects) as well as abiotic and biotic external drivers. The final GAM formulations are presented in Tab. 6-1 and have explained variances (adjusted R^2) of 35 – 80%. Across most of the final models positive density effects were the most important predictor. The relationships between the modelled stage abundance and the density of the preceding stage or the reproducing females in the previous or same season were mainly linear in the log-log space, as indicated by an edf close to 1 (Fig. 6-3). In 2 models partial effects of some density terms were slightly zero-inflated, i.e. the autumn N and F abundance in the C13_{aut}-model as well as the F autumn abundance from the previous year in the F_{win} model. Both N and F are generally infrequent during the autumn season. Including these terms in the F_{win}- and C13_{aut}-model decreased the generalized cross validation value, increased the explained variance from 46% to 54% and 32% to 57% respectively and also improved residuals and were kept therefore in. Nevertheless, care should be taken in the interpretation of their parameter estimates and especially of the non-linear effect F density effect in the C13_{aut}-model (edf > 3).

Impacts of the hydro-climatic variables were in contrast rather stage- and season-specific and highly non-linear. We observed significant temperature effects on females in winter and early copepodites in spring and summer. While the relationships were dome-shaped in winter and

LIFE CYCLE DYNAMICS OF A KEY COPEPOD OVER LONG TIME SCALES |

Table 6-1: Summary results of the final Generalized Additive Models (GAM) and the alternative threshold formulations (TGAMs) used to describe *P. acuspes* stage abundances in each season. Coefficients are given for linear terms in the GAM. Subscript asterisks indicate the significance of each predictor. The adjusted R² (in %) are given for all models, the genuine cross-validation (gCV) scores only for competing GAMs and TGAMs. Models with a less optimal performance, i.e. with a higher gCV score, are marked in grey letters.

season	response variable	model type	formulation	adj. R ² (%)	gCV
winter	C45 _{win}	GAM	$C45_{win,y} = 3.85 + 0.4 \times C45_{aut,y-1}^{**} + g(PI_y^{***}) + \varepsilon_{win,y}$	57.3	0.614
		TGAM	$C45_{win,y} = 6.4 + \varepsilon_{win,y} + \begin{cases} g_1(PI_y^{***}) & \text{if } PI \leq 0.8778 \\ f(C45_{aut,y-1}^{***}) + g_2(PI_y^{***}) & \text{if } PI > 0.8778 \end{cases}$	69.1	0.876
	F _{win}	GAM	$F_{win,y} = 5.38 + f(F_{aut,y-1}^{**}) + g(T_{win,y}^{*}) - 1.41 \times PI_y^{***} + \varepsilon_{win,y}$	48.7	0.65
		TGAM	$F_{win,y} = 4.51 + g_1(PI_y^{***}) + \varepsilon_{win,y} + \begin{cases} f(F_{aut,y-1}^{***}) & \text{if } PI \leq 0.8261 \\ g(T_{win,y}^{**}) & \text{if } PI > 0.8261 \end{cases}$	54.7	0.621
spring	N _{spr}	GAM	$N_{spr,y} = 5.71 + 0.41 \times F_{spr,y}^{***} + g(BSI_y^{*}) + \varepsilon_{spr,y}$	52.0	-
	C13 _{spr}	GAM	$C13_{spr,y} = 1.21 + 0.54 \times N_{spr,y}^{***} + 0.49 \times T_{spr,y}^{***} + \varepsilon_{spr,y}$	35.0	-
	F _{spr}	GAM	$F_{spr,y} = 1.11 + 0.62 \times C45_{win,y}^{**} + g(S_{spr,y}^{***}) - 1.001 \times PI_y^{+} + \varepsilon_{spr,y}$	65.6	0.926
		TGAM	$F_{spr,y} = 4.26 + g_1(S_{spr,y}^{***}) + \varepsilon_{spr,y} + \begin{cases} f_1(C45_{win,y}^{***}) + g_2(BSI_y^{***}) + g_3(PI_y^{**}) & \text{if } PI \leq 0.7331 \\ f_2(C45_{win,y}^{*}) & \text{if } PI > 0.7331 \end{cases}$	79.3	1.489
summer	C13 _{sum}	GAM	$C13_{sum,y} = 4.5 + 0.28 \times N_{spr,y}^{***} + 0.29 \times F_{sum,y}^{***} + g(T_{sum,y}^{***}) + \varepsilon_{sum,y}$	60.4	-
	C45 _{sum}	GAM	$C45_{sum,y} = 3.67 + 0.53 \times C13_{sum,y}^{***} - 0.73 \times PI_y^{**} + \varepsilon_{sum,y}$	60.8	0.421
		TGAM	$C45_{sum,y} = 7.1 + f_1(C13_{sum,y}^{***}) + g_1(PI_y^{**}) + \varepsilon_{sum,y} + \begin{cases} g_2(S_{sum,y}^{**}) & \text{if } PI \leq 0.5708 \\ 0 & \text{if } PI > 0.5708 \end{cases}$	66.1	0.395
autumn	C13 _{aut}	GAM	$C13_{aut,y} = 2.99 + 0.44 \times C13_{sum,y}^{**} + 0.18 \times N_{aut,y}^{*} + f(F_{aut,y}^{*}) + g(BSI_y^{*}) + \varepsilon_{aut,y}$	47.4	-
	C45 _{aut}	GAM	$C45_{aut,y} = 0.75 + 0.27 \times C45_{sum,y}^{+} + f(C13_{aut,y}^{*}) + g_1(S_{aut,y}^{**}) + g_2(PI_y^{**}) + \varepsilon_{aut,y}$	58.7	0.572
		TGAM	$C45_{aut,y} = 7.07 + f_1(C13_{aut,y}^{***}) + \varepsilon_{aut,y} + \begin{cases} f_2(C45_{sum,y}^{***}) + g_1(S_{aut,y}^{***}) & \text{if } PI \leq 0.8955 \\ g_2(PI_y^{***}) & \text{if } PI > 0.8955 \end{cases}$	72.9	0.463

⁺ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

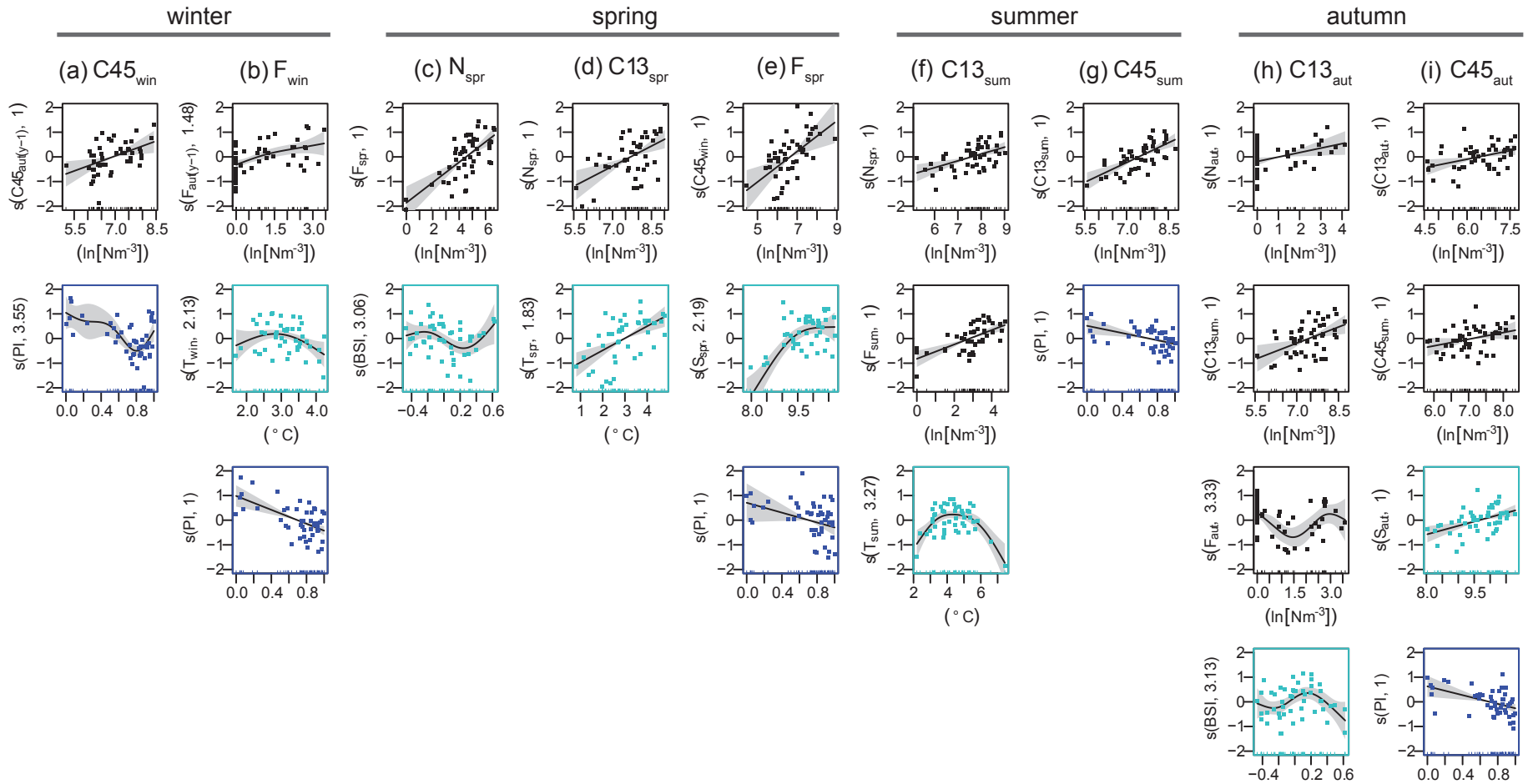


Figure 6-3: Results of the statistical modelling: Partial plots from the final GAMs showing the effect of each covariate. The density (black), hydroclimatic (cyan), and predatory (blue) effects are presented for each stage-specific model from (a) to (i). Values on the y-axis indicate the effect that the term on the x-axis has on the modelled and $\ln(X+1)$ transformed seasonal stage abundance. Numbers in parentheses on the y-axis indicate the estimated degrees of freedom. Solid lines indicate the smoothed (non-) parametric trend, shaded areas indicate the pointwise 95% CI. The rug along the x-axis indicates the location of the observations. As salinity, BSI and PI are dimensionless, no units are presented on the x-axis.

summer (Fig. 6-3b,f), the effect on the spring early copepodites was almost linear (Fig. 6-3d). Complex non-linear, albeit weak relationships with the BSI were derived for N in spring and C13 in autumn. C45 and F (with the exception of winter) were in contrast to the younger stages mainly affected by salinity. We found a strong positive and linear effect of salinity on late copepodites in autumn and a positive, but saturating non-linear effect for F in spring (Fig. 6-3e,i). Predation was in all final models an important driver for older stages, although not significant for spring F. The effect of predation was generally linear and negative (Fig. 6-3b,e,g,i).

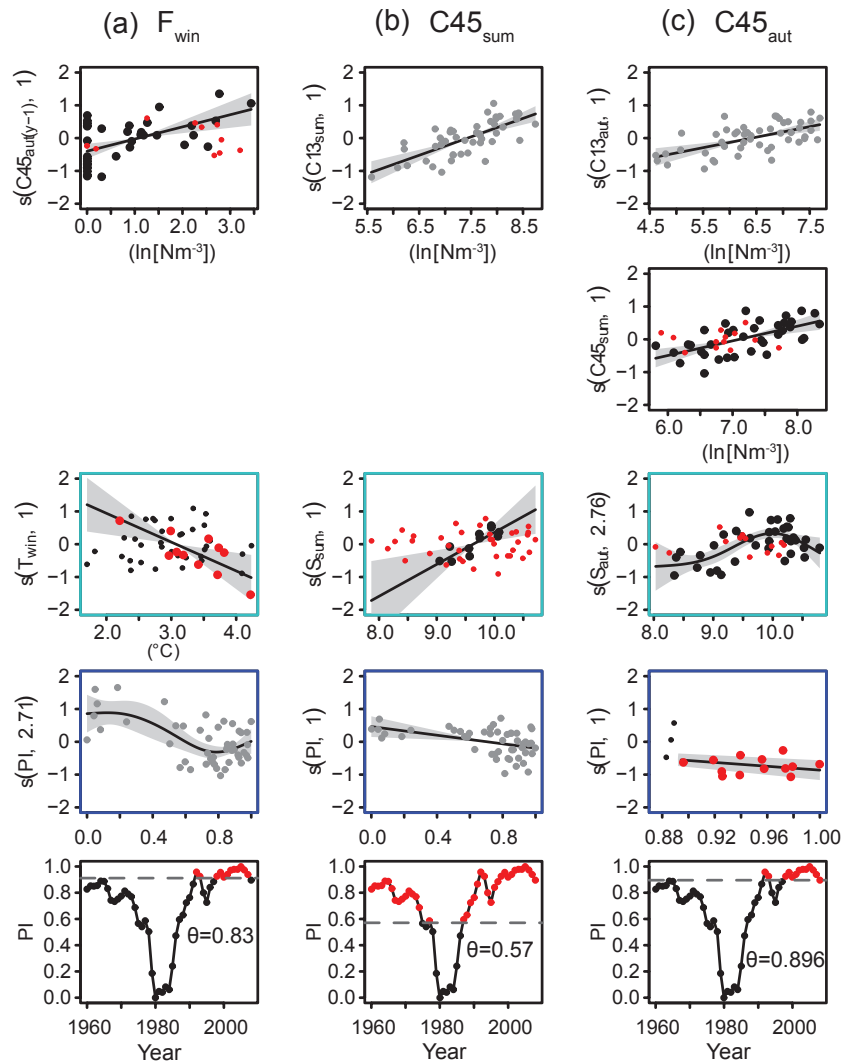


Figure 6-4: Statistical threshold models (TGAM) that performed better than the corresponding GAM. Partial plots showing the main additive or non-additive effects of density (black), hydro-climate (cyan), and predation (blue) are presented together with the regime assignment to the actual values of threshold variable (PI) for (a) F in winter, (b) C45 in summer, and (c) C45 in autumn. Additive effects (i.e. no threshold dividing into two different state effects) are indicated by grey coloured residuals. Non-additive effects are indicated by black and red residuals for the low and high predation regime respectively. Big-sized residuals specify here the regime with the significant effect. Values on the y-axis indicate the effect that the term on the x-axis has on the $\ln(X+1)$ transformed seasonal stage abundance. Numbers in parentheses on the y-axis indicate the estimated degrees of freedom. Solid lines indicate the smoothed (non-) parametric trend, shaded areas indicate the pointwise 95% CI. As salinity and PI are dimensionless, no units are presented on the x-axis. The lower row displays the long-term evolution of the PI with those values that determined the high regime shown in red and those for the low regime in black. The actual threshold value (θ) of each model is also given.

Non-additive interactions

We tested for thresholds that distinguish between high and low predation regimes, i.e. non-additivity, for C45 and F models (Fig. 6-4). We found the threshold formulation to be preferred to their fully additive equivalents for the C45 in summer and autumn as well as for F in winter (Tab. 6-1). For C45 the models indicate a stronger bottom-up regulation through salinity and density effects of C45 (in autumn) during the low predation regime (Fig. 6-4b,c). Above the predation threshold, the bottom-up effects diminished and in autumn the negative predation effect became significant. In summer, predation was a significant predictor for late copepodites irrespective of the predation regime and the predation threshold was lower (0.571) compared to autumn (0.896), together indicating a stronger predation effect in summer.

Female dynamics in winter also alternated depending on the level of predation (Fig. 6-4a). During a low predation pressure the density effect was stronger, while in times of high predation pressure, temperature was significantly and linear negatively related to F abundance. The predation threshold was rather high (0.826), indicating the predominance of the density effect. Predation was a significant predictor for winter F independent of the predation regime.

Discussion

Internal life cycle dynamics

Our statistical modelling approach demonstrated that density effects explain most of the variability in *Pseudocalanus acuspes* long-term dynamics. We identified the N production in spring, generally a critical phase in copepod dynamics, to depend almost exclusively on spring F abundance. Spring F population size in turn is determined by the overwintering stock of late copepodites as already suggested for *Pseudocalanus* sp. in Dabob Bay (Ohman 1985) and in the Baltic Sea (Peters *et al.* 2006). Nevertheless, in all seasons, individual life stage abundance depended significantly on the abundance of the previous stage or reproducing females either in the same season or the season before. Statistical relationships hereby were mostly linear in the log-log space as has been shown in life stage models of e.g. fish species (Ciannelli *et al.* 2005, Dingsør *et al.* 2007).

A weakness of our data set is the low temporal resolution of only seasonal sampling, which is usually too low to model the fast life cycles with overlapping generations of zooplankton species such as calanoid copepods. Although Baltic *P. acuspes* is described to have a rather slow development with mainly one annual generation (Renz & Hirche 2006), making it a suitable species for our modelling exercise, five "environmental cohorts" of females have been identified during the year in a more detailed analysis (Peters *et al.* 2006). We accounted for the uncertainty in observing the life cycle inherent in our data set by testing for various density effects between life stages within a season and the preceding season. This resulted in two final models, which included partly rather inconclusive stage effects (Fig. 6-3b,g), e.g. the effect of the generally low

abundant autumn F on the relatively abundant winter F. Nevertheless, the general patterns of stage succession emerging from our statistical analysis give us confidence to have included the main life cycle pattern of our model species.

Effects of hydro-climatic drivers

In addition to the prevailing density effects, external factors influence the dynamics of *P. acuspes*. As temperate species, the effects of hydro-climatic variables differed clearly between seasons. Even more pronounced differences were observed between individual life stages, reflecting the variations in their realized niches (Helaouët & Beaugrand 2009, Helaouët *et al.* 2011). Younger stages of *P. acuspes*, i.e. N and C13, that reside in the upper water column, responded stronger to local thermal conditions, indicated by the BSI and water temperature. Older stages, i.e. C45 and F, that live in deeper water layers are mainly determined by deepwater salinity.

Large-scale, low-frequency climatic indices have proved to be suitable predictors for long-term changes in the ecology of marine zooplankton (e.g. Fromentin & Planque 1996, Beaugrand *et al.* 2003, Chiba *et al.* 2006, Turner *et al.* 2006) by reducing complex space and time variability of local weather conditions into simple measures (Stenseth *et al.* 2003). In our analysis however we only found weak effects of the local climate index BSI on N in spring and the C13 in autumn. Möllmann *et al.* (2008) similarly only observed a weak climate effect on total *P. acuspes* spring biomass, indicating that direct hydrographic conditions may be more important for this species.

Not surprisingly, although not shown before for Baltic *P. acuspes*, we found a strong temperature effect on C13 abundances in spring and summer. By applying non-parametric models we further identified a non-linear relationship that suggests an optimum range of 4-5 °C for the realized thermal niche. Juvenile copepodites are known to depend particularly on temperature, affecting growth rates, development times and moulting rates (Vidal 1980a,b, Hirst & Bunker 2003, Dzierzbicka-Glowacka 2004, Liu & Hopcroft 2008). However, with increasing body size, and hence age, growth rate becomes less temperature-dependent (Vidal 1980a, Dzierzbicka-Glowacka 2004). Younger copepodite stages have therefore optimized their growth at higher temperatures, even if food supply is low, whereas under similar food conditions older stages have a higher growth at lower temperatures (Vidal 1980a). This might explain why we did not find temperature effects for older stages except for the not very abundant F in winter. Our results indicate that younger *P. acuspes* stages in the Baltic Sea prefer higher temperatures than *P. acuspes* in the Chukchi Sea (Hopcroft & Kosobokova 2010) but lower temperatures as e.g. *Calanus finmarchicus* in the North Atlantic (Helaouët & Beaugrand 2009). Previous long-term studies in the Baltic Sea, in contrast, could not find significant relationships between *P. acuspes* biomass and temperature (Dippner *et al.* 2000, Möllmann *et al.* 2000). In these studies, however, no stage-specific responses were investigated; hence, any temperature response of C13 might have been superimposed by the other stages.

P. acuspes in the Baltic Sea is generally perceived as being more driven by salinity than temperature, since the brackish water may display sub-optimal reproductive conditions (Renz & Hirche 2006). Consequently, in our analysis, salinity had the strongest and most significant impact on female abundance in spring. During this main reproduction season, females inhabit the deeper and more saline parts of the water column where they can avoid osmotic stress and hence save energy for their gonad development and reproduction (Möllmann *et al.* 2003, 2008). Slightly weaker effects of deepwater salinity were observed in autumn for C45 in both GAM and TGAM models. We found for C45 in summer only a slight effect in the TGAM model. Except for the lack of a winter effect, our results support previous long-term studies of total *P. acuspes* in the Baltic Sea showing strongest correlations between deepwater salinity and total biomass in spring and autumn (Möllmann *et al.* 2000). Slight differences between studies might be due to the stage-specific nature of our study, differential depth ranges used or through the longer time-period covered.

Despite the generally positive influence of higher salinity, which has been observed by several authors before (Ojaveer *et al.* 1998, Möllmann *et al.* 2000, 2003, Renz & Hirche 2006), we found non-linear relationships with the effects to be stronger at lower salinities (< 10). Above this threshold higher salinities did not significantly lead to higher abundances. This indicates a value of 10 to be a threshold where salinity is not any longer the limiting factor.

Predation effects

As predation by planktivorous fish has been shown to influence *P. acuspes* dynamics before (Möllmann & Köster 2002, Casini *et al.* 2008) we here found significant predation effects, particularly in winter. Similar to other studies (Casini *et al.* 2008, Möllmann *et al.* 2008, Llope *et al.* 2011) these biotic interactions were mostly linear. Only in winter we observed a few years with high abundances of C45 to occur concurrently with high predation pressures. This coincidence is ecologically difficult to explain and may indicate observation error related to our measure of predation.

In the absence of planktivorous fish stock sizes for the entire study period, we used an indirect measure of predation. We used the inverse of the cod parent stock size because of an inverse relationship between the top-predator and its main forage species sprat during the recent three decades. Among the shortcomings of this procedure is that this relationship may not be stable and hence not valid for the additional period investigated here. Furthermore, the other large planktivorous fish stock of the Baltic (i.e. herring) is disregarded in our analysis, since earlier studies were not able to find a significant negative relationship with zooplankton (Möllmann *et al.* 2008, Casini *et al.* 2008). Eventually our predation index does not reflect mis-matches in the co-occurrence of sprat and *P. acuspes* due to the seasonal migration pattern of the planktivore. In summer to autumn sprat usually leaves the deeper Baltic basins where *P. acuspes* resides hence lowering the predation pressure.

In spite of the uncertainty in our predation index the results of our statistical modelling exercise give us confidence in the approach. We found significant negative relationships with the predation index only for C45 and F, which is in accordance to size-specific foraging of copepods (Möllmann & Köster 2002). Furthermore, previous studies on feeding ecology have shown sprat to prey on *P. acuspes* during winter and spring (Möllmann & Köster 2002, Möllmann *et al.* 2004), which supports our results of the predominance of the predation effect during winter. Eventually our study support results from earlier studies that show significant top-down control of *P. acuspes* by sprat based on using shorter time series (Möllmann & Köster 2002, Casini *et al.* 2008).

Non-additive relationships – changes between bottom-up and top down control

Relationships between bottom-up and top-down control variables may not be stable in marine ecosystems (Frank *et al.* 2007, Casini *et al.* 2009). We were therefore interested in non-additive effects between explanatory variables and applied a non-additive threshold formulation of GAMs to our data. We could demonstrate that density effects as well as effects of hydro-climatic variables depended on the predation pressure on C45 and F. For example, late copepodites and females in the previous season determined strongly the abundances in autumn and winter as long as their numbers were not reduced by a very high predation pressure. Stige *et al.* (2009) made a similar observation for the Barents Sea and found a positive association between spring and summer zooplankton biomass only under a low feeding regime of capelin. Furthermore, in our study the salinity effect on *P. acuspes* C45 in summer and autumn diminished under high predation pressure. A similar decoupling of zooplankton dynamics from climate/hydrography by high predator abundances has also been observed for the Black and Barents Seas (Stige *et al.* 2009, Llope *et al.* 2011) as well as for the Baltic Sea for a shorter time series (Casini *et al.* 2009). Our findings regarding the temperature effect are in contradiction to earlier studies as we found a negative temperature effect on winter females of *P. acuspes* only during a high predation regime. We hypothesize that the negative effect of temperature may act permanently, but become noticeable only if population abundance is remarkably reduced by high predator density. With regard to the debate whether zooplankton is bottom-up or top-down regulated, our study results add to the increasing evidence that both regulatory processes can alternate and act simultaneously (Frank *et al.* 2007, Casini *et al.* 2009, Stige *et al.* 2009).

Conclusions

The results of our integrative statistical analysis have shown that dynamics of animal population such as the copepod *P. acuspes* are driven by a combination of internal and external drivers. In Fig. 6-5 we summarized these complex interactions conceptually. Density effects between the different life stages of *P. acuspes* explain most of the variability in interannual dynamics, while

external driver have significant stage-specific, often non-linear and in some cases non-additive effects. Important to note is that the external and internal processes interact so that external environmental drivers not only directly influence a particular life stage during a certain season, rather their effect progresses through the life cycle affecting stages in subsequent seasons.

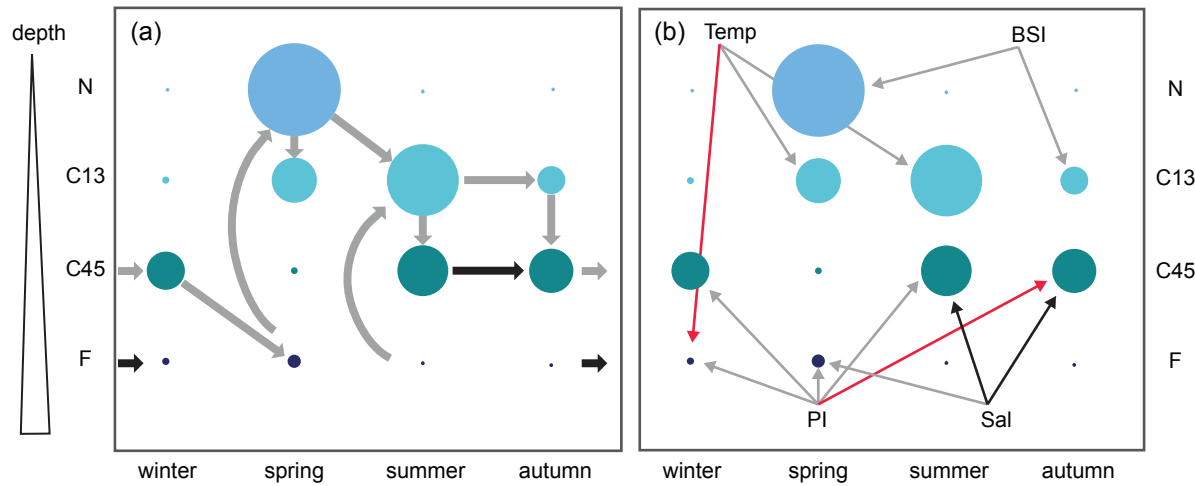


Figure 6-5: Conceptual diagram of the annual life cycle of *Pseudocalanus acuspes* showing (a) density effects, i.e. the relationships between successive stages, and (b) the external effects of temperature (Temp), the local climate index (BSI), salinity (Sal) and predation (PI) represented by grey arrows. Internal and external effects that are only significant under a low or high predation pressure are indicated by black and red arrows respectively. Weak significant density effects (p -value < 0.01) are not presented here. The sizes of the solid circles of each stage group in all four seasons (i.e. yearly quarter) are approximate representations of the proportional contributions of each stage group to the total seasonal abundances. The winter season represents hereby the overwintering period, spring the reproduction period, and summer and autumn the accumulation period.

These insights allow us to explain the long-term population dynamics of our model species during the recent five decades. The strong increase of nauplii and particularly C13 at the beginning of the 1970s was initiated by the combined effect of positive anomalies of the local climate index BSI and related higher temperatures that fell in the optimum range. Due to density effects, this increase in abundance propagated to C45, particularly in summer. A high predator population however suppressed a stronger increase of the older stages until the mid 1970s, when predation pressure ceased. The resulting peak for these life stages was stabilized by the positive effect of high salinity conditions in the deepwater and density effects of older stages which both acted even stronger under a low predation regime. The following decline at the mid-/end 1980s started with the continuous decrease of salinity and the simultaneous onset of strong sprat predation, both reducing the survival of older stages and leading consequently to lower numbers of offspring. The high positive anomalies in the climate conditions together with water temperatures above the optimum in 1989 additionally caused a reduction in the stock of young *P. acuspes* stages. Similarly, the second peak for C45 stages in winter and the resulting females and nauplii in spring can be explained by the synergistic effect of constantly increasing deepwater salinities and a short-term drop of predation pressure. The recent increase of C13 individuals in summer and autumn is explainable by water temperatures moving into their

optimum range and climate conditions that prevail at more neutral levels (i.e. BSI anomalies around zero).

Our study demonstrates the importance of integrative modelling approaches that include density effects for the life cycle dynamics as well as their interaction with season- and stage specific hydro-climatic effects. Particularly when evaluating the increasing impacts of climate change and anthropogenic pressures on animal populations. Our results furthermore add to the increasing knowledge on the importance of variability in top-down and bottom-up control for regulating long-term population dynamics. Eventually we emphasize that integrative time series modelling approaches such as presented here rely fundamentally on the continuation of monitoring programs of high spatial and temporal resolution.

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Supporting Information

SI text

Data handling

Prior to the analysis, data were visually examined for outliers and in the case of being too influential in the model (Cook's distance value > 1 or residual values $< -2 / > +2$) removed. As exclusion criteria we used the Cook's distance method (Quinn & Keough 2002) and removed data points with Cook's distance values > 1 as well as data points that had residual values $< -2 / > +2$ (Zuur *et al.* 2007) and/or caused smoothing functions that were ecologically not interpretable to be significant that wouldn't be otherwise. Explanatory variables were tested for collinearity using Pearson correlation coefficient and a variance inflation factor (VIF) of 3 was used as an exclusion criterion (Zuur *et al.* 2007). Missing values were estimated by calculating a 4-year mean, based on the two previous and the two following years.

Outlier

F_{win} model: We removed the year 1992, since this year represented an outlier in the y-space (F_{win} abundance of 0 N/m^3). Including the year would have lead to the same final model in which the Cook's distance indicated no strong influence (Cook's distance value = 0.38). Nevertheless, the residual value was with < -3 beyond the acceptable range and caused the residuals in general to be not normal distributed, a significant autocorrelation for the lag of six years and a bad model fit.

$C13_{spr}$ model: We removed here the year 1983, since this year represented an outlier in the y-space ($C13_{spr}$ abundance of 0 N/m^3). Including the year would have lead to the same final model in which the Cook's distance indicated no strong influence (Cook's distance value = 0.36). Nevertheless, the residual value was with < -6 beyond the acceptable range and caused the residuals in general to be not normal distributed and a bad model fit.

We further removed the three years 1993-1995. Although not too influential for the final model in general (Cook's distances < 0.2), these data points caused a weak negative effect of female density while auto-regressive effects were in all other final models positive. Excluding these years made this effect insignificant while the remaining partial effects and the explained variance were kept almost the same. Including the three years and removing the F_{spr} term in the model instead would have reduced the model fit considerably. Beside a low density of females, nauplii were also less abundant during these years. Although $C13_{spr}$ stages showed a positive dependence with nauplii, their abundances were fairly high and did not reflect the modelled value. For simplicity reasons, we decided to remove these exceptional years even though we lost some information.

$C13_{sum}$ model: Year 1983 was removed in this model since this year represented an outlier in the x_1 -space ($C13_{spr}$ abundance of 0 N/m^3). Although Cook's distance (0.06) as well as the residual

value < 0.5) did not indicate a too strong influence, the outlier caused the otherwise not significant covariate C13_{spr} to have a significantly negative effect, for which it was difficult to find an ecological interpretation.

Supporting references

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Supporting tables and figures

Table 6-S1: Number of samplings per year in winter (win), spring (sum), summer (sum), and autumn (aut) (i.e. in each yearly quarter).

year	win	spr	sum	aut	year	win	spr	sum	aut
1960	2	18	24	12	1985	4	8	8	3
1961	24	10	20	11	1986	2	7	12	2
1962	15	11	21	10	1987	3	7	9	8
1963	8	11	10	13	1988	2	14	11	4
1964	12	12	12	10	1989	6	11	6	6
1965	5	11	11	5	1990	1	11	10	6
1966	0	17	11	10	1991	2	11	8	0
1967	10	9	8	3	1992	1	0	0	0
1968	7	0	0	0	1993	0	11	0	4
1969	2	2	0	3	1994	4	7	3	4
1970	4	8	4	3	1995	2	7	4	6
1971	4	2	4	1	1996	4	8	14	5
1972	7	9	4	6	1997	7	10	11	7
1973	3	6	0	0	1998	0	7	11	7
1974	9	0	0	0	1999	6	8	4	3
1975	5	10	7	6	2000	3	10	12	6
1976	0	14	7	7	2001	6	11	6	7
1977	5	12	8	3	2002	6	12	12	7
1978	3	5	4	6	2003	10	11	12	8
1979	0	0	4	13	2004	8	10	12	10
1980	6	5	9	2	2005	0	26	12	16
1981	4	6	7	4	2006	13	10	17	17
1982	4	10	12	9	2007	13	16	15	13
1983	2	1	6	3	2008	11	8	12	9
1984	4	3	8	4					

Table 6-S2: List of variables used in the GAM and TGAM analyses with their definition and data source. The seasonal stage abundances were included in the models either as response variables or as auto-regressive covariates. The BSI, salinity, temperature and PI variables represent the external covariates.

variable	definition	data source/type	
$N_{spr}, N_{sum}, N_{aut}$	$\ln(X+1)$ -transformed nauplii abundances (N/m^3) in spring (Apr-Jun), summer (Jul-Aug), and autumn (Oct-Dec) in SD28	BIOR survey	zooplankton
$C13_{spr}, C13_{sum}, C13_{aut}, C13_{aut(y-1)}$	$\ln(X+1)$ -transformed abundances of copepodite stages 1-3 (N/m^3) in spring (Apr-Jun), summer (Jul-Aug), and autumn (Oct-Dec; same) in year y (not indicated) or the previous year ($y-1$) within SD28	BIOR survey	zooplankton
$C45_{win}, C45_{spr}, C45_{sum}, C45_{aut}, C45_{aut(y-1)}$	$\ln(X+1)$ -transformed abundances of copepodite stages 4-5 (N/m^3) in winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Aug), and autumn (Oct-Dec) in year y (not indicated) or the previous year ($y-1$) within SD28	BIOR survey	zooplankton
$F_{win}, F_{spr}, F_{sum}, F_{aut}, F_{aut(y-1)}$	$\ln(X+1)$ -transformed female abundances (N/m^3) in winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Aug), and autumn (Oct-Dec) in year y (not indicated) or the previous year ($y-1$) within SD28	BIOR survey	zooplankton
BSI	Baltic Sea Index; mean value of winter months Dec-March. BSI calculations exist either based on sea level pressure values obtained from the NCEP (US National Centers for Environmental Prediction) or the SMHI (Swedish Meteorological and Hydrological Institute) data bank. Both time series differ slightly in their temporal coverage, causing deviations in the overall mean and consequently in the calculated monthly anomalies in overlapping years. In this study, the full time series (1970-2008) of the SMHI based BSI was used, since it is considered to better reflect the local situation (A. Lehmann, IFM-GEOMAR, pers. comm.) For the missing years 1960 – 1969, the index is based on NCEP data.	IFM-GEOMAR	
$S_{win}, S_{spr}, S_{sum}, S_{aut}$	mean salinity in the halocline region (70-100 m depth); averaged across the winter (Feb-Mar), spring (Apr-May), summer (Jul-Aug), and autumn (Oct-Nov) season within SD 28	bottle data from ICES database	
T^1_{spr}	mean temperature in 0 – 40 m depth; averaged across the spring (Apr-May) season within SD 28	bottle data from ICES database	
$T^2_{spr}, T^2_{sum}, T^2_{aut}$	mean temperature in 20 – 60 m depth; averaged across the spring (Apr-May), summer (Jul-Aug), and autumn (Oct-Nov) season within SD 28	bottle data from ICES database	
$T^3_{win}, T^3_{spr}, T^3_{sum}, T^3_{aut}$	mean temperature in 40 – 80 m depth; averaged across the winter (Feb-Mar), spring (Apr-May), summer (Jul-Aug), and autumn (Oct-Nov) season within SD 28	bottle data from ICES database	
PI	predation index based on Eastern Baltic cod spawning stock biomass (SSB); to mimic the predation pressure by planktivorous sprat we used inversely scaled values between 0 and 1. For this, we calculated the ratio between the difference of the annual SSB to the time series maximum and the overall min./max. range	VPA estimate	

SD 28 = ICES subdivision 28, representing the Eastern Gotland Basin

Table 6-S3: Overview of covariates included in the full GAM and TGAM. We tested for autoregressive effects by including stage abundances from the same or the previous season; these were chosen based on knowledge of their annual life cycle. Hydro-climatological variables were included as abiotic and predation as biotic external variable. Bold letters indicate variables that remained in the final model and had a significant effect.

season	modelled stage	model	autoregressive variable	external variable
winter	C45 _{win}	GAM	C13 _{aut(y-1)} , C45_{aut(y-1)}	BSI, S _{win} , T ³ _{win} , PI
		TGAM	C13 _{aut(y-1)} , C45_{aut(y-1)}	BSI, S _{win} , T ³ _{win} , PI
	F _{win}	GAM	C13 _{aut(y-1)} , C45 _{aut(y-1)} , F_{aut(y-1)}	BSI, S _{win} , T³_{win} , PI
		TGAM	C45 _{aut(y-1)} , F_{aut(y-1)}	BSI, S _{win} , T³_{win} , PI
spring	N _{spr}	GAM	C45 _{win} , F _{win} , F_{spr}	BSI , S _{spr} , T ¹ _{spr}
	C13 _{spr}	GAM	F _{win} , F_{spr} , N_{spr}	BSI*, S _{spr} , T²_{spr}
	F _{spr}	GAM	C45_{win} , F _{win}	BSI, S_{spr} , T ³ _{spr} , PI
		TGAM	C45_{win}	BSI , S_{spr} , T ³ _{spr} , PI
summer	C13 _{sum}	GAM	N_{spr} , C13 _{spr} , F _{spr} , N _{sum} , F_{sum}	BSI, S _{sum} , T²_{sum}
	C45 _{sum}	GAM	N _{spr} , C13 _{spr} , F _{spr} , C13_{sum} , F _{sum}	BSI*, S _{sum} , T ³ _{sum} , PI
		TGAM	C13 _{spr} , C13_{sum}	BSI, S_{sum} , T ³ _{sum} , PI
autumn	C13 _{aut}	GAM	N _{sum} , C13_{sum} , F _{sum} , F_{aut} , N_{aut}	BSI , S _{aut} , T ² _{aut}
	C45 _{aut}	GAM	C13 _{sum} , C45 _{sum} , F _{sum} , C13_{aut}	BSI, S_{aut} , T ³ _{aut} , PI
		TGAM	C45_{sum} , C13_{aut}	BSI, S_{aut} , T ³ _{aut} , PI

* excluded from analyses due to collinearity (VIF > 3)
See for the abbreviations Table 6-S2

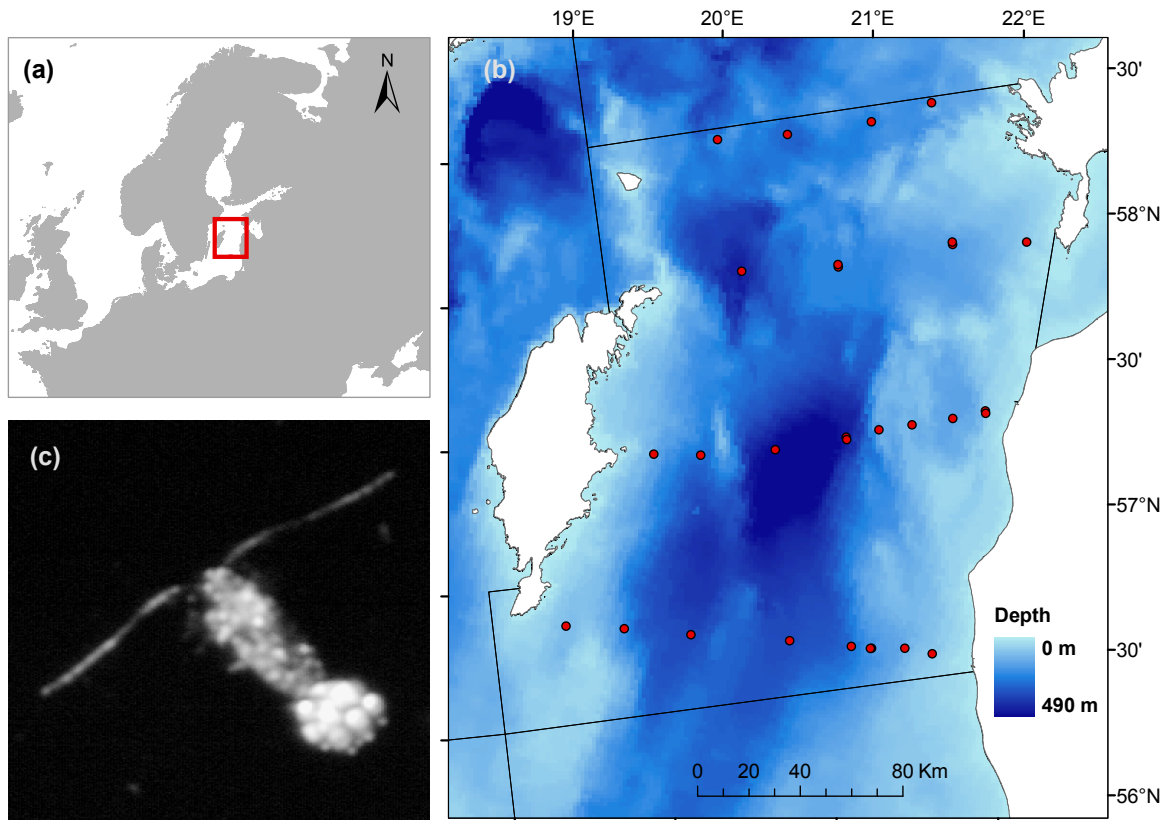
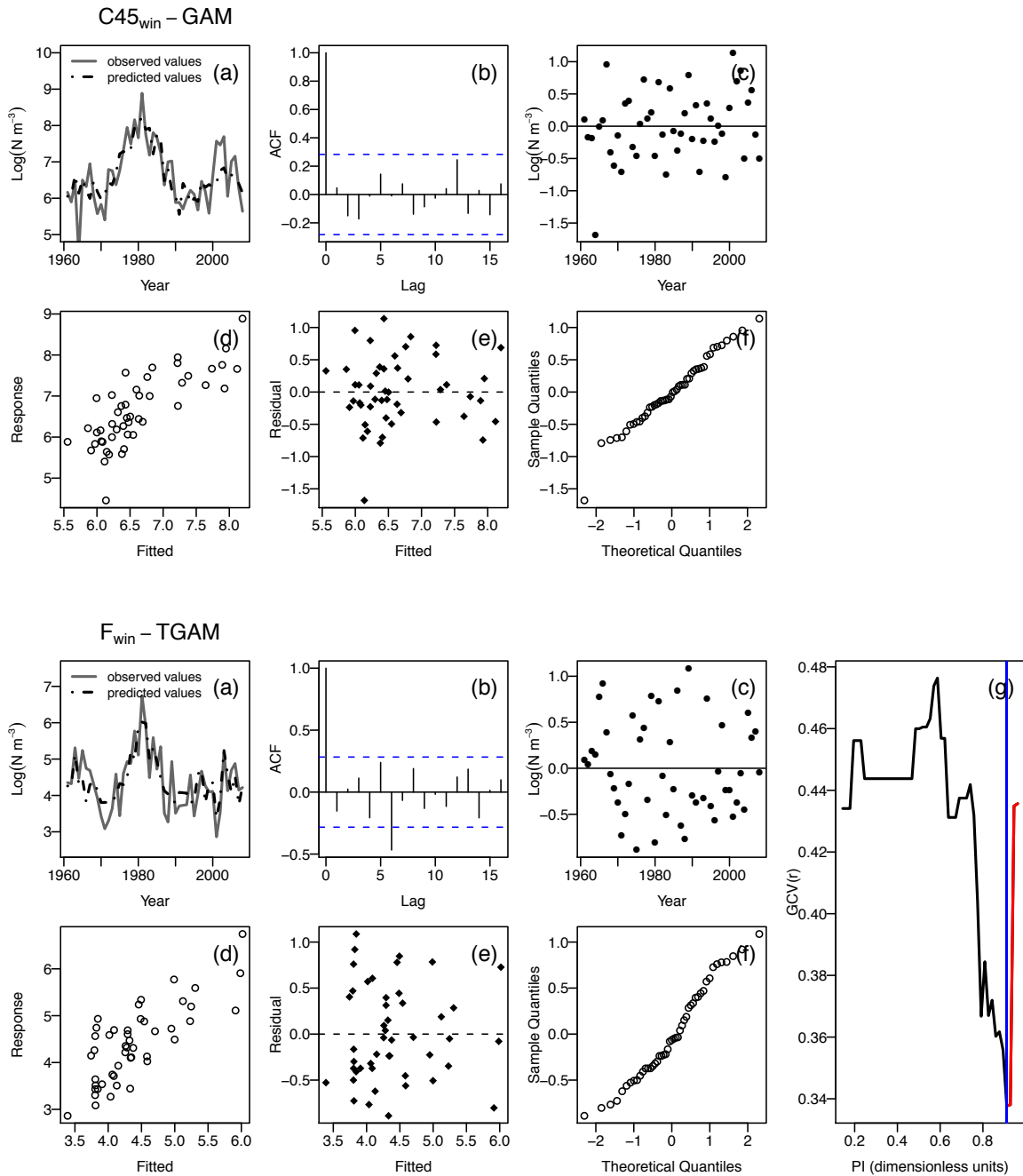
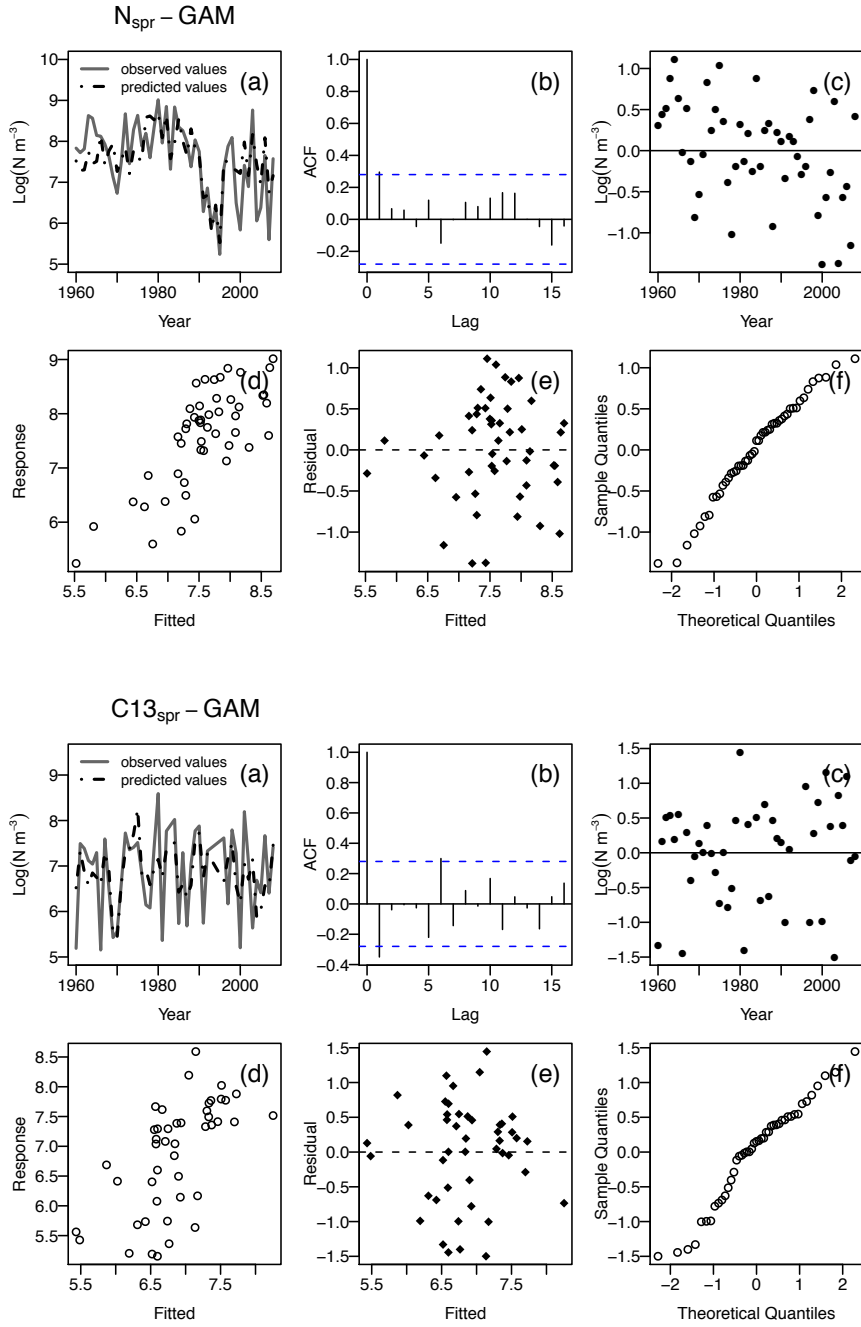
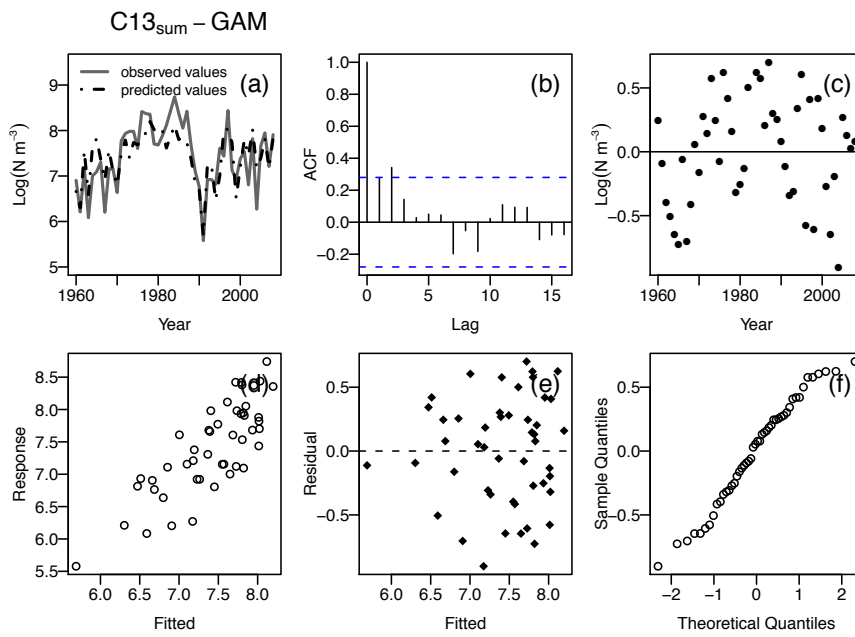
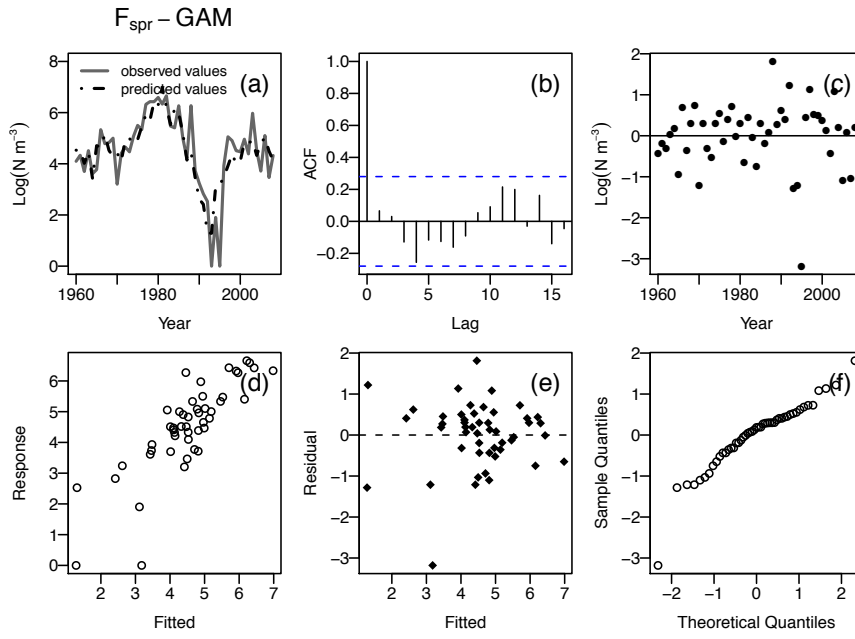


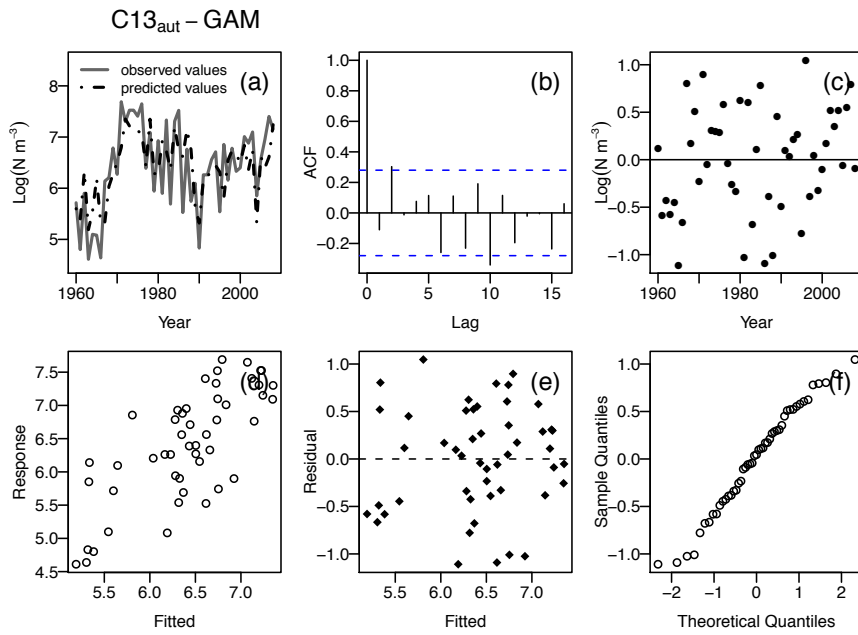
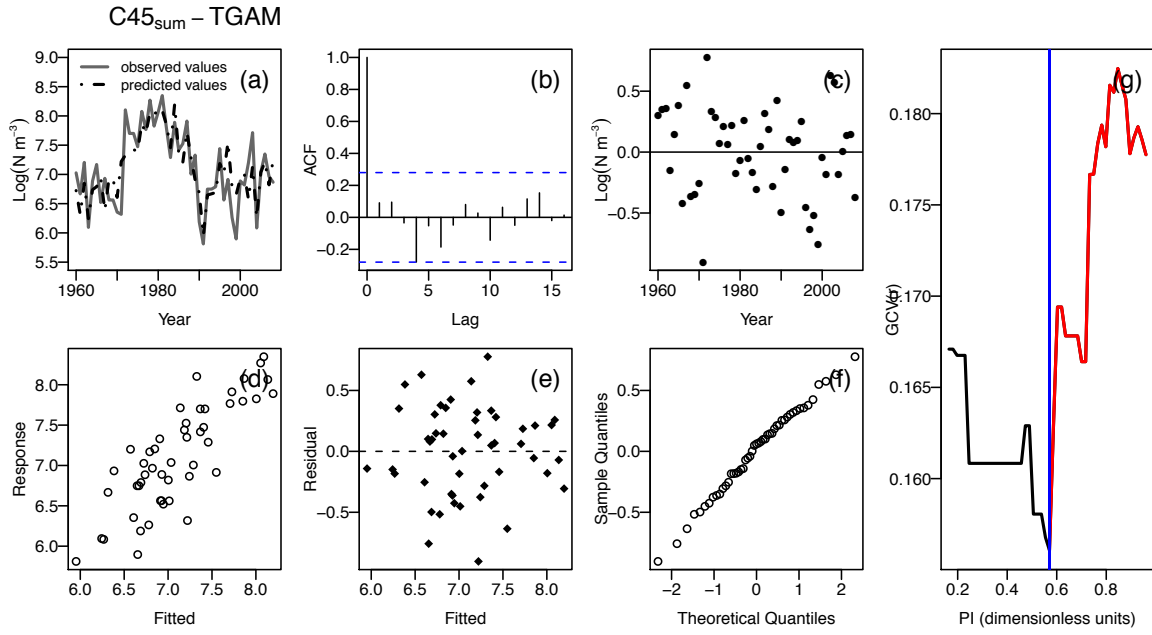
Figure 6-S1: Baltic Sea and *Pseudocalanus acuspes*. (a) Map showing the location of the Baltic Sea within Europe. (b) Main zooplankton stations (sampled > 20 times during the studied time period) in the Gotland basin (ICES subdivision 28, Central Baltic Sea). (c) Photograph of an egg-sac carrying *P. acuspes* female taken *in situ* with the video plankton recorder (source: Klas O. Möller)

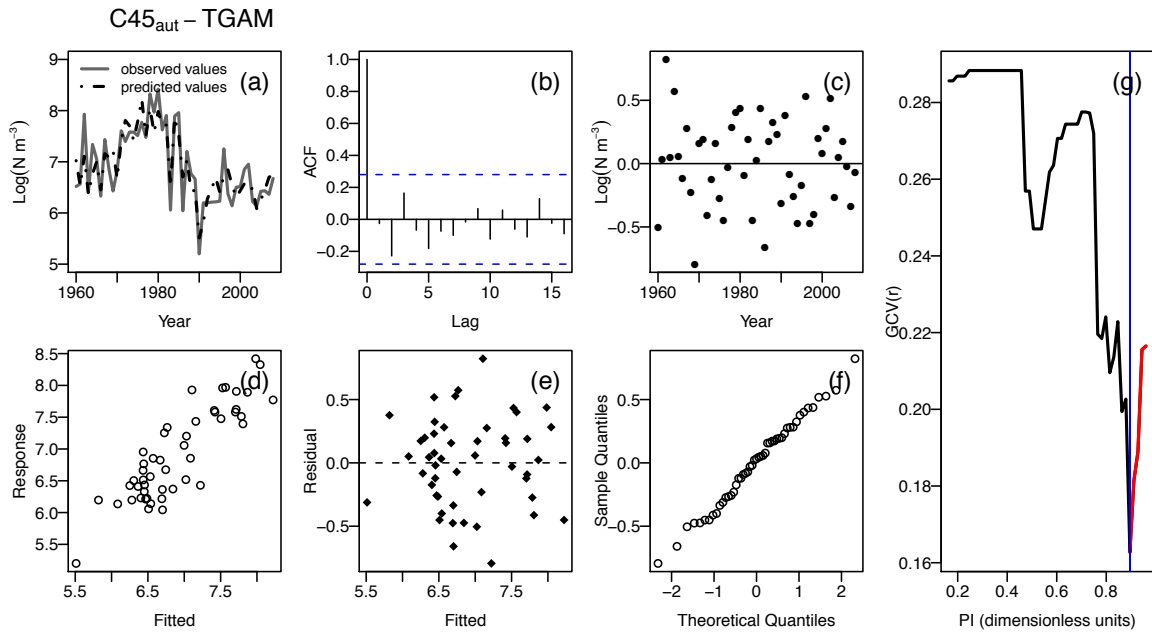
Figures 6-S2: Diagnostic plots of the final GAM or TGAM formulations. The model fitness is indicated by a comparison of (a) the observed vs. the predicted time series and (d) the fitted vs. each response value. Temporal dependence was evaluated by (b) the auto-correlation function plot (ACF), in which the significance level is indicated by the blue line, and (c) by the residual behaviour over time. Homogeneity (fitted vs. predicted values) and normality (Q-Q-Plot) are indicated by (e) and (f) respectively. The threshold estimation (generalized cross validation minimization) and the threshold value (blue line) of the predation index defining the low (black) and high (red) regime are given for each TGAM in (g).











7 A novel approach to modelling life cycle dynamics of a key marine species under past and future environmental changes

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Abstract

Identifying key indicator species, their life cycle dynamics, and their driving forces is an important step in a sound ecosystem-based management. But similarly important is an understanding of past and present species dynamics and how these influence future dynamics, which can be helpful in planning and decision-making processes. Here we show, and quantify, for the key copepod *Pseudocalanus acuspes* how the sensitivities to environmental drivers are strongly stage- and season-specific and how indirect effects on the following stage can amplify the direct environmental impact. We developed a single life cycle model, by linking stage-specific models that incorporate linear, non-linear, and non-additive density, climate, and food web effects and used it to simulate past long-term dynamics by retrospectively changing environmental conditions and project future dynamics under different climate and predation scenarios. Our novel modelling approach captured reliably the historical *P. acuspes* population dynamics and identified copepodites IV-V in winter and females in spring as the stages most sensitive to direct and indirect effects of the main drivers salinity and predation. Most importantly and interestingly our model projected a shift (i.e. a collapse) in *P. acuspes* population size when salinity levels drops to levels historically unreported. Our approach demonstrates that zooplankton has the hitherto unused potential as an integrative indicator of ecosystem change under multiple global change drivers (i.e. climate, fisheries, eutrophication), providing information of ecosystem state dynamics for modern ecosystem-based management approaches.

Key words: *Pseudocalanus acuspes*, critical life stages, future projected stock collapse, density-dependence

Introduction

Research on ecological futures has become increasingly important under the cumulative effects of a changing climate and further anthropogenic pressures such as eutrophication and overfishing. Reliable predictions of likely future ecosystem states are necessary for improving planning and decision-making processes (Clark *et al.* 2001, Carpenter 2002). However, studying the future can not only strengthen the bridge between science and management (Coreau *et al.* 2009), it can also aid in building new scientific knowledge (Pace 2001). Modelling is one possibility next to conducting experiments to understand and predict past and present dynamics of populations within ecological systems (Sutherland 2006, Jørgensen 2008). To identify how past and present population dynamics influence the future dynamics can be as important as identifying the drivers (Coreau *et al.* 2009). Hence, model-based predictions have been widely adopted as a heuristic tool in ecological future research and have been applied to various species in terrestrial and marine ecosystems (DeMaster *et al.* 2001, Huang *et al.* 2011, Kaschner *et al.* 2011). The use of short- and medium-term predictions in fish stock assessments as a basis for deriving advice on fishing quotas to governments and international regulatory bodies is one example where ecological future research has become indispensable in conservation management. Predictions can also help improving the mechanistic understanding (Pace 2001); a process that should be iterative: a better understanding supported by predictions leads to better models which then improve predictions.

However, every future prediction should only be considered as one probabilistic realization with a range of uncertainty attached to it. Predictions generally face several constraints: they can yield significant correlations although based on a poor understanding (Pace 2001) and they estimate an outcome under highly specific conditions assuming that future conditions affect for example a species in a similar way as past conditions. Predictions are further associated with great uncertainties due to initial and boundary conditions, or parameter and structural uncertainty. Consequently, literature is developing on how to quantify and present this uncertainty (Doak *et al.* 2008, Cook *et al.* 2010). An alternative is given by the use of projections, which are predictions conditional on future scenarios. Projections have the advantage to assess a broad range of potential future ecosystem states and to explore possibilities in ecosystems with important uncertainties rather than to predict a unique future (Carpenter 2002). Projections have gained increasing appreciation in recent years, particularly in conservation science and the decision-making process with a focus on socio-ecological scenarios (Tansey *et al.* 2002, Bohensky *et al.* 2006, Langmaed *et al.* 2009).

In marine future research, most studies focus on single species or communities of higher trophic levels (Lindegren *et al.* 2009, 2010, Barbraud *et al.* 2011, DeMaster *et al.* 2011, Cheung *et al.* 2011) or on primary production (Litchman *et al.* 2006, Jang *et al.* 2011). Instead, zooplankton species have been rather inadequately represented despite their great abundance and vital role

in mediating the energy flow from primary producers to consumers, as well as their importance in the microbial food web and the biological pump (Richardson 2008, Turner 2002, 2004). Zooplankton has been furthermore demonstrated as a very suitable indicator of the effect of climate change on aquatic ecosystems and long-term changes in marine zooplankton (Planque & Taylor 1998, Möllmann *et al.* 2000, Mackas & Beaugrand 2010). A few studies have emerged now in which bioclimate envelope models have been applied to project future geographic distributions of zooplankton species in marine systems (Helaouët & Beaugrand 2009, Helaouët *et al.* 2011, Letessier *et al.* 2011, Reygondeau & Beaugrand 2011). However, projections of zooplankton dynamics using simulation models that incorporate biotic interactions and non-linearity are sparse (but see Llope *et al.* (2011)).

An important, yet underrepresented task in projections of animal populations is the consideration of life cycle dynamics (Russell *et al.* 2012). Different life stages may have different environmental niches and hence vary in their adaptive ability to local climate conditions. Stage-specific differences in thermal tolerance have been demonstrated for instance among eggs, larvae, and pupal of the moth species *Manduca sexta* (Kingsolver *et al.* 2011) or juveniles and adults of the diamondback watersnake (*Nerodia rhombifer*) (Winne & Keck 2005). Seasonal components in the stage-specific response to environmental drivers can be additionally relevant as shown for Soay sheep (Coulson *et al.* 2001). Population dynamics are even more complex as species are not only driven by their abiotic environment but strongly interact with other species in the community. Species interactions such as competition or predation can have a great influence on the spatial and temporal dynamics of a species (Guisan & Thuiller 2005, Poloczanska *et al.* 2008), being sometimes the main driver as observed in trophic cascades (Pace *et al.* 1999, Frank *et al.* 2007). In the light of this complexity, Russell *et al.* (2012) have recently advocated a more integrated approach in ecosystem predictions, including the identification of key species, critical life stages as well as their main interactions.

In this study we for the first time link empirically derived linear, non-linear and non-additive statistical relationships of individual life stages with their environment into an integrative, complex stage-resolved population dynamic model for a key zooplankton species. Our model species is *Pseudocalanus acuspes* from the Central Baltic Sea, where it is an important ecosystem component, contributing significantly to a recent reorganization of the system (Möllmann *et al.* 2009). Generally, the genus *Pseudocalanus* spp. is one of the dominant zooplanktonic species in the world ocean and one of the most ubiquitous animals in the world (Corkett & McLaren 1978; Kane 1993; Richter 1995; Nielsen & Andersen 2002). Using our novel modelling approach we address the two major aims of future research in ecology. First, we improve our knowledge on the ecology of *P. acuspes* by simulating the historic population dynamics under different environmental conditions. This helped us identifying periods and life stages of particular vulnerability as well as to investigate the propagation of climate effects through the animal's life cycle. Second, we investigated potential futures of our model species by conducting stochastic

projections of the population's response to one climate and a number of fisheries management and eutrophication scenarios. Our novel approach demonstrates that zooplankton has the hitherto unused potential as an integrative indicator of ecosystem change under multiple global change drivers (i.e. climate, fisheries, eutrophication), providing information on ecosystem state dynamics for modern ecosystem-based management approaches.

Material and Methods

Data

Zooplankton

Abundance ($N \cdot m^{-3}$) data for *P. acuspes* are derived from a database of a zooplankton monitoring programme of the Institute of Food Safety, Animal Health and Environment (BIOR) in Riga, Latvia. The sampling is conducted seasonally since the 1960s, usually in February, May, August and October, with a variable number of stations in the Eastern Gotland Basin (see Fig. 6-S1b, SI in manuscript 2). The sampling gear, a Juday Net (Unesco 1979), has a mesh size of 160 μm and an opening diameter of 0.36 m. It is operated vertically and considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be slightly underestimated. Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a maximum depth of 150 m. During analysis, abundance of nauplii (N), early copepodites I – III (C13), later copepodites IV – V (C45) as well as adult females (F) were enumerated. For our simulation study, stage-specific abundance data were averaged across stations and season (i.e. annual quarters) and covered the period 1960 – 2008. The $\ln(X+1)$ – transformation was applied to all seasonal stage abundance data of *P. acuspes* to reduce intrinsic mean-variance relationships.

Environmental data

The modelling exercise in manuscript 2 revealed hydrographic variables temperature and salinity as well as predation (consumer control) to be the most important drivers of stage-specific long-term dynamics of *P. acuspes*. Additionally a local climate index (Baltic Sea Index – BSI; Lehmann *et al.* 2002) had a significant, although weak effect. Since no modelled future time series for the BSI is available we decided not to include this variable in our simulation study. Summer temperature time series were computed for the midwater (20-60m) shown to affect early copepodite stages. Salinity in the deepwater layer (70-100 m) affects late copepodite (i.e. C45) and adult stages from spring to autumn. Hydrographic time series were compiled to match the timing of the zooplankton sampling, i.e. April-May for spring, July-August for summer and October-November for autumn.

In our retrospective simulation exercise we used observed data from the period 1960 – 2008, derived from a database of the International Council of the Exploration of the Sea (ICES;

<http://www.ices.dk>) and BIOR. For our future projections we used data for 1974-2098 that were generated by the coupled physical-biogeochemical model BALTSEM (BALTic sea Long-Term large-Scale Eutrophication Model; Gustafsson 2000, 2003). BALTSEM is driven by output from a regional climate model (Döscher *et al.* 2002) that was forced with lateral boundary data from a large-scale coupled atmosphere-ocean general circulation model ECHAM5/MPI-OM (Meier *et al.* 2011) for one realization of the A1B emissions scenario (A1B1) The A1B scenario belongs to the A1 scenario family, one of the four marker scenarios chosen by the Intergovernmental Panel on Climate Change (IPCC) (2000), representing a world of rapid economic growth and rapid introduction of new and more efficient technology. This intermediate scenario predicts a global temperature rise of 2.8 °C together with a likely range of 1.7 – 4 °C in the first 21st century and was favoured over the other more extreme ones.

In addition to hydrographic variables, predation has been shown to affect later copepodite stages and females (manuscript 2; Möllmann & Köster 2002). These stages of *P. acuspes* represent major prey items for both Baltic planktivorous fish species herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Möllmann *et al.* 2004). However, the population size of *P. acuspes* is mainly controlled by sprat (Möllmann *et al.* 2008; Casini *et al.* 2008). Using sprat as an indicator for predation pressure was unfortunately not possible due to lacking data of stock size estimates from fish stock assessments prior to 1974 (ICES 2011). We therefore developed a predation index (PI) based on stock size estimates for cod (*Gadus morhua*) (manuscript 2). Eastern Baltic cod is the major piscivore in the Baltic Sea and its stock size is inversely related to the stock size of sprat (Casini *et al.* 2008; Möllmann *et al.* 2008). For the retrospective simulation study, we used spawning stock biomass (SSB) estimates for cod from official stock estimates that date back to 1966 (ICES 2011) and extended the time series back to 1960 using estimates by Eero *et al.* (2007). The combined dataset was inverted to mimic the predation pressure by planktivorous sprat and scaled to values between 0 and 1 (see Tab. 6-S2, SI in manuscript 2).

For our future projections, we derived four PI for the years 1974 – 2098 based on cod stock size estimates that were modelled using an Ecopath with Ecosim (EwE) food web model for the Baltic Proper (BaltProWeb, Tomczak *et al.* 2012) under different combined nutrient and fisheries management scenarios (see Fig. 7-1). Food-web model runs were forced by output from BALTSEM (i.e. time series of biogeochemical variables computed using BALTSEM) for the same climate scenario A1B and two nutrient load scenarios (BSAP and BAU), which were calculated from the product of nutrient concentrations and volume flows (Gustafsson *et al.* 2011). The BSAP scenario was designed according to the Baltic Sea Action Plan (BSAP), where the atmospheric deposition is reduced to 50% and the nutrient concentrations in rivers according to HELCOM (2007, but see for more details Gustafsson *et al.* 2011); the business as usual (BAU) scenario represents an increase in nutrient concentrations in rivers while atmospheric conditions remain at current levels (Gustafsson *et al.* 2011). The two fisheries management strategy scenarios tested for a cod fishing mortality of $F=0.3$, being in line with the present cod-

recovery-plan (EC No. 423/2004), and a cod fishing mortality of $F=1.1$, representing the average fishing mortality between 2002-2006 (ICES 2011). The four nutrient-fishery scenarios were named as BSAP high ($F=1.1$) and low F ($F=0.3$) as well as BAU high and low F .

Since the cod biomass trajectories modelled by BaltProWeb represented adults (ages ≥ 4) and not strictly the spawning stock (as in manuscript 2), the modelled cod time series for the hindcasted years 1974-2008 displayed the same trend but proportionally lower values as the observed time series. We hence rescaled the PI by basing the values 0 and 1 by the minimum and maximum of the projected cod time series during these past years. A comparison of the hindcasted *P. acuspes* stage abundances for the period 1974-2008 using the PI from the observed and modelled cod data showed only slight deviations and, hence, verified this approach (Fig. 7-S4c, in Supporting Information SI).

Statistical modelling

Model building

Statistical relationships of subsequent life stages with environmental variables derived in manuscript 2 were linked according to Llope *et al.* (2011) to simulate the observed intra- and inter-annual population dynamics of *P. acuspes* (Fig. 7-1). We initialized our simulations at year y with the first observation of late copepodites (C45) in winter and further on predicted female abundance in spring and consecutively the various seasonal life stage abundances throughout the year. Predictions of C45 in autumn then served as input for winter C45 at year $y+1$ starting the next year cycle.

We used only statistical models that contained significant relationships between successive stages (i.e. density terms). We dropped significant, albeit weak density terms for stages for which no statistical models could be applied in manuscript 2 due to their low abundances. Most of the stage-specific abundance-environment relationships we linked in our simulation models represent the class of Generalized Additive Models (GAMs) (Tab. 7-1). Relationships for winter females and C45 in summer and autumn represent the non-additive threshold formulation of GAMs (TGAM) which incorporate different relationships conditional on a threshold variable (Ciannelli *et al.* 2004), in our case the PI. When covariates displayed linear relationships to life stage abundance, GAMs were refitted with a linear term. We however used smoothers for all covariates to let the model be flexible when refitting to data subsets or on predicted data.

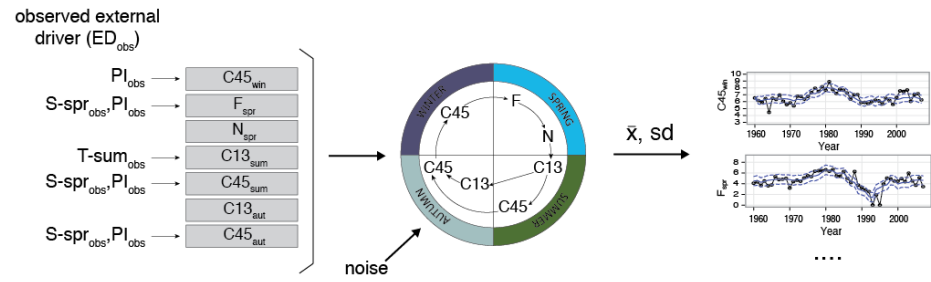
In all simulations we added random noise to the biotic variables by re-sampling (with replacement) the residuals from the model, trained on the observed time series data. For each model we draw the residual sample from the same season in a year in order to preserve the

A NOVEL APPROACH TO MODELLING LIFE CYCLE DYNAMICS |

Table 7-1: Overview of the final Generalized Additive Models (GAM) and the alternative threshold formulations (TGAMs) we selected for our simulation. These are based on the relationships derived in manuscript 2 (see Tab. 7-1). The fitted models were coupled in the presented order to simulate the observed intra- and inter-annual population dynamics of *P. acuspes*.

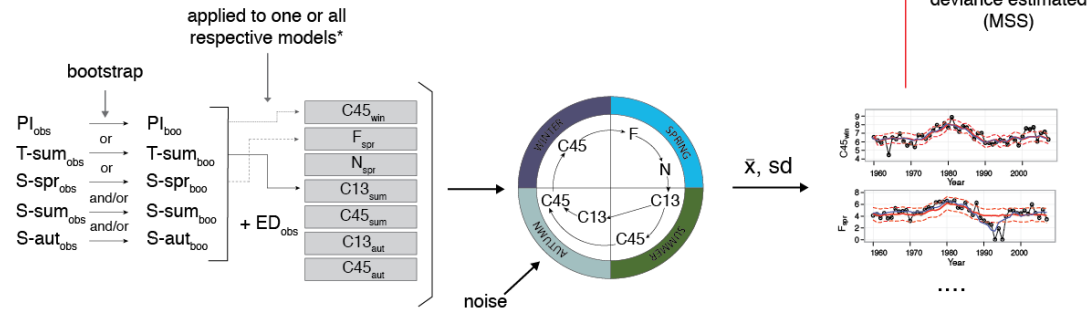
No.	season	response variable	model type	formulation
1	winter	C45 _{win}	GAM	$C45_{win,y} = b + f(C45_{aut,y-1}) + g(PI_y) + \varepsilon_{win,y}$
2	spring	F _{spr}	GAM	$F_{spr,y} = b + f(C45_{win,y}) + g(S_{spr,y}) + g(PI_y) + \varepsilon_{spr,y}$
3	spring	N _{spr}	GAM	$N_{spr,y} = b + f(F_{spr,y}) + \varepsilon_{spr,y}$
4	summer	C13 _{sum}	GAM	$C13_{sum,y} = b + f(N_{spr,y}) + g(T_{sum,y}) + \varepsilon_{sum,y}$
5	summer	C45 _{sum}	TGAM	$C45_{sum,y} = b + f(C13_{sum,y}) + g_1(PI_y) + \varepsilon_{sum,y} + \begin{cases} g_2(S_{sum,y}) & \text{if } PI \leq r \\ 0 & \text{if } PI > r \end{cases}$
6	autumn	C13 _{aut}	GAM	$C13_{aut,y} = b + f(C13_{sum,y}) + \varepsilon_{aut,y}$
7	autumn	C45 _{aut}	TGAM	$C45_{aut,y} = b + f_1(C13_{sum,y}) + \varepsilon_{aut,y} + \begin{cases} f_2(C45_{sum,y}) + g_1(S_{aut,y}) & \text{if } PI \leq r \\ g_2(PI_y) & \text{if } PI > r \end{cases}$

Step 1: Hindcast simulation under observed environmental conditions - suitability of model approach



Step 2: Hindcast simulations under changed environmental conditions - Sensitive life stages and propagation of effects

* For each simulation run, one bootstrapped driver is used to force only one stage model (e.g. PI_{boot} for $C45_{winter}$ or $T-sum_{boot}$ for $C13_{summer}$) while the rest is forced by ED_{obs} . Additionally, PI_{boot} is used for all relevant stage models and similarly $SS-spr/sum/aut_{boot}$.



Step 3: Projections based on four different scenarios

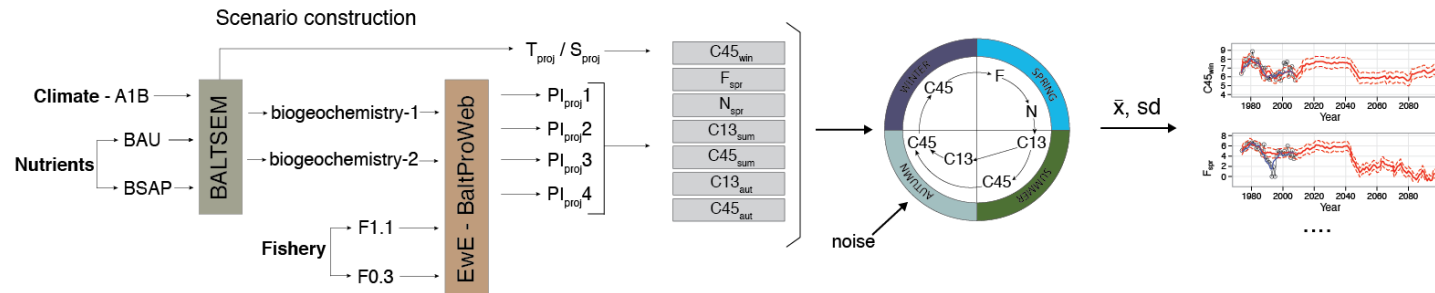


Figure 7-1: Conceptual diagram of the study design (steps 1-3). Single stage models of nauplii (N), young copepodites I-III (C13), old copepodites IV-V (C45) and females (F) were linked to a life cycle model and forced by observed past external drivers (step 1), testing for alternative past environmental conditions (step 2) and future projected conditions (step 3).

contemporaneous correlation of errors. 1000 Monte Carlo simulations were run for each model from which the mean and the standard deviation were calculated.

Model validation

The predictive performance of the coupled simulation model was tested by calculating Pearson's correlation coefficients r for the relationship between observed and mean predicted time series of each life stage model. Since predictions might be biased in a consistent direction, despite a perfect correlation ($r=1$), we did a model calibration as proposed by Potts & Elith (2006). We applied a simple linear regression between observed and mean predicted values (i.e. observed = $b + m \cdot \text{predicted}$), which provides information on the bias and consistency of the prediction indicated by the intercept term b and the slope m , respectively. If the model is perfectly calibrated, b should be zero and m should be one. Our models were derived from a relatively small dataset (< 50 observations). The smoothing terms are therefore likely to be influenced by single, extreme data points and often specific to this particular set of data. Consequently, a subset might lead to different amounts of smoothing for each covariate. We assessed their robustness by fitting the individual models to a subset of the observed data. For this, datapoints from five randomly sampled years (i.e. approx. 10%) were removed and the GAMs re-estimated for each simulation run.

Retrospective analysis of environmental effects and their life cycle propagation

The first goal in using our novel simulation model was to identify the strength of the effects of environmental drivers on the different *P. acuspes* life stages as well as to investigate their indirect effects on subsequent stages, i.e. the propagation of these effects within the life cycle. Hence, we performed bootstrapping on each environmental covariate within our simulations, either for single seasons or for the entire year (see step 2 in Fig. 7-1). In detail, we ran 1000 simulations for each analysis in which we created a vector of bootstrapped samples (with replacement) from the particular driver and predicted the seasonal abundance of the stage of interest based on this bootstrap. From the predicted time series we calculated the mean deviance to the predicted time series with fixed (i.e. observed) environmental conditions as mean sums of squares (MSS) and compared the succession of deviance between stages.

Projections of potential futures

Eventually we used our life cycle simulation model of *P. acuspes* for projections using temperature and salinity data derived by BALTSEM (based on the A1B climate scenario) and predation indices (PI) derived using BaltProWeb (based on the four management scenarios; 2 nutrient loads x 2 cod fisheries management scenarios; see above and step 3 in Fig. 7-1). We started each simulation in 1974, using again the observed winter abundance of late copepodites C45 as initial condition, and fed the models with projections of hydrography and PI until 2098. By this, we were able to assess the performance of the simulation based on projected

environmental drivers in comparison to the observations. To allow for comparisons with other lower or high trophic level models, which often use total biomass values during the main production seasons, we calculated the mean total biomass from spring-summer by multiplying the seasonal stage abundances of the mean projection, including its standard deviation, with their individual wet weights after back-transformation (Hernroth 1985), and by calculating the total biomass of all stages within the season and then averaging between spring and summer.

Results and Discussion

Performance and robustness of the linked life cycle model

Our novel modelling approach performed generally well in simulating the historical *P. acuspes* population dynamics. Predictions by the coupled model captured reliably the observed trends, while smoothing the high-frequent year-to-year variability (Fig. 7-2). The model validation exercise further indicated no strong bias despite a slight but consistent underestimation of seasonal abundances. Furthermore, we found the statistical relationships to be robust as simulations based on randomly sampled subsets of the observed data deviated little in mean and standard deviation from time series derived from the full dataset (Fig. 7-S1, SI).

The simulation model performed best for females (F) in spring and late copepodites (C45) in winter and autumn (correlation between modelled and observed time series $r=0.8$, $r=0.76$, and $r=0.75$, respectively). Simulated summer dynamics of early copepodites (C13) and C45 correlated as well fairly good with observations, although displaying a slight overestimation during the 1960s and an underestimation of the peak abundances during the 1970s and 1980s. (Fig. 7-1). Predictions of spring N abundance was less accurate since we used only spring F as predictor (explaining 44% of the N variance), but removed the BSI term (see Material and Methods).

The statistical model for C13 in autumn had a lower performance ($r=0.3$), predicting a rather constant time trajectory but missing the observed increase during the early 1970s. The poor model performance is likely due to the removal of explanatory variables (i.e. autumn F and N as well as BSI) compared to manuscript 2, which explained together 30% of the total variance. For the overall life cycle dynamics, however, the poor model fit for this stage-group was of less importance since predicted abundances of the subsequent life stages in autumn (i.e. C45) fitted well to observations. In general, estimation of early life stage abundances (i.e. N and C13) is difficult in *P. acuspes* and zooplankton in general since peak egg production is variable in time, and development times are short and sensitive to the prevailing temperatures (Renz *et al.* 2007, Vidal 1980, Liu & Hopcroft 2008). A resulting sampling bias may explain the strong year-to-year variability in our observed time series of earlier *P. acuspes* life stages as well as higher standard deviations in the model simulation.

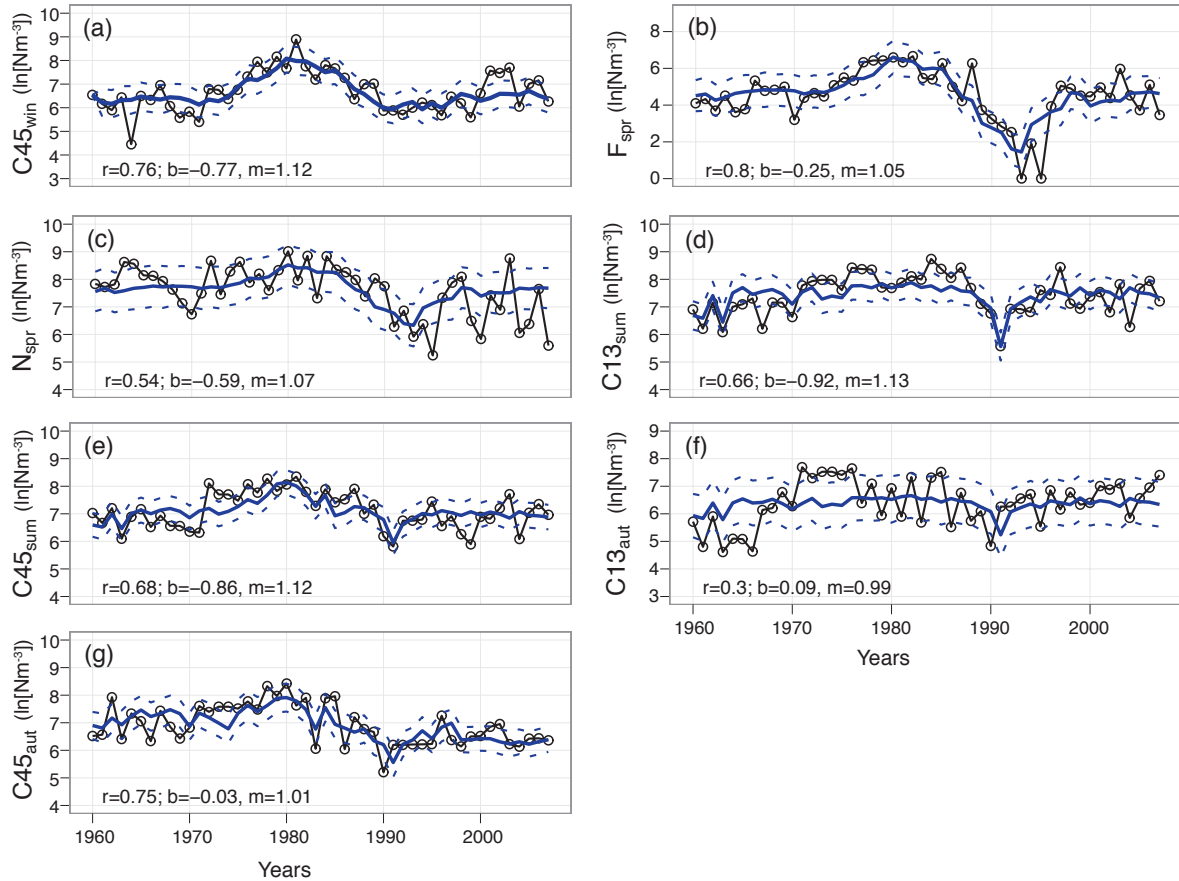


Figure 7-2: Predicted hindcast of seasonal stage abundances from our coupled life cycle model. Simulations were started using the first observation of C45 winter abundances of the series (in 1960) from which the female spring abundance and consecutively the various seasonal stage abundances within this and the following years were predicted (from (a) to (g)). The blue, solid lines represent the means of the 1000 Monte Carlo simulations, the blue, dashed line the standard deviations. The black line with circles represent the observed time series. Pearson's correlation coefficient r between observed and mean predicted time series are given together with the calibration intercept (b) and slope (m).

Vulnerability of life stages to environmental change

The model validation exercise gave us confidence that our simulation model reliably captures the population dynamics of *P. acuspes*. Hence, we first used the coupled model to simulate the past, which allowed us to examine the responses of the different life stages to variable environmental conditions. The predicted time series of each model run are presented in the Supporting Information (Fig. 7-S2.1 - 7-S2.10). We identified periods and life stages of particular vulnerability by evaluating their responses to changes in environmental drivers, measured as the degree of deviance between simulations with randomized (i.e. bootstrapped) and observed (i.e. fixed) environmental conditions.

The results of our bootstrapping analysis show that in the life cycle of *P. acuspes* C45 in winter and F in spring are the stages most sensitive to the main environmental drivers salinity and predation. We observed F abundance in spring under randomized salinity to be constantly lower than in the fixed simulation (Fig. 7-S2.1b). More importantly, the strong decline in C45 abundance during the early 1990s was not reproduced, evidencing the negative effect of the

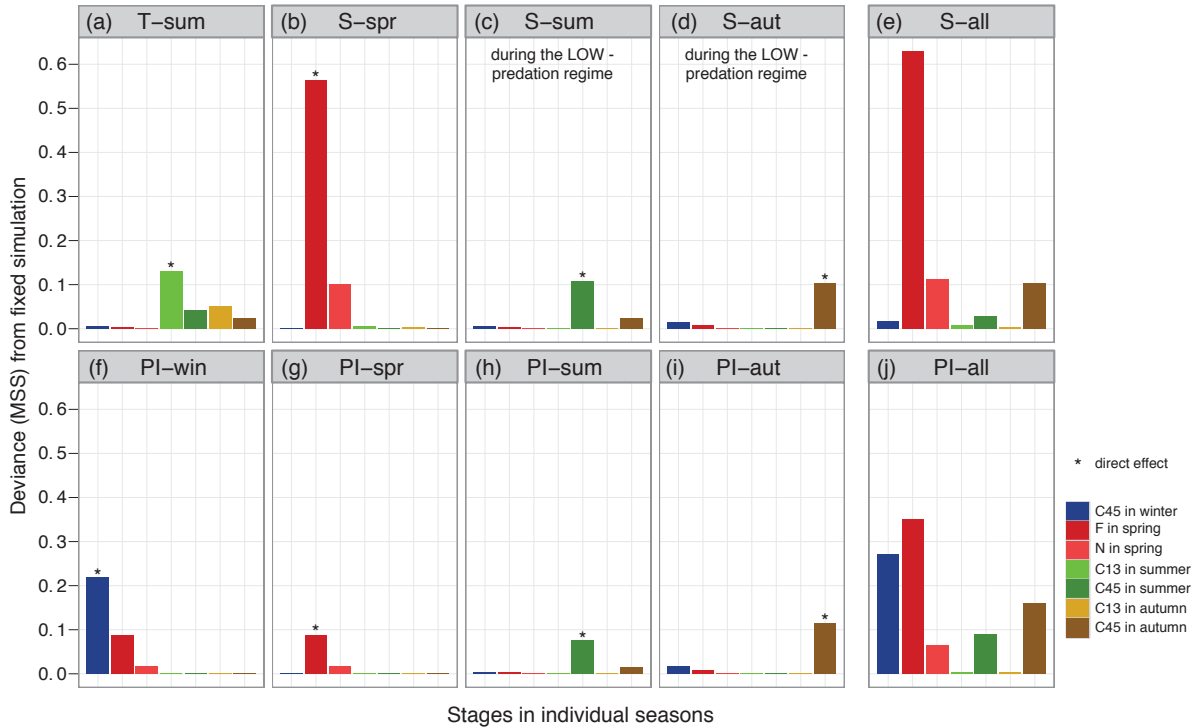


Figure 7-3: Direct and indirect effects of changes in environmental conditions. The mean sums of squares (MSS) between mean predicted seasonal stage abundances from the fixed simulation and the simulations where environmental covariates were bootstrapped. That is, temperature in summer (a), salinity in spring (b), summer (c), autumn (d) and all three seasons together (e), as well as PI in winter to autumn (f-i) and the whole year (g).

decrease in deepwater salinity. Predictions of F abundance in spring displayed by far the highest deviance (Fig. 7-3b), highlighting the importance of environmental forcing during their reproductive period. It has been shown earlier that spring females inhabit the deeper and more saline water layers to avoid osmotic stress and to save energy for their gonad development and reproduction (Möllmann *et al.* 2000, Renz & Hirche 2006). We further found C45 to be the stage-group most vulnerable to predation, especially during winter (Fig. 7-3f). Hence, predation pressure explained well the observed peak in *P. acuspes* abundance around 1980. Our results are in accordance with previous studies showing sprat to prey on *P. acuspes* mainly during winter and spring (Möllmann & Köster 2002, Möllmann *et al.* 2004). During these seasons C45 reside in deeper Baltic water layers where they most likely overwinter in an active diapause with inhibited moulting, reduced metabolism and growth, despite an ongoing but lower foraging activity (Norrbin 1990, Renz & Hirche 2006). This strategy has been adapted to resist unfavorable conditions (Cohen 1970) and in consequence makes the animals less likely to be influenced by hydrography. On the other hand, their slow mobility may lead to a higher vulnerability to sprat predation (Norrbin 1992).

Beside the main effects on environmental drivers for C45 in autumn and F in spring, we further observed non-additive effects of salinity for C45 in summer and autumn only during a low predation regime. Hence, predicted time series of C45 abundance in summer and autumn derived by our randomized simulations differed from the fixed simulations only during low or high

predation regimes, respectively (see Fig. 7-S2.2e, 7-S2.3g). Effects of temperature were generally weak and restricted to copepodite stages in summer and autumn.

In addition to direct effects of environmental drivers on life stages of *P. acuspes* we investigated the indirect effects on subsequent life stages, i.e. the propagation of external effects within the life cycle, by comparing the deviation between the bootstrapped and fixed model predictions in subsequent stage-specific abundances. The direct effect of an environmental variable in a particular season was mainly translated to the next, directly linked stage only. Evidence for this is derived by the low or absent deviance estimate of life stages not subsequent to each other (Fig. 7-3), as well as by the strong agreement between time series predicted with randomized and fixed environmental covariates (Fig. 7-S2.1 - 7-S2.10). Similarly did climate impacts not propagate to later life stages in fish dynamics (Stige *et al.* 2010). We found the lack of propagation of environmental effects within the life cycle to be most pronounced in spring, when only a relatively small proportion of the high deviance in predicted F abundances, caused by bootstrapping the spring salinity conditions, is visible in the N prediction (Fig. 7-3b). However, if environmental changes affect several stages throughout the year as in the case of predation and salinity, the indirect effects on the following stage can amplify the impact of the direct effects. For instance, changes of predation pressure in winter not only affect the dynamic of C45 winter abundances but also of F in spring (Fig. 7-3f) as they depend on the survival of the overwintering stock (Ohman 1985, Peters *et al.* 2006). Consequently, the female stock in spring is in both respects negatively affected by an overall increase of predation pressure - by the lower number developing from the surviving winter C45 stages and by the direct predation mortality. This amplification is indicated by the strong increase in deviance of predicted female spring abundance under a simulation of bootstrapped PI within all seasons (Fig. 7-3j), which could explain the particularly strong predation effect identified for the spring stock in previous studies (Kornilovs *et al.* 2001, Möllmann & Köster 2002, Möllmann *et al.* 2008). It further strengthens the suggestion of females in spring representing the most critical life stage and period.

Projection of a future shift

After using our novel simulation model to investigate the ecological processes that have caused past dynamics of *P. acuspes*, we used the model to evaluate potential futures of our target species. To this end we combined the A1B climate scenario with four predation scenarios that are the result of a combination of two nutrient load and cod fisheries management scenarios. The actual future projections start in 2010, while the period from 1974 to 2009 serves as a calibration period for the environmental drivers. The projected *P. acuspes* stage abundance time series of each model run are presented in the Supporting Information (see Suppl. Fig. 7-S3.1 - 7-S3.4).

The forcing variables for our life cycle model of *P. acuspes* were derived both from BALTSEM and BaltProWeb. The main and most drastic feature of the A1B climate scenario is a strong and

abrupt decrease in deepwater salinity from 10 to 8 around 2040 (Fig. 7-S4b). Summer temperature instead is expected to increase continuously from about 5 to 8 °C with high inter-annual fluctuations (Fig. 7-S4a). Predation of sprat on *P. acuspes* will likely depend on the level of cod fishing pressure. Under a high fishing mortality (i.e. BAU high F and BSAP high F) the cod stock is expected to collapse independent of nutrient loads and climate (Lindegren *et al.* 2010), leading to a strong control of *P. acuspes* by sprat (Fig. 7-S4c). Under the target fishing mortality of the stock recovery plan (F=0.3), cod is expected to recover during the period of 2020 to 2040. However, latest during 2040 the cod stock will likely decrease again due to decreasing salinities affecting reproductive conditions (Lindegren *et al.* 2010). The timing and magnitude of the future cod decrease and hence an increase in predation pressure on *P. acuspes* will be conditional on the nutrient load scenario (Fig. 7-S4c). During the high nutrient load, business as usual scenario (BAU) cod would display a stronger and earlier collapse compared to the lower target loads attached to the Baltic Sea Action Plan (BSAP). The mechanism behind this detrimental effect of higher eutrophication on the cod stock are most likely reduced oxygen conditions negatively affecting cod egg survival (Köster *et al.* 2003). The effect of different fishing mortality levels on cod (F=1.1 vs. F=0.3) is strongly visible across trophic levels during the period of 2020 – 2040 (Fig. 7-4). Here, *P. acuspes* biomass is increasing under low cod fishing mortality as a response to an increasing cod stock resulting in lower predation pressure by sprat (Fig. 7-4 b, d). In contrast, when the cod stock is depleted under a high fishing pressure, maximal predation pressure by sprat will also deplete the *P. acuspes* biomass (Fig 7-4 a, c). This result shows the predominant importance of the cod stock for food web structure in the Baltic (Casini *et al.* 2008, 2012, Möllmann *et al.* 2008, 2009).

The common feature across all four projected *P. acuspes* future trajectories is the abrupt, hence regime-shift like (Scheffer *et al.* 2001; Scheffer and Carpenter 2003) decline in *P. acuspes* biomass in synchronicity to the drastic decrease in salinity around 2040 (Fig. 7-4). Under the assumed climate scenario the biomass of the copepod dropped in all nutrient load and fishery scenarios to levels lower than observed before. The population collapse will furthermore occur irrespective of the biomass level before 2040 which was strongly determined by the level of predation pressure (see above). The major driver of this collapse of the *P. acuspes* population are most likely the low salinity conditions in the second half of the 2000s as a result of the assumed climate scenario (A1B). The low salinity of < 9 in the deepwater would be the main driver limiting the population growth (but see below).

Our future simulations indicate non-additive effect of the environmental drivers of *P. acuspes* and the importance of ecological thresholds (Casini *et al.* 2009). We found the population collapse around 2040 to be largely independent of the level of predation pressure on *P. acuspes* as a result of the two different cod management scenarios. Only during the most favourable cod stock scenario with low fishing mortalities and low eutrophication (BSAP-F0.3) a minor positive cascading effect on *P. acuspes* is visible, but on a very low population level only (Fig. 7-4d).

Hence the main driver of change is the low salinity, and indeed deepwater salinities < 9 likely prevailing under the assumed climate scenario during the last 60 years of our century have rarely and only sporadically been observed before. Hence, 9 can be assumed an ecological threshold where salinity drives *P. acuspes* dynamics independent of predation level. Casini *et al.* (2009) have shown based on a retrospective analysis that a threshold in control of Baltic zooplankton exists. They defined the threshold in a reverse fashion determining the predation level that outperforms the control by the abiotic environment. Here we show reversely that under an assumed climate change and freshening of the Baltic Sea salinity will control *P. acuspes* biomass independent of the predation level. As shown above and earlier (Möllmann *et al.* 2000, manuscript 2), the salinity is mainly affecting F abundance during reproduction in spring and hence indirectly nauplii production (Renz & Hirche 2006).

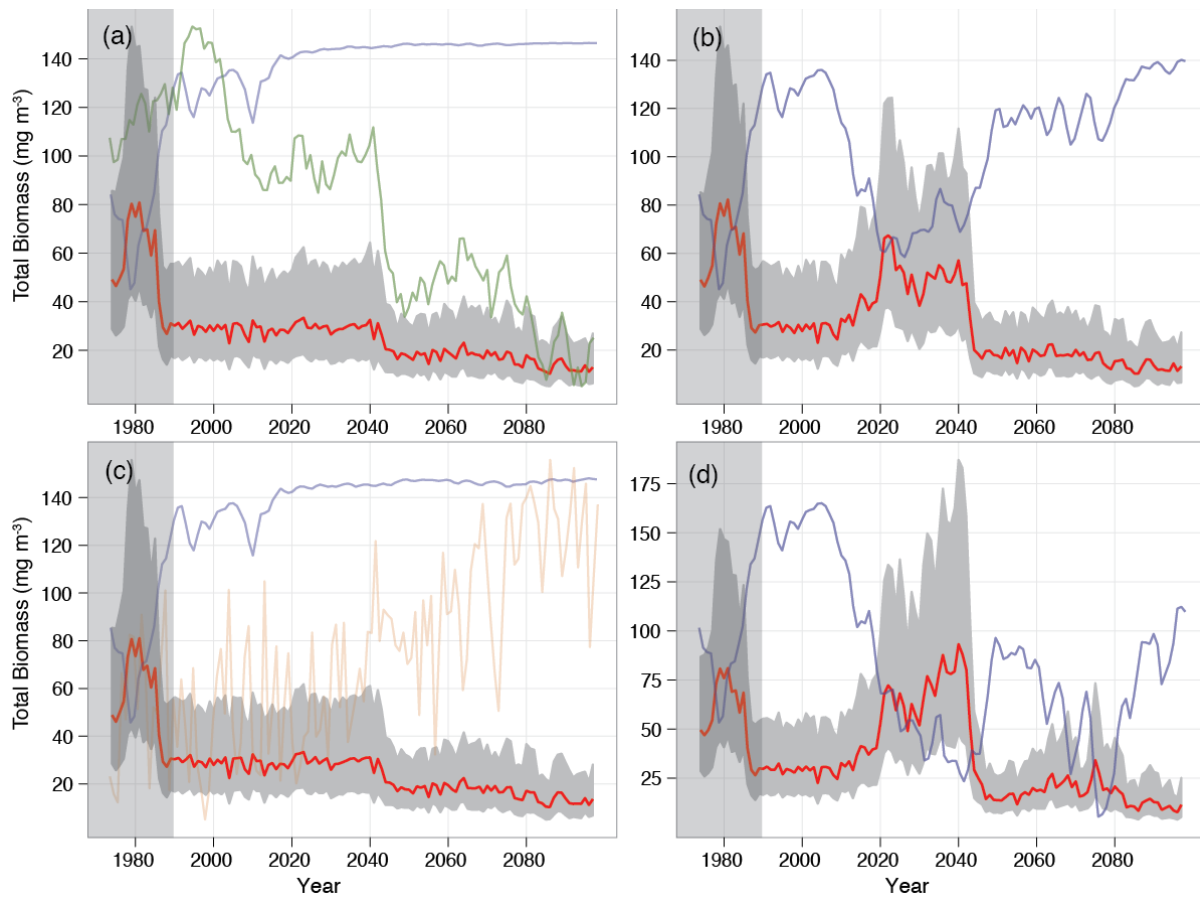


Figure 7-4: Future projections of total biomass in the main production period (spring-summer), starting in 2010, under one salinity-temperature scenario (A1B) and four predation pressure scenarios based on two different nutrient load scenarios (BSAP, BAU) in combination with two fishery management scenarios (high F, low F): (a) BAU high F, (b) BAU low F, (c) BSAP high F, (d) BSAP low F. The red lines together with the shaded areas represent the mean projected biomasses and their standard deviations. The projected trend of salinity conditions is illustrated in (a) as green line, temperature conditions in (c) as yellow line. The four projected PI trends are illustrated in blue in each scenario (a-d).

In contrast to salinity, temperature played only a minor role in the future simulations of *P. acuspes*, as they are projected to remain within the optimal range for the affected C13 stages,

exceeding this range only after 2080 (i.e. > 6 °C). Different nutrient loadings affected *P. acuspes* in our model only indirectly via their effect on the predation level. In this respect, one of the drawbacks of our model is that food components are not included, particularly as resource-induced competition may be a factor inducing density-dependence in *P. acuspes*. Reduced salinity conditions may generate osmotic stress in female *P. acuspes*, increasing respiration rate and energy requirements and eventually food demand. Higher rates of primary production due to higher nutrient loads might therefore have a compensating effect, which we did not account for due to a lack of long-term data.

As expected our projections of *P. acuspes* biomass bear high estimates of uncertainty, indicated by the standard deviation, particularly for the period between 2020 and 2040 under low predation pressure regimes (Fig. 7-4 b, d). But despite this uncertainty the major dynamics described above clearly emerged. Generally, due to the various uncertainties inherent in future extrapolations, either model-based (Thuiller 2004, Pearson *et al.* 2006, Beaumont *et al.* 2007) or evolutionary-based (Hoffmann & Sgrò 2011), the projected time series should not be regarded as certain future outcome. Instead, our projection exercise proves to be a useful tool to identify interacting dynamics and potential population responses, which otherwise would not be resolved.

Identifying the mechanisms and drivers leading to the future shift

We further investigated the mechanisms that have caused the shift in *P. acuspes* dynamics c. 2040 in our model simulations. As we above identified C45 in winter and F in spring to be the most vulnerable life stages, we assumed the survival rate $F/C45$ to be critical for overall population dynamics of our model species. $F/C45$ over time displayed a strong synchronicity with overall future population dynamics of *P. acuspes*, including the strong and abrupt decrease around 2040 (Fig. 7-5). The shift in our model is largely independent of the future predation scenarios used in the simulations, hence pointing towards the overwhelming importance of the climate-induced salinity decrease. However, between the shift and 2080 we see a period of low but variable survival rates induced by predation. Variability is highest under the BSAP-scenarios depending on the level of predation on *P. acuspes* induced by the two different cod management scenarios (Fig. 7-5b). After 2080 the survival rate $F/C45$ is simulated to be very unstable with high fluctuations induced by the very low F abundances projected by the model.

Density-dependence is generally considered as a mechanism stabilizing animal population dynamics (Sinclair & Pech 1996, Bjørnstad & Grenfell 2001). The importance of density-dependence in population dynamics has been controversially debated for decades (Nicholson 1933, Andrewartha & Birch 1954, Turchin 1999), and only recently its role in zooplankton long-term dynamics has been acknowledged. Ohman *et al.* (2002) and Plourde *et al.* (2009) observed

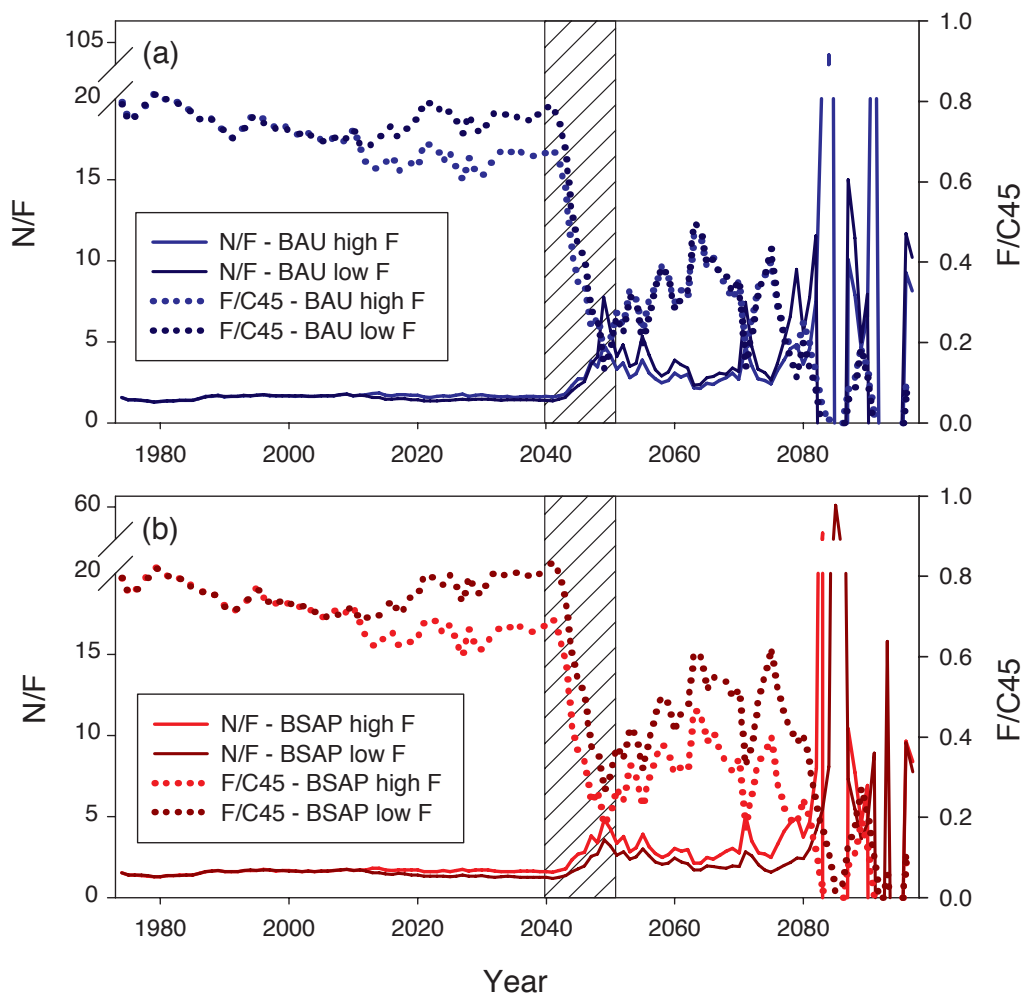


Figure 7-5: Projected temporal developments of production rates in spring (N/F) and survival rates from winter to spring (F/C45) under both cod fishery scenarios (low/high F) in combination with (a) the high nutrient loading (BAU) scenario and (b) the low nutrient loading scenario (BSAP).

mortality rates of eggs and nauplii of *Calanus finmarchicus* to depend on the number of females during the growth period. Hence, we investigated the survival of N in relation to F abundance. Interestingly, we found an increase in survival of N matching in time the shift around 2040 and showing a strong density-dependence at low levels of *P. acuspes* F abundance (Fig. 7-5). Cannibalism and food supply are generally major sources for density-dependence in zooplankton (Ohman *et al.* 2002, Plourde *et al.* 2009). Both mechanisms are not well investigated for *P. acuspes* in the Baltic Sea. Nevertheless, the genus *Pseudocalanus* sp. has been generally considered as not food-limited (Corkett & McLaren 1978, Davis 1984, Ohman 1985) because of their low food requirements such as for maximal ingestions rates, development, and maximum body size (Paffenhöfer & Harris 1976, Vidal 1980a,b) and sufficient ambient concentrations of phytoplankton. A recent comparison of female growth characteristics between *P. elongatus* in the North Sea and *P. acuspes* by Renz *et al.* (submitted) has confirmed that for *P. elongatus* food is not a limiting factor. In contrast, however, *P. acuspes* shows relatively low production rates related to restricted food availability. Because of the stratified hydrographic condition in the Baltic

Sea, with its permanent halocline around 60 to 70 m depth and a thermocline that develops in summer, physical and food conditions can be challenging. During the late spring and summer season, when the thermocline has established, phytoplankton production is restricted to the upper mixed layer (van Beusekom *et al.* 2009). Except for the nauplii, *P. acuspes* stages inhabit the layers below the thermocline and hence are dependent on sinking algae, microzooplankton or detritus (Peters *et al.* 2006, Möller *et al.*, in press). After the degradation of the spring bloom food concentrations can strongly decrease to maximal $90 \mu\text{g C l}^{-1}$ (van Beusekom *et al.* 2009), which is regarded as limiting for growth rates of *P. acuspes* (Renz *et al.*, submitted).

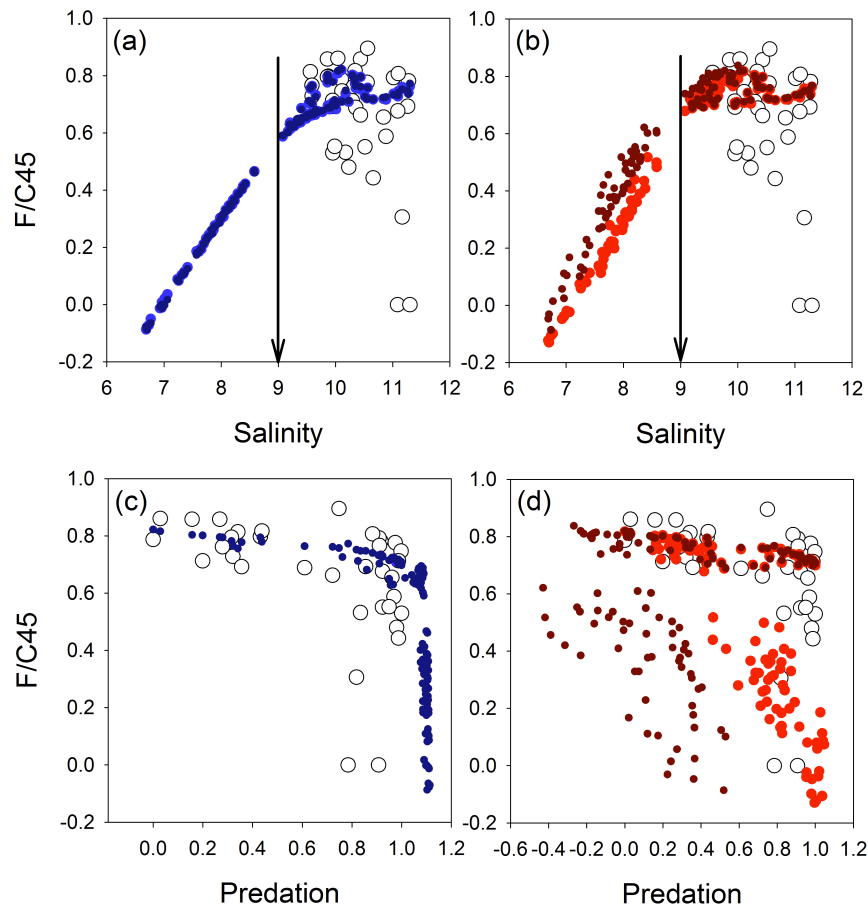


Figure 7-6: Relationships between survival from C45 to F and environmental drivers salinity and predation under scenarios of high F (a,c) and low F (b,d) in combination with the BAU (light blue and red) or the BASP (dark blue and red) scenario.

Despite the indications for increased offspring production of Baltic *P. acuspes* at extremely low F abundance, our future simulations show that density-dependence could not compensate for the strong reduction of survival from C45 to F in relation to salinity (Fig. 7-5). Hence, we investigated the development of F/C45 to the main environmental drivers salinity and predation (Fig. 7-6). Relating the survival rate to salinity clearly demonstrates the salinity to be the main driver for the future shift in our model simulations. While historically (except of three low F/C45 outliers) and in the projections until 2042, there is no relationship between the survival rate, from 2043 onwards and during salinities <9 we observed a strong linear decrease of F/C45 with salinity. This

relationship is independent of the predation scenario used, showing only a slight delay of the decrease in survival under low cod fishing mortality and the BSAP nutrient load scenario (both leading to lower predation on *P. acuspes*; Fig. 7-6b). The secondary importance of predation for our projected future shift in *P. acuspes* dynamics is also demonstrated by the relationship of F/C45 to the predation index (PI). The decrease in F/C45 occurs only at very high predation levels under most of the environmental scenarios and occurs even under reduced predation in the low cod fishing and BSAP nutrient load scenario (Fig. 7-6d).

Conclusion

Using a novel, statistically-based life cycle model we showed that *P. acuspes* as an originally arctic marine species will be endangered through the assumed freshening of the Baltic Sea as a result of future changes in climate (Meier *et al.* 2006). The level of population response will certainly depend on the level of the decrease in salinity which is conditional on the magnitude of the assumed climate change, for which we used only one realisation (A1B) in our study. Nevertheless, reduced salinities are a common feature in the Baltic under most projections of future climate (Meier *et al.* 2006). Our model simulations, alike some earlier process-based and time series studies (Möllmann *et al.* 2000, Renz & Hirche 2006), further identified key life stages that were affected by environmental change. Most importantly and interestingly our model projected a shift (i.e. a collapse) in *P. acuspes* population size when salinity levels dropped to levels historically unreported. Our life cycle model is hence able to anticipate the ecological dynamics under novel environmental futures and can serve as a tool for modern ecosystem-based management of the Baltic Sea, where *P. acuspes* is a key species that affects strongly the overall food web dynamics (Möllmann *et al.* 2008). As zooplankton is still underappreciated as an indicator for the management of marine ecosystems, we suggest similar models of key zooplankton species to be developed for other areas of the world ocean. Last but not least, our modelling approach shows the value for future projections of ecological systems, not only for management, but also for a better understanding of ecological dynamics (Coreau *et al.* 2009). Using our novel model we were able to identify critical stages in the life cycle of our model species, the most important environmental drivers and an ecological threshold in the response of the population to future environmental change. These findings may be the starting point for new field and laboratory investigations on Baltic *P. acuspes* and may fuel similar studies on other key zooplankton species.

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Supporting Information

Supporting figures

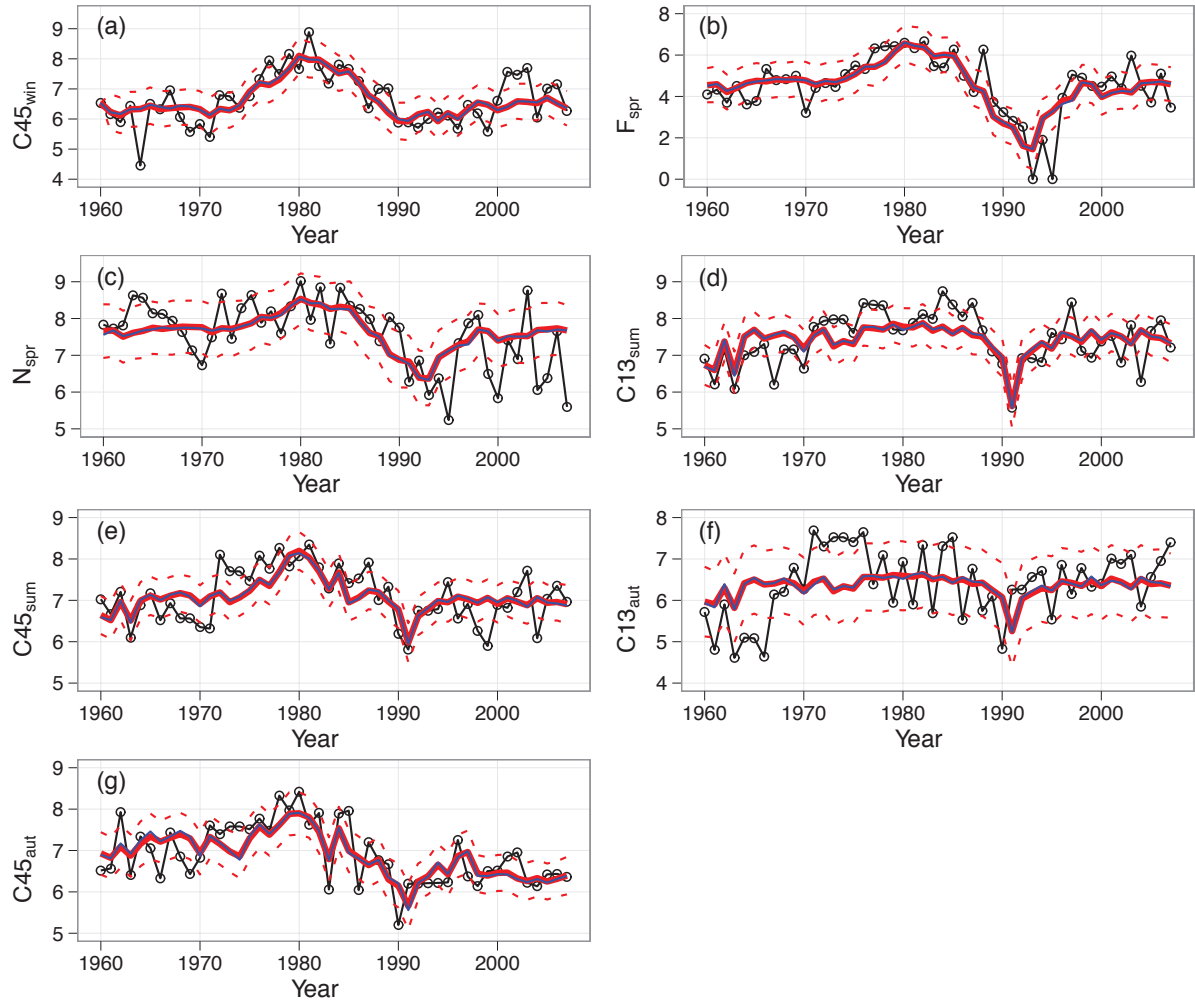
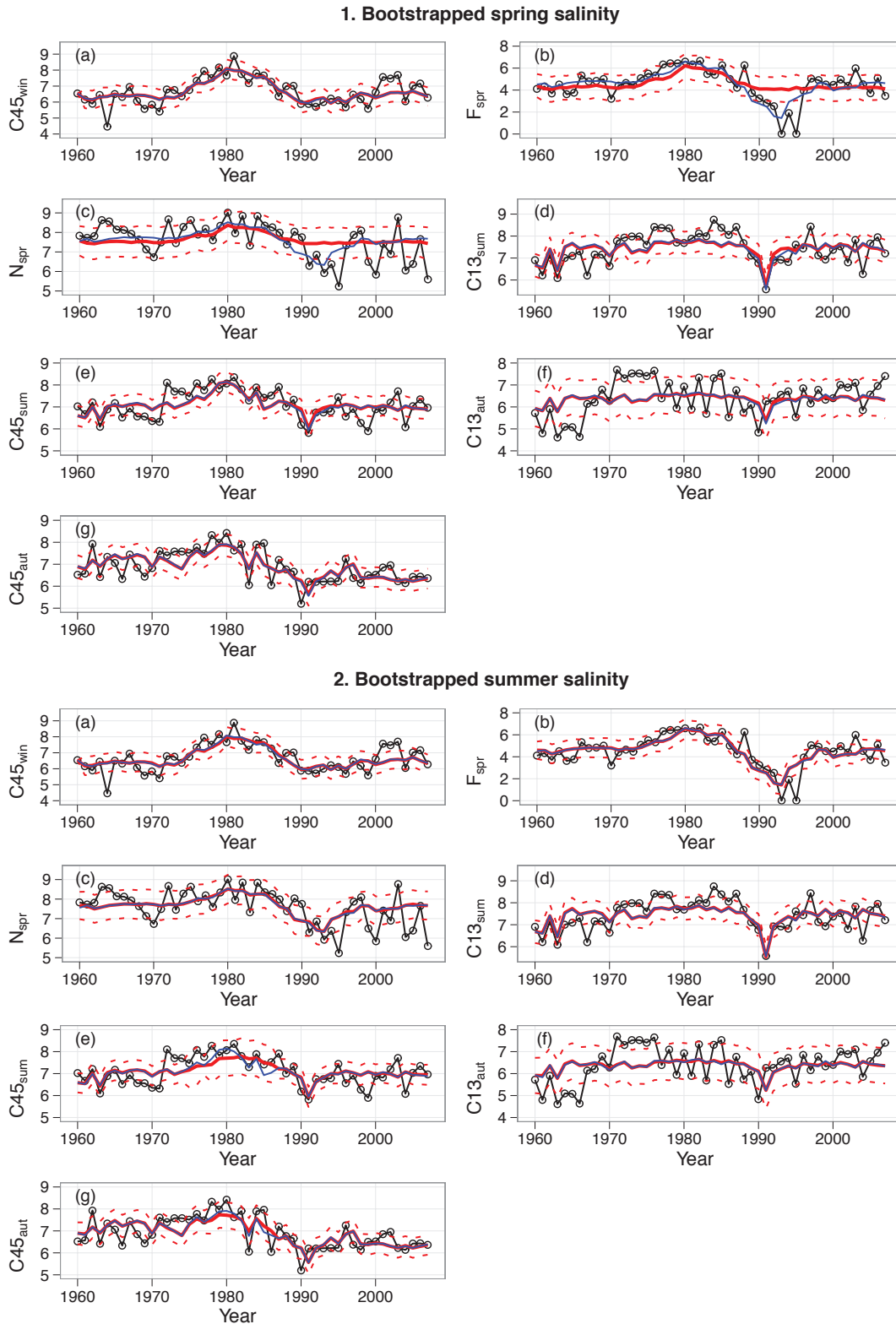
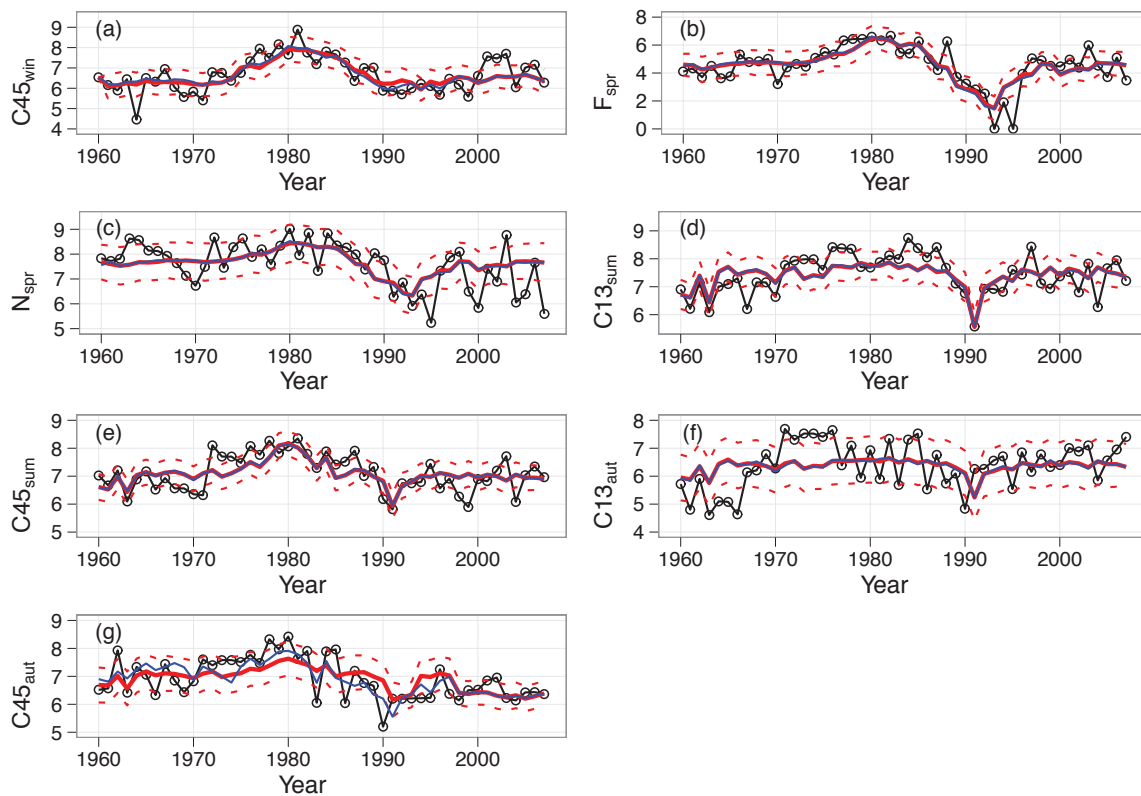


Figure 7-S1: Evaluation of model robustness. The simulated time series of seasonal stage abundances based on individual models that were fitted on a subset of data (i.e. five randomly sampled years (i.e. approx. 10%) were removed and the GAMs re-estimated for each simulation run.) vs. models fitted on the full data set are presented. The red, solid lines represent the means of the 1000 Monte Carlo simulations based on subsets, the red, dashed line the standard deviations. The overlying, blue solid lines represent the mean of the 1000 full data set Monte Carlo simulations. The observed time series are illustrated as black line with circles.

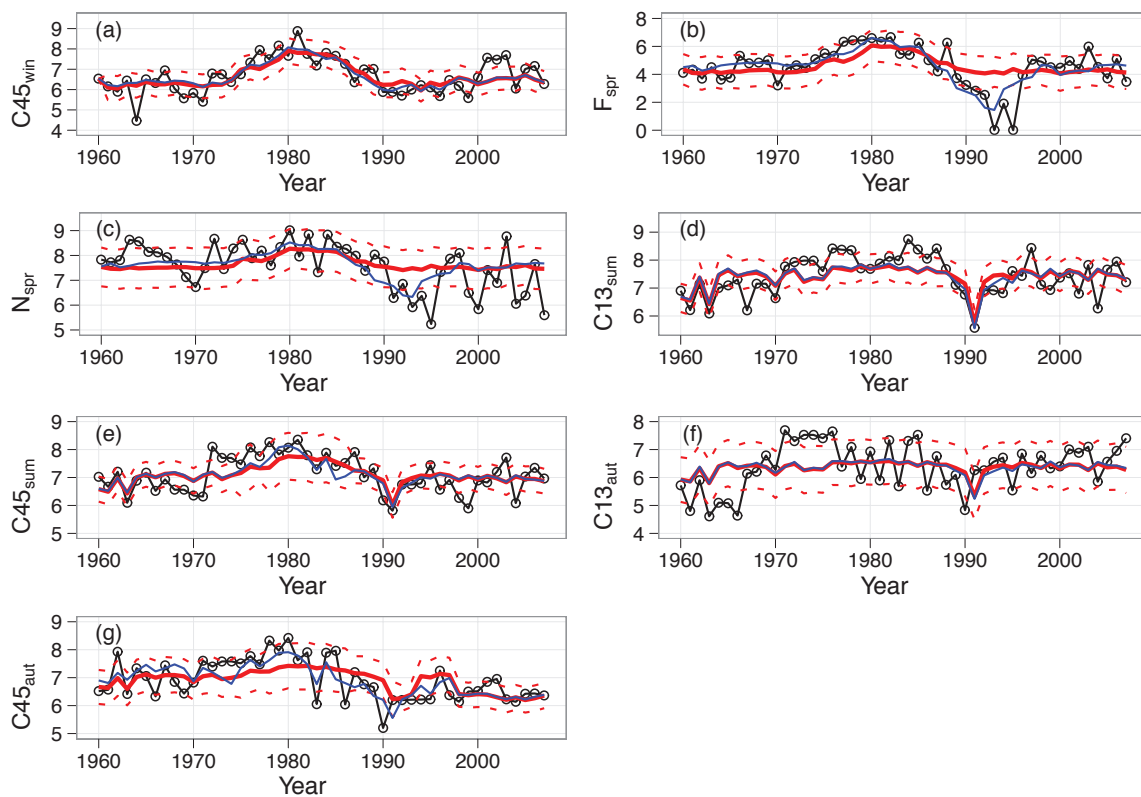
Figure 7-S2.1 - 7-S2.10: Simulation of past stage dynamics under bootstrapped environmental conditions. For each simulation in which time series of single environmental covariates were in one or several seasons bootstrapped, predicted time series of seasonal stages abundances are presented. The red, solid lines represent the means of the 1000 Monte Carlo simulations, the red, dashed line the standard deviations. The overlying, blue solid lines represent the mean of the 1000 Monte Carlo simulations from the fixed model (i.e. based on observed environmental conditions). The observed time series are illustrated as black line with circles.



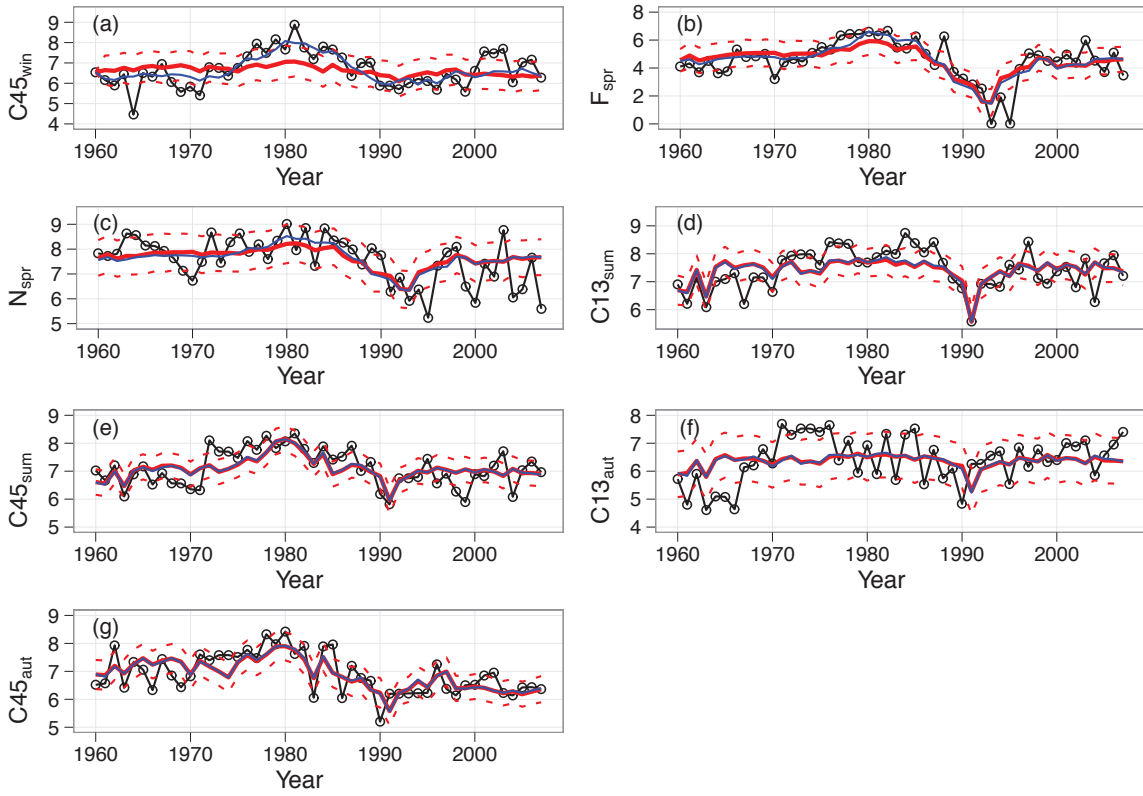
3. Bootstrapped autumn salinity



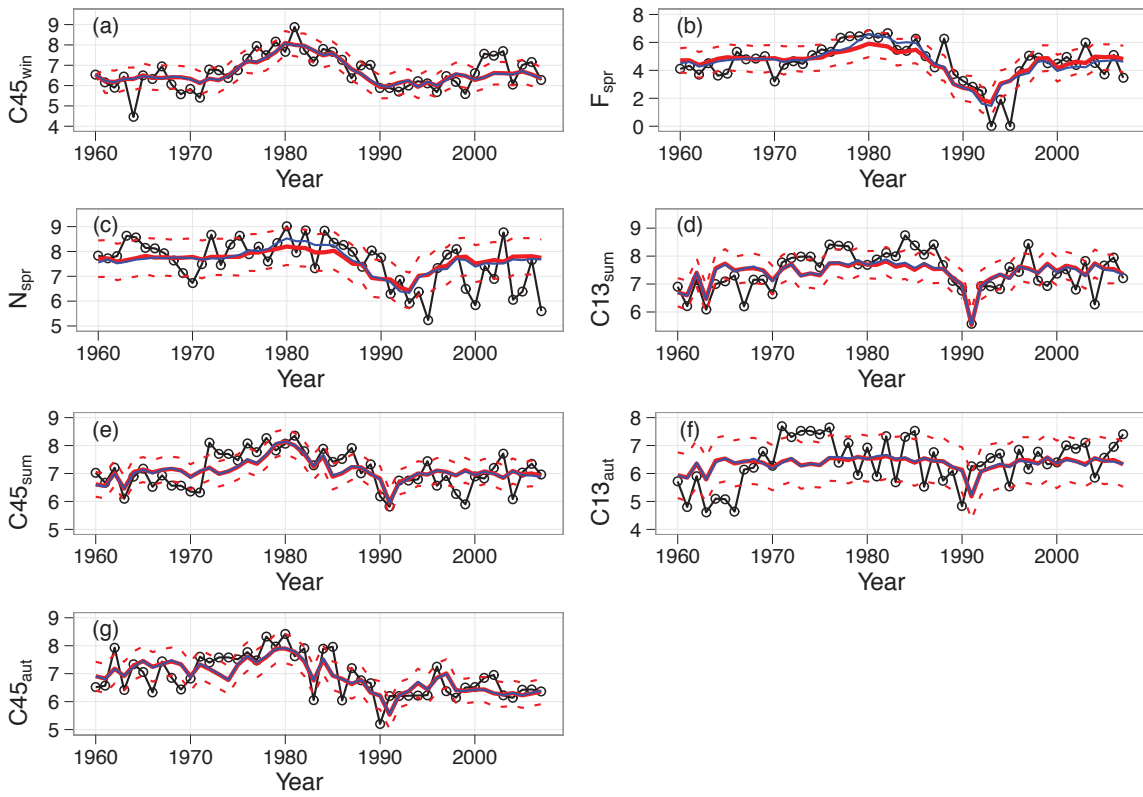
4. Bootstrapped summer - autumn salinity



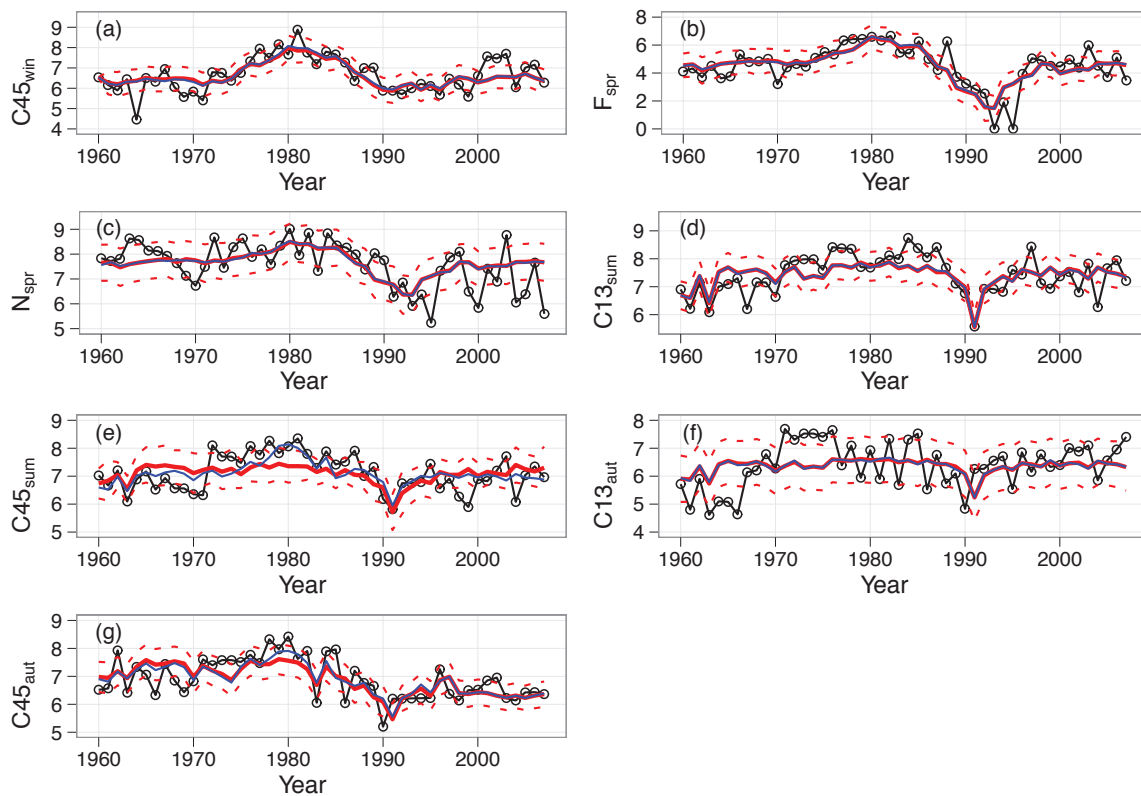
5. Bootstrapped winter PI



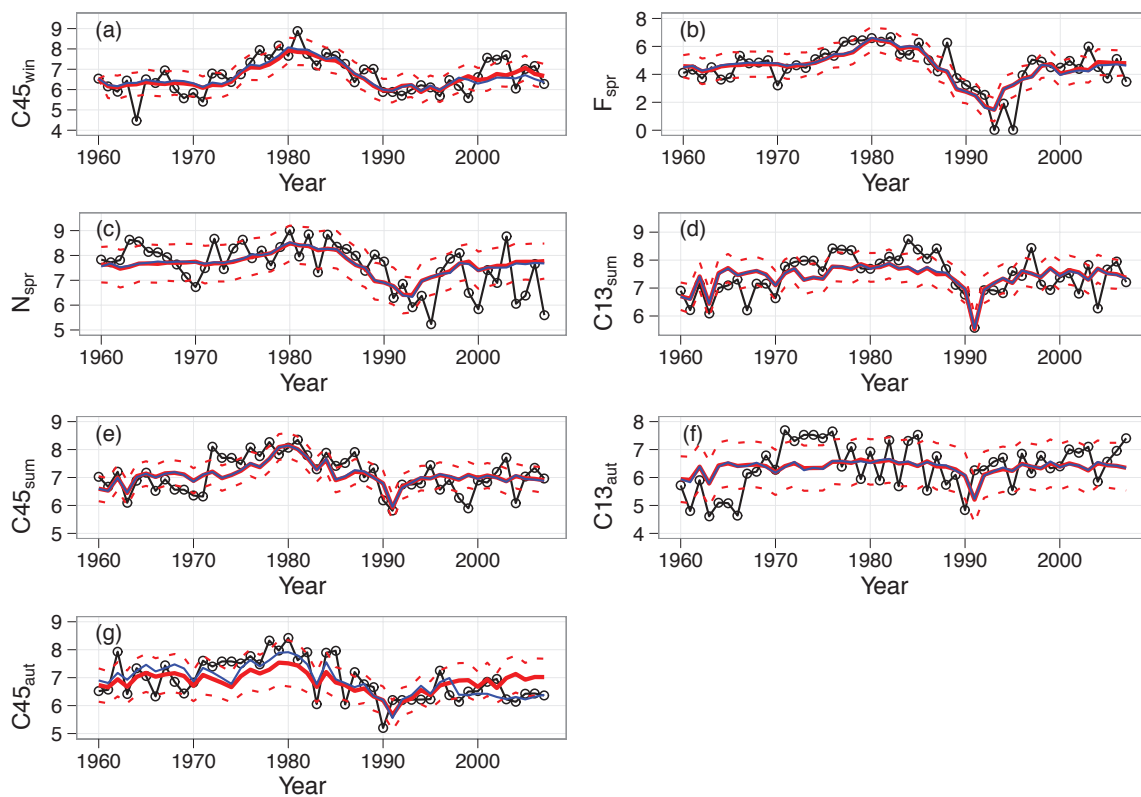
6. Bootstrapped spring PI



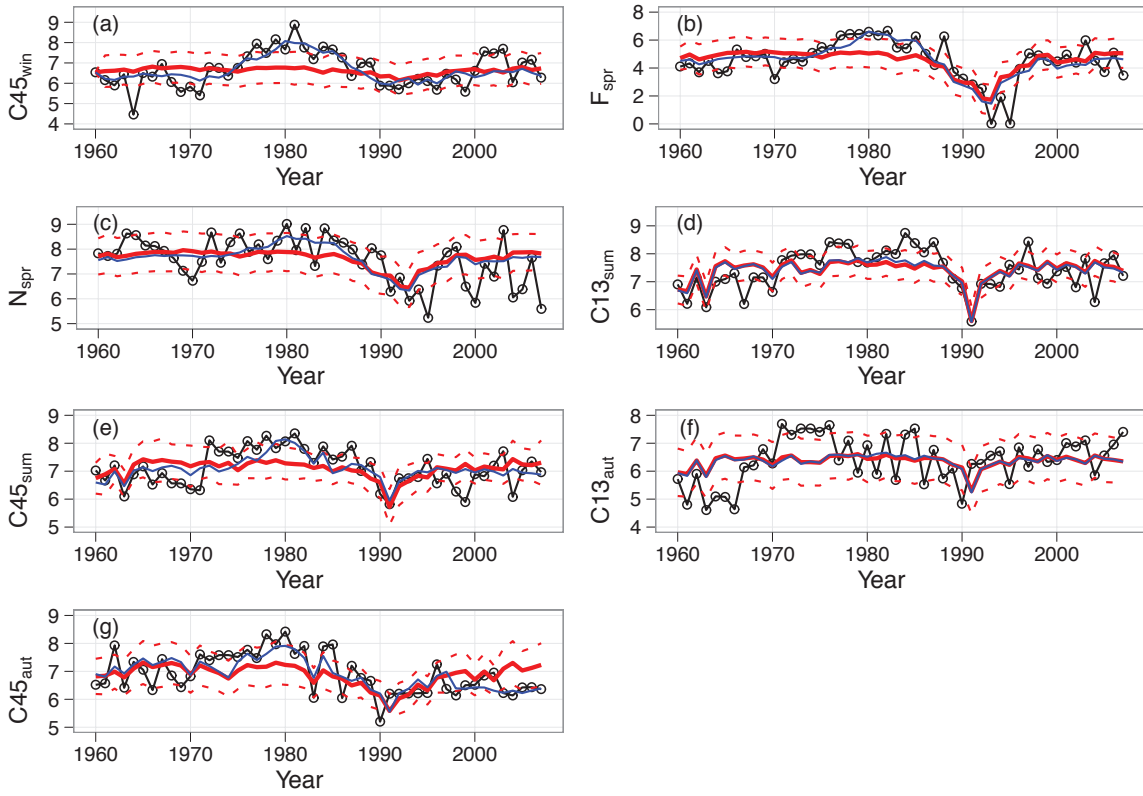
7. Bootstrapped summer PI



8. Bootstrapped autumn PI



9. Bootstrapped winter- autumn PI



10. Bootstrapped summer temperature

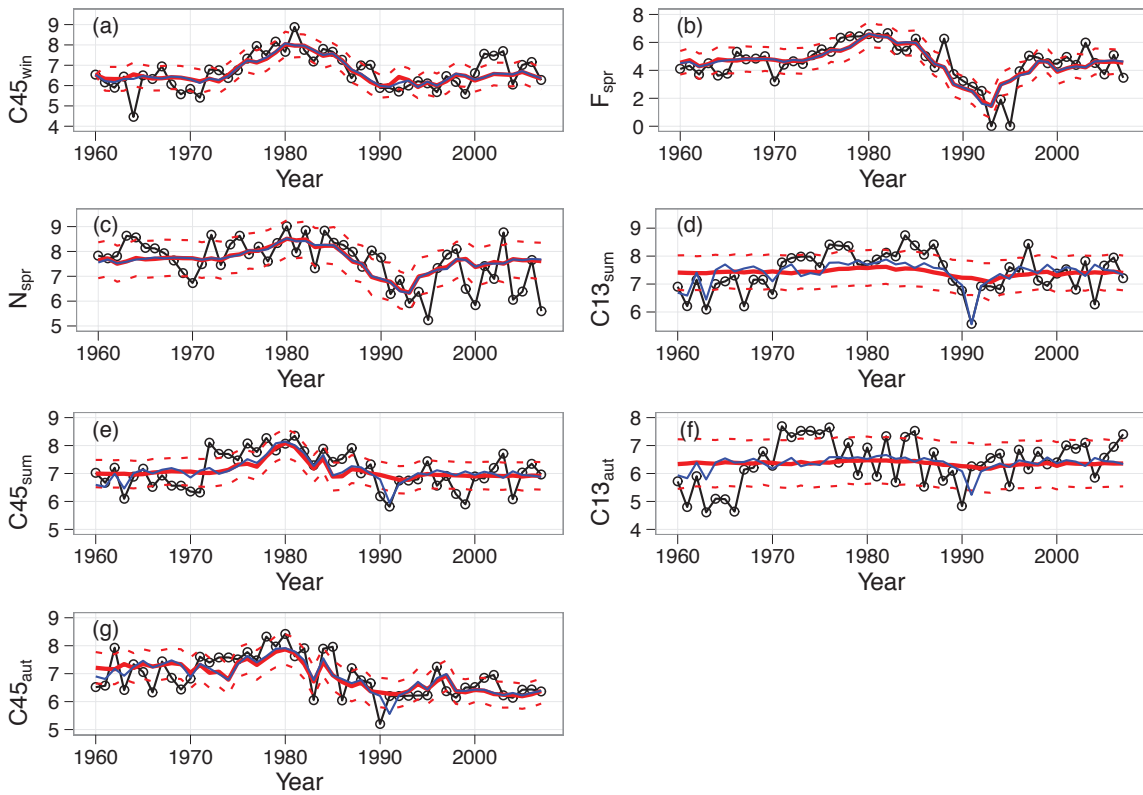
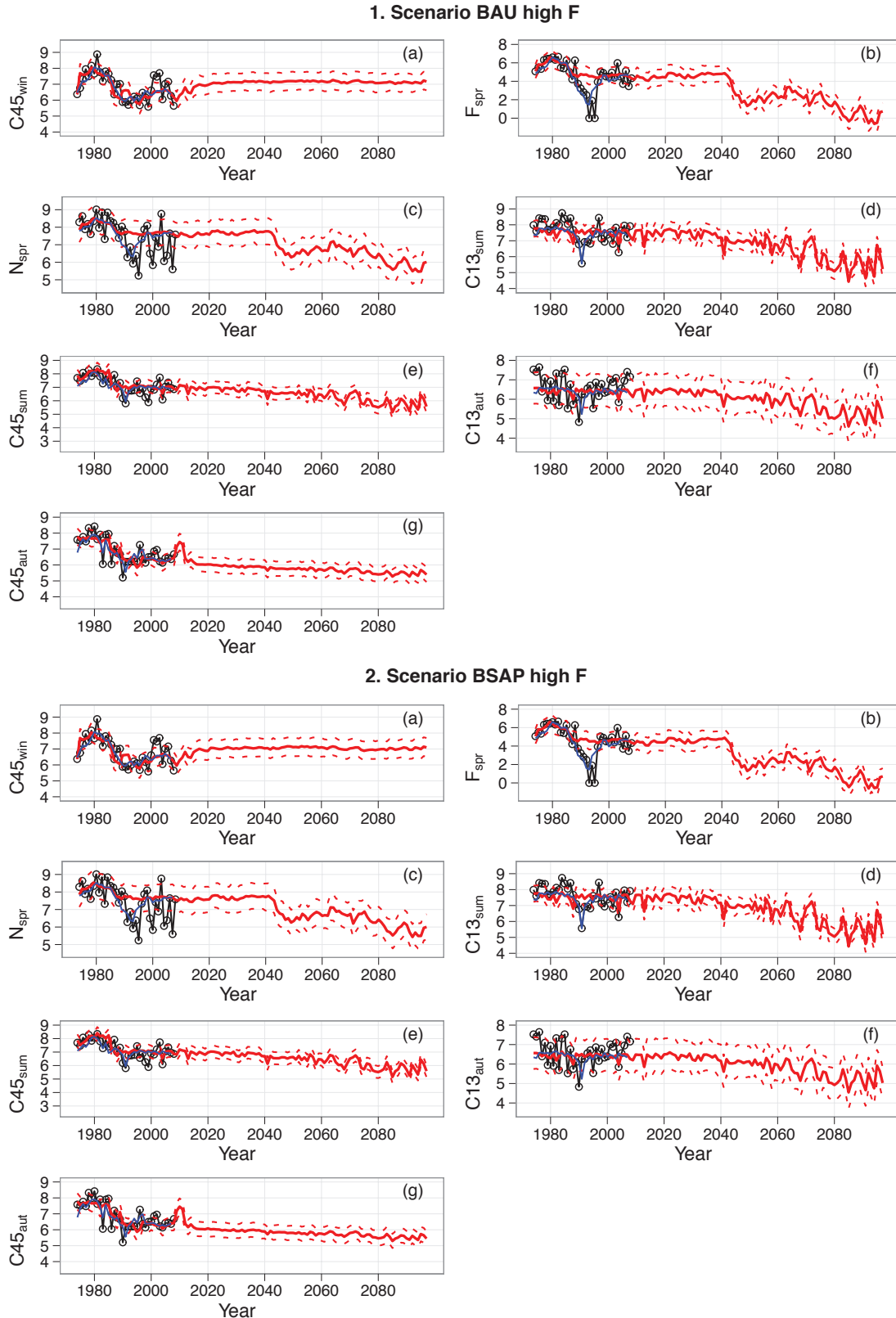
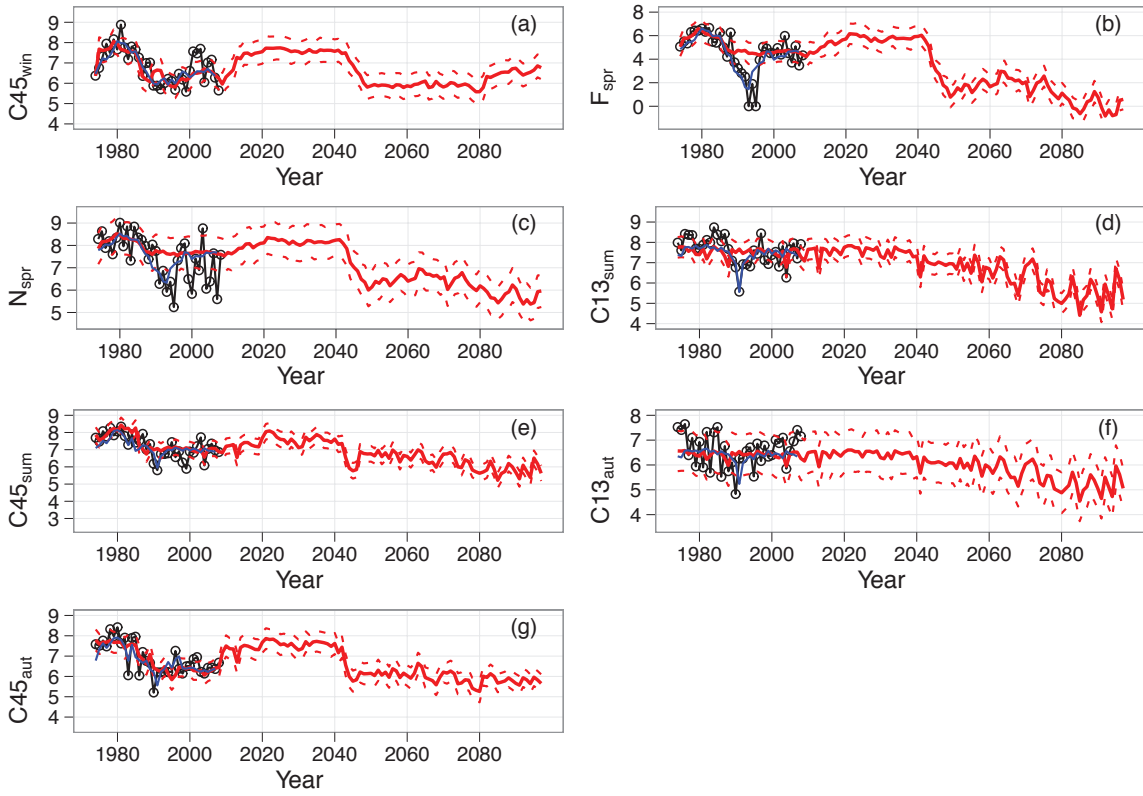


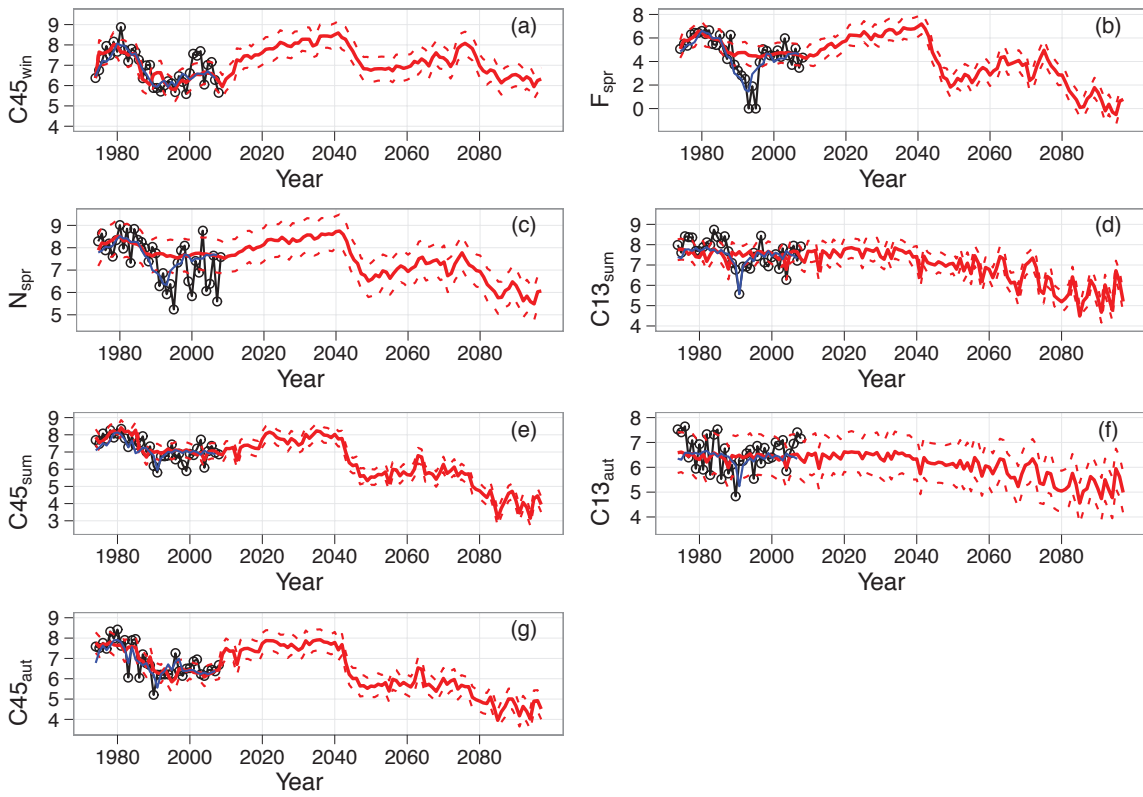
Figure 7-S3.1 - 7-S3.4: Projected future long-term stage dynamics under one climate (A1B) and four predation pressure scenarios based on two different nutrient load scenarios (BSAP, BAU) in combination with two fishery management scenarios (F1.1 or high F, F0.3 or low F). The red, solid lines represent the means of the 1000 Monte Carlo projections, the red, dashed line the standard deviations. The past observed time series (black line with circles) and the hindcast simulation (blue solid line) are provided for comparison.



3. Scenario BAU low F



4. Scenario BSAP low F



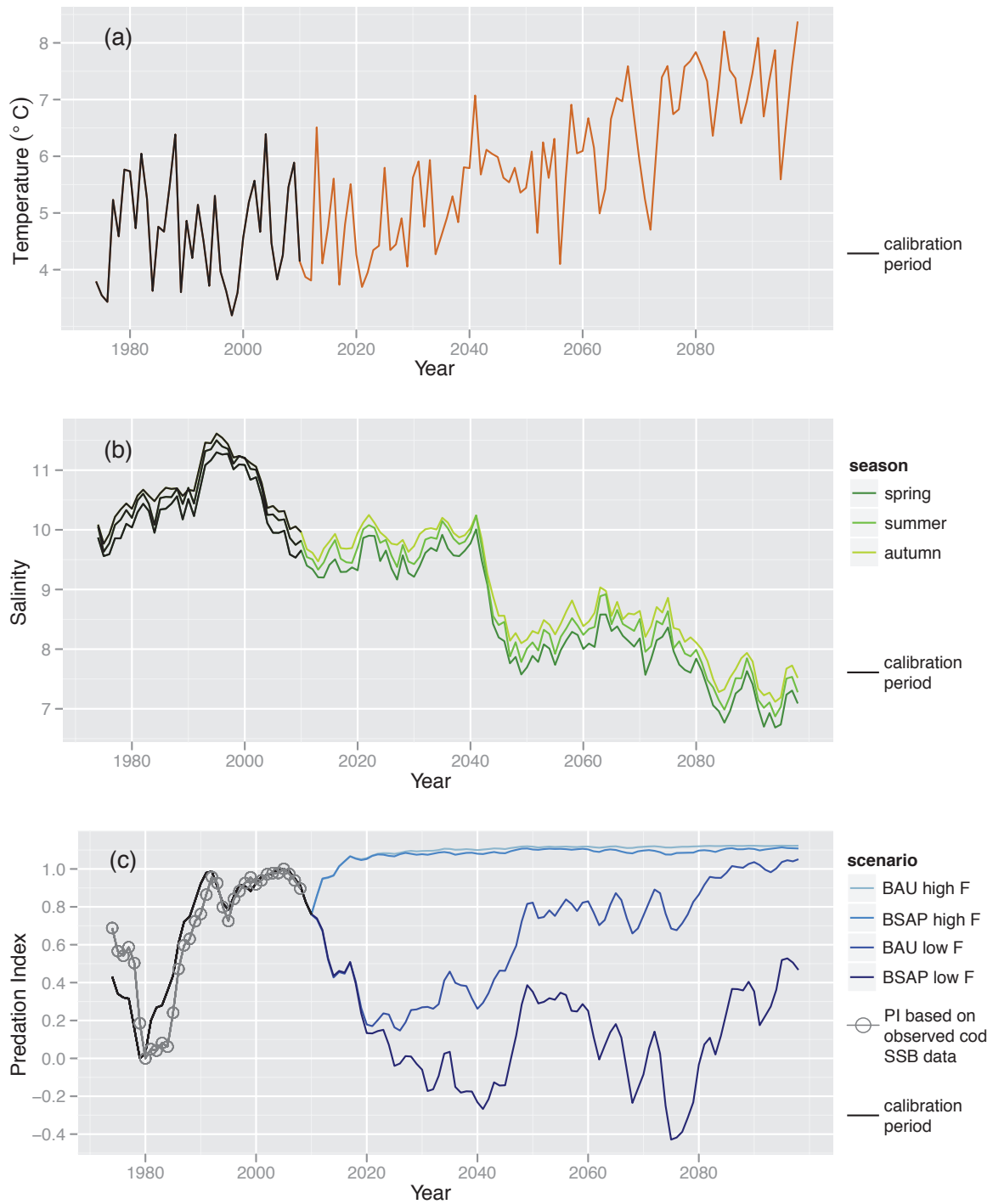


Figure 7-S4: Projected future dynamics of the environmental drivers based on the BALTSEM and BaltProWeb model simulations.

8 Early detection of ecosystem regime shifts: a multiple method evaluation for management application

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Abstract

Critical transitions between alternative stable states have been shown to occur across an array of complex systems. While our ability to identify abrupt regime shifts in natural ecosystems has improved, detection of potential early-warning signals previous to such shifts is still very limited. Using real monitoring data of a key ecosystem component, we here apply multiple early-warning indicators in order to assess their ability to forewarn a major ecosystem regime shift in the Central Baltic Sea. We show that some indicators and methods can result in clear early-warning signals, while other methods may have limited utility in ecosystem-based management as they show no or weak potential for early-warning. We therefore propose a multiple method approach for early detection of ecosystem regime shifts in monitoring data that may be useful in informing timely management actions in the face of ecosystem change.

Introduction

Transitions between alternative states, i.e., regime shifts, have been shown to occur across an array of complex systems (Venegas *et al.* 2005, May *et al.* 2008), including ecosystems (Scheffer *et al.* 2009). Our ability to identify abrupt shifts in real ecosystems has improved through advances in theory and statistical methods (Andersen *et al.* 2009). However, these methods are primarily designed to detect regime shifts once having occurred. Recent theoretical studies suggest that several indicators may be used as early-warnings of an approaching transition (Scheffer *et al.* 2009). Although needed for short-term management efforts to maintain key ecosystem goods and services, empirical applications of early detection of abrupt shifts in real ecosystems have so far mainly been limited to experimental studies (Drake & Griffen 2010, Carpenter *et al.* 2011) or paleo-climatic reconstructions over vast temporal scales (Livina & Lenton 2007, Dakos *et al.* 2008).

Several early-warning indicators have been proposed to describe the temporal dynamics of complex systems close to a critical transition (Scheffer *et al.* 2009). The basic rationale behind these indicators lies in the fact that the recovery of a system to equilibrium after a perturbation becomes slower close to a transition (van Nes & Scheffer 2007). This phenomenon is known as 'critical slowing down' (Wissel 1984) and causes the variance and autocorrelation in the fluctuations of a system to increase prior to a regime shift (Scheffer *et al.* 2009, Held & Kleinen 2004, Carpenter & Brock 2011). In addition, the spatial dynamics of complex systems may also change close to a transition, where alterations in the spatial patterns of variance and correlation of key ecological features may serve as a complimentary set of early-warning indicators (Guttal & Jayaprakash 2009, Dakos *et al.* 2010, Donangelo *et al.* 2010). Although the merit of these indicators is that they can be detected across an array of ecosystems and types of transitions (Dakos *et al.* 2011), their disadvantage is that they require long time series of high resolution for their estimation. Moreover, the potential for early-detection in practice is based on the assumption that the time series accurately represent the response of the ecosystem around its present equilibrium state (Scheffer *et al.* 2009). Since ecological monitoring records are typically of limited length, lack detailed information on spatial distribution patterns of key organisms, and often include substantial measurement error, the practical use of any of the proposed early-warning indicators for ecosystem management may prove problematic. Given that these limitations can lead to both false positive and false negative signals (Scheffer *et al.* 2009), the use of multiple spatial and temporal indicators should ideally be considered (Dakos *et al.* 2011) and alternative methods should be tested (Carpenter & Brock 2011). Yet, studies of early-warning signals in real ecosystems have so-far been restricted to only a narrow range of possible temporal (Dakos *et al.* 2008) or spatial indicators (Litzow *et al.* 2008).

Large-scale patterns of ecosystem change have been observed in marine ecosystems across the Northern hemisphere (Link *et al.* 2009, Möllmann *et al.* 2011), including the Baltic Sea (Möllmann *et al.* 2009). A key question for marine management is whether these regime shifts could have

been detected by early-warning indicators. Using real monitoring data of the copepods *Pseudocalanus acuspes* and *Acartia* spp., two key indicator species significantly contributing to the reorganization of the Baltic Sea ecosystem (Fig. 8-1) (Möllmann *et al.* 2009), we here apply a set of methods for detecting trends and structural breaks in time series, i.e., (i) temporal and spatial indicators of critical slowing down, (ii) trend analysis and (iii) shiftograms (see Material and Methods), as alternative tools for early-detection of regime shifts. Lastly, we assess all early-detection methods, covering both temporal and spatial processes, in order to evaluate their practical use in forewarning the major regime shift that occurred in the Baltic Sea during the late 1980s (Fig. 8-1) (Möllmann *et al.* 2009).

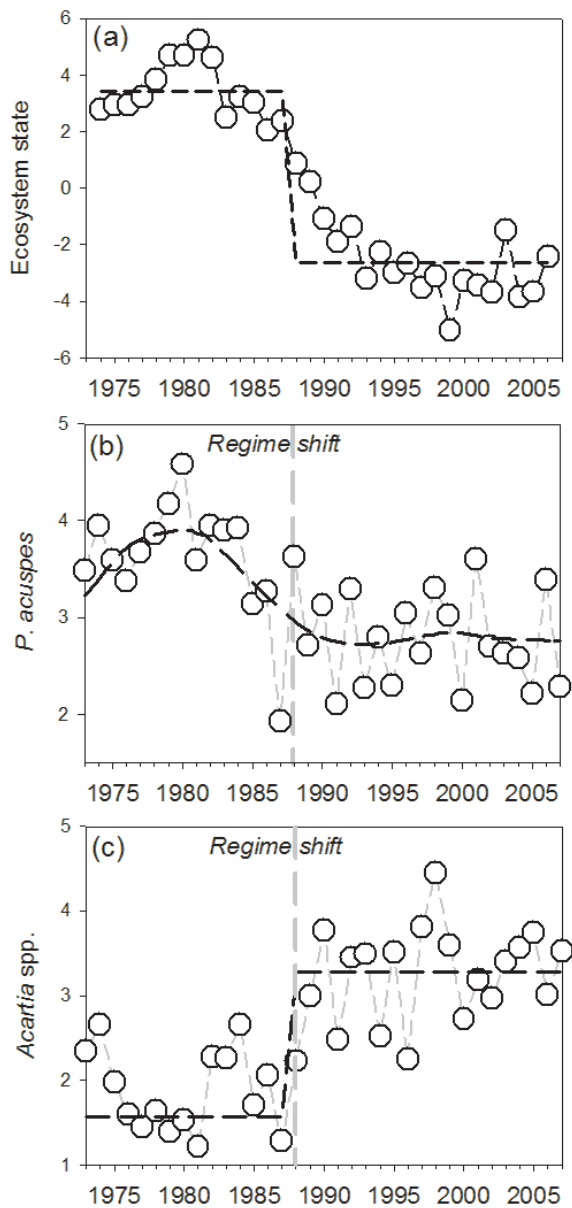


Figure 8-1: Ecosystem dynamics of the Central Baltic Sea illustrated by the first principle component of a principle component analysis of biotic time series (a). A significant break point based on the Sequential Regime Shift Detection Method illustrates the ecosystem regime shift in the late-1980s (dashed). Long-term dynamics of the selected early-warning indicators, *Pseudocalanus acuspes* (b) and *Acartia* spp. (c) during the corresponding time period (1974-2008) with the associated regime shift in 1988-1989 (grey). The black dashed lines illustrate two different types of transitions, i.e., gradual changes or a sudden (pulse) transitions, respectively.

Material and Methods

Ecosystem characteristics and data considerations

The Baltic Sea is a large semi-enclosed sea (Fig. 8-S1), which due to its brackish nature is characterized by low species diversity, but high productivity. Climatic conditions since the late 1980s have significantly changed the living conditions for plant and animal populations inhabiting the area, caused by increasing temperatures and decreasing salinity and oxygen levels (Möllmann *et al.* 2008). In addition to climate forcing, anthropogenic impact from overfishing and eutrophication likely contributed to the abrupt regime shift, which included trophic cascading involving several trophic levels (Casini *et al.* 2009, Möllmann *et al.* 2009). The regime shift occurred during a transition period between 1988 and 1993, where all external drivers were on extreme levels (Möllmann *et al.* 2009). Given the difficulty of detecting the exact timing of regime shifts (Andersen *et al.* 2009), we assume (for the purpose of this study) the major changes to have happened already in 1988 (Fig. 8-1a). We used *Pseudocalanus acuspes* and *Acartia* spp., two key zooplankton species in the Central Baltic Sea food web significantly contributing to the reorganisation of the ecosystem, as indicators for the regime shift (Möllmann *et al.* 2009). The population sizes of these zooplankton species changed drastically during the regime shift (Fig. 8-1b,c), which had strong implications for their major predators, such as larval cod (Hinrichsen *et al.* 2002, Voss *et al.* 2003, Möllmann *et al.* 2008), as well as the main planktivores in the ecosystem, i.e., herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Möllmann *et al.* 2005). Due to their pivotal role as mediators between lower trophic levels and the fish community (Möllmann *et al.* 2003), their rapid response to climate variability (high sensitivity to salinity and temperature, respectively), *P. acuspes* and *Acartia* spp. serve as suitable indicators for the ecosystem regime shift in the Central Baltic Sea. Furthermore, long-term temporally and spatially resolved monitoring programs (Möllmann *et al.* 2000), i.e., monthly coverage of sampling stations from 1960 and onwards, are available for both species. In order to assess the ability to detect abrupt regime shifts sufficiently in advance for management, we applied a set of early-detection methods on spatially aggregated and disaggregated (by sampling stations and areas; Fig. 8-S1) data set of *P. acuspes* and *Acartia* spp. biomass covering the period 1960-2008. Since the primary aim of the study is to investigate and evaluate potential early-warning signals, we chose to focus on and present results on method performance during the time-period immediately preceding and following the regime shift (i.e., 1982-1993). We used data representing spring as this is the main reproductive season of the copepods (Hansen *et al.* 2006, Renz & Hirche 2006).

Indicators of critical slowing down

We measured temporal variance (as the standard deviation; SD) and autocorrelation at lag-1 (AR(1)) in detrended time series of average spring biomass of *P. acuspes* and *Acartia* spp. within a 10, 15 and 20-year sliding window, following the approach by Dakos *et al.* (2008). Temporal variance (Carpenter & Brock 2006) and autocorrelation at lag-1 (Held & Klein 2004) are expected

to rise prior to a critical transition, as approaching an unstable equilibrium would theoretically lead to a larger degree of instability (e.g. Carpenter & Brock 2006, Dakos *et al.* 2008, Hewitt & Thrush 2010). While temporal variance was measured as the SD of detrended time series (of equal sample size), a relationship between the mean of a population and its variance often exists when comparing different samples in space (Litzow *et al.* 2008). Hence, spatial variance was estimated by the coefficient of variation (CV; $100 \cdot \text{SD} / \text{mean}$) (Litzow *et al.* 2008) correcting for the mean across all stations from the entire sampling area (Fig. 8-S1). Similar to temporal variance it has been shown that spatial variance or the coefficient of variation increases before a catastrophic shift (Guttal & Jayaprakash 2009, Donangelo *et al.* 2010). In addition, spatial correlation may also change close to a shift (Dakos *et al.* 2011). Here, we estimated spatial correlation across sampling stations using the Moran's I test (Legendre & Legendre 1998). In order to reduce bias from uneven sampling between years, we randomly selected 6, 8 and 10 stations per year and estimated the mean correlation coefficient and associated p-value for each year after 1000 random draws.

Trend analysis

In a second set of methods we applied statistical methods for assessing recent trends in the zooplankton time series. Although not specifically designed for early detection of regime shifts, the idea of using trend analysis as an early-warning signal lies in the possibility of detecting a slight increase in the rate of change (either in an upward or downward trend) in advance of a critical transition in an ecological time series. The approach is based on fitting non-linear Generalized Additive Models (GAM) (Wood 2006) and estimating second derivatives (f'') as a proxy for statistically significant acceleration in the rate of change (slope) of ecological time series (Fewster *et al.* 2000, Trenkel & Rochet 2009). While the first approach relies on an *a priori* specified degree of smoothing (Fewster *et al.* 2000), the second method (Trenkel & Rochet 2009) applies a routine for selecting optimal numbers of regression splines (degree of smoothing; df). In order to reduce potential bias due to the selection of regression splines, we performed the trend analysis using two levels of degrees of freedom (df = 10 and 20).

Shiftograms

The third approach was not primarily designed for early detection either, but rather for the identification and detection of regime shift. It is based on the evaluation of statistical time series models including structural breaks and combines several statistical indicators into a so-called "shiftogram" (Gröger *et al.* 2011). The shiftogram approach is an iterative procedure combining econometric time series analysis and quantile methods displaying the gradual or rapid transition towards a local minimum (i.e. structural break-point) by making use of time series features and quality-of-fit criteria, such as the corrected Akaike's information criterion (AICC) and a joint significance test (p-joint) of all parameters related to a particular type of structural break. These quality-of-fit criteria may be regarded as indicators of an imminent shift, illustrated by a potential

decrease in AICC and p-joint statistics prior to a shift. Moreover, we used the AICC and p-joint test into an “alertogram” that primarily uses the negative slope of the AICC or p-joint values prior to a potential structural break by fitting a linear regression and performing assessments of false positives (type I error; probabilities of false warning) and false negatives (type II error; probabilities of false no-warnings) based on slope F tests. As neither the trend analysis nor the shiftogram approaches are developed as strictly early-detection methods, but for shift identification, we also refitted the GAMs and shiftograms on shortened time series until the major regime shift in 1988, in order to test whether they can be used to give early-warning, or whether they simply detect the shift once it is underway or even after it has occurred.

Method assessment

The full set of early-warning methods were assessed in terms of (i) the potential for detecting early-warnings signals in the selected indicator time series, (ii) how far in advance early-warning signals could potentially be detected, (iii) associated methodological assumptions and drawbacks influencing early-detection and (iv) applicability to real ecosystem management in terms of data requirements. While the trend analysis and shiftogram approach may quantitatively evaluate the first two criteria (i.e., by performing statistical tests), no predefined reference levels exist to objectively assess the performance of our ecological indicators of critical slowing down, nor the possibility to theoretically crash test the methods against a simulated (modelled) spatio-temporal data set (e.g., Guttal & Jayaprakash 2009, Dakos *et al.* 2010, Donangelo *et al.* 2010, Carpenter & Brock 2011, Dakos *et al.* 2011). In order to minimize the extent to which subjectivity and expert judgement influence the interpretation and assessment of our results, we argued that a potential signal may be alerted when an indicator value exceeds or falls below the upper and lower 95% confidence interval of its historical (cumulative) distribution prior to a regime shift. However, note that the above exercise is not suited for a direct comparison between methods *per se* but to assess how under the constraints of real ecological time series similar to ours, different approaches may or may not work, and which assumptions and drawbacks may pose the greatest challenges in terms of early-warning detection and applicability to management.

Results and Discussion

In order to assess the ability to detect abrupt regime shifts sufficiently in advance for management, we applied three sets of early-detection methods on spatially aggregated and disaggregated monitoring data of *Pseudocalanus acuspes* and *Acartia* spp. biomass from 1962 to 2008: (i) temporal and spatial indicators of critical slowing down (Dakos *et al.* 2008, Litzow *et al.* 2008); (ii) trend analyses aimed at detecting changes in the rate of change in time series (Fewster *et al.* 2000, Trenkel & Rochet 2009); and (iii) shiftograms, i.e. statistical indicators developed to identify structural breaks in time series (Gröger *et al.* 2011).

Indicators of critical slowing down

Temporal variance of *P. acuspes* (measured as standard deviation, SD) strongly increased two years before the regime shift in 1988 (Fig. 8-2a), but still remained below the upper confidence interval of its historical distribution. In the case of *Acartia* spp. the temporal variance also increased one year prior to the regime shift, but exceeded the upper confidence interval first after the shift had occurred (Fig. 8-2b). Overall the strength of the increase in SDs depended on the number of years used for the sliding window, being strongest when using a 10 year window (Fig. 8-S2). On the contrary, temporal autocorrelation analysis demonstrated a marked and significant decline in AR(1) parameters (below the lower confidence level) preceding or coinciding with the regime shift (Fig. 8-2c,d); regardless of the number of years used for the sliding window (Fig. 8-S2). Since early-warning detection depends on the choice of metric, the use of sliding windows, and constraints in the length of the time series, the potential of temporal indicators of critical slowing down for early-warning may be limited.

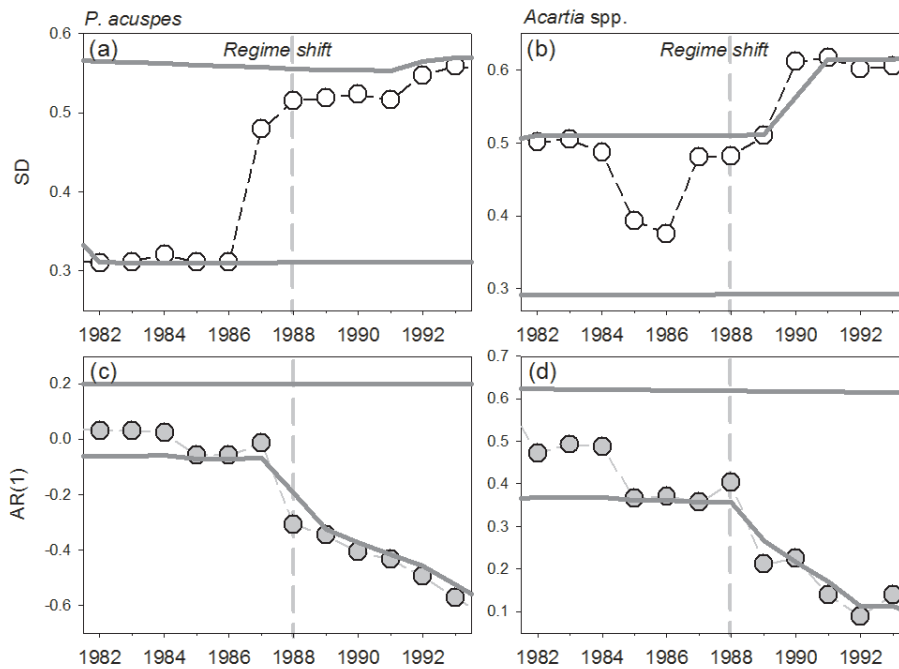


Figure 8-2: Temporal variance (estimated as standard deviations, SD) and the first-order autocorrelation coefficient (AR(1)) for *P. acuspes* (a,c) and *Acartia* spp. (b, d) estimated within sliding windows of 10 years. Vertical dashed lines mark the timing of the regime shift in the late 1980s and grey solid lines the upper and lower 95% confidence intervals.

In contrast to the temporal analysis, spatial approaches for detecting patterns in either variance or correlation yielded rather similar results. The spatial variance in *P. acuspes* displayed strong inter-annual fluctuations and a significant increase in the coefficient of variation (CV) one year ahead of the regime shift (Fig. 8-3a), while *Acartia* spp. showed decreasing CV below the lower confidence interval only after the shift (Fig. 8-3b). The reason for opposite patterns in spatial CVs may originate from the pronounced differences in abundance trends, i.e., illustrating a decrease in *P. acuspes* (Fig. 8-1b) and increase in *Acartia* spp. (Fig. 8-1c), where decreasing abundances

may simply increase spatial CVs and vice versa. Furthermore, our results show a continuous increase and decrease in CVs throughout the period, thus partly inconsistent to the theoretical expectation of critical slowing down, which predicts a decrease in variance after a shift as the system reaches its new equilibrium. Whether simply driven by the long-term abundance trends or caused by dynamics not yet having reached (stable) equilibrium, the discrepancies between theory and practical application deserve further attention.

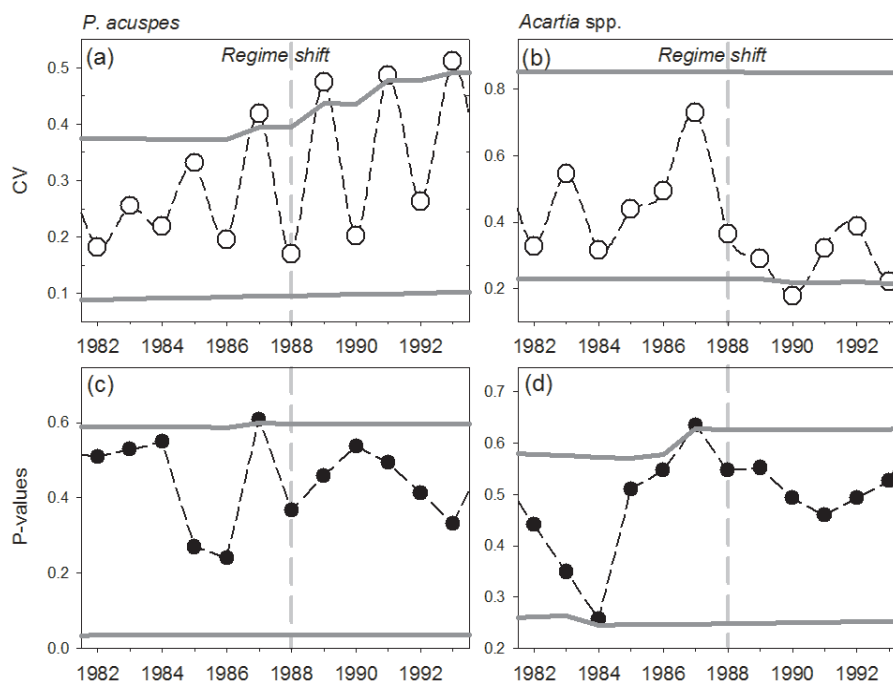


Figure 8-3: The coefficient of variation (CV) and degree of spatial correlation for *P. acuspes* (a, c) and *Acartia* spp. (b, d) estimated as the mean significance (p-value) of spatial correlation across 8 randomly assigned stations. Vertical dashed lines mark the timing of the regime shift in the late 1980s and grey solid lines the upper and lower 95% confidence intervals.

The spatial (Moran's I) correlation showed p-values exceeding their upper confidence intervals one year in advance of the regime shift for both species (Fig. 8-3c,d). This may indicate a strong fragmentation of the zooplankton distribution well before the population sizes changed prior to the regime shift (e.g., even 6-7 years before the shift for *P. acuspes*; Fig. 8-S3a). In the case of *P. acuspes* this can be explained by the distribution of adults in deep water layer confined by oxygen conditions from below and salinity conditions from above (Hansen *et al.* 2006, Renz & Hirche 2006). Reduction of oxygen and salinity levels due to a lack of inflows from the North Sea since the early 1980s, a major cause of the Baltic ecosystem regime shift (Möllmann *et al.* 2009), reduced the spatial extent of suitable reproductive habitat for the copepod. Hence, habitat fragmentation may have caused parts of the population to become spatially isolated from each other which may have impaired reproductive capabilities and resulted in the population decline (Möllmann *et al.* 2003). Nevertheless, it has to be noted that our knowledge on the spatial dynamics of *P. acuspes* and *Acartia* spp. is still limited. We are therefore unable to provide a solid interpretation of the observed distribution patterns. Hence, the elevated heterogeneity in the

distribution pattern, i.e., the consecutive peaks in p-values during the late-1980s (Fig. 8-S3a), may simply represent the natural spatial variability in the dynamics of Baltic Sea copepods and thus render the derived early-warning signals as potential false alarms.

Contrary to temporal indicators of slowing down, spatial approaches for detecting changes in correlation and variance patterns (Guttal & Jayaprakash 2009, Litzow *et al.* 2008, Dakos *et al.* 2010) are not primarily constrained by methodological assumptions associated with a particular method, but are influenced by the quality and consistency of monitoring programs in space and time. However, our spatial analysis of critical slowing down seems robust to the random resampling of monitoring stations, e.g. spatial correlation between stations in each year showed consistent dynamics based on repeated random draws of 6, 8 and 10 stations, respectively (Fig. 8-S3), indicating that potential bias from uneven sampling between years may be of less importance or successfully accounted for by performing proper sensitivity analysis.

Trend analysis

The trend analysis (Fewster *et al.* 2000) indicated potential early-warning signals given by a significant decreasing and increasing trend for *P. acuspes* and *Acartia* spp. prior to the regime shift (Fig. 8-4). When refitted to the time-period preceding the regime shift (1960-1987), significant change points were detected between 1986 and 1987 (Fig. 8-S4), while when excluding year 1987 no change was detected before the regime shift. In the complimentary trend analysis (Trenkel & Rochet 2009), applying a routine for selecting the optimal numbers of regression splines, a significant increase in the rate of decline was indicated between 1985 and 1987 (Tab. 8-S1), as illustrated by a negative f' (slope) and a positive f'' (acceleration). As in the previous example, no significant trend or change point was detected when excluding also 1987.

The trend analysis seems to be highly dependent on the length of time series and the numbers of regression splines used during fitting of the generalized additive models (GAMs; Fig. 8-4). These assumptions influence the degree to which potential signals may resemble true early-warning signals, hence undermining the robustness of advice originating from such analysis. As an example of potential methodological bias, the choice of the numbers of regression splines results in differences in the number of change points detected, as well as in the timing of these changes (Fig. 8-4). Even when statistically optimizing the number of splines (Trenkel & Rochet 2009), the length of the time series may influence the number and timing of significant change points being detected. However, it should be noted that trend analysis approaches were not primarily designed for early detection of regime shifts, but as an effective tool for detecting recent trends and change points in ecological time series (Fewster *et al.* 2000, Trenkel & Rochet 2009).

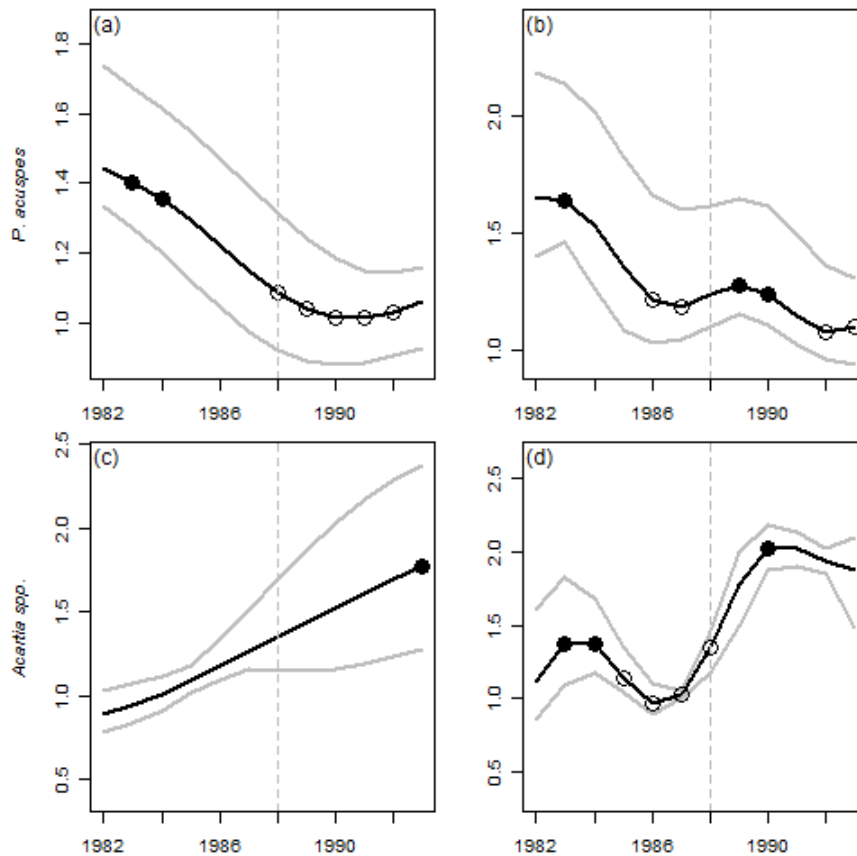


Figure 8-4: Smoothed time series of *P. acuspes* and *Acartia* spp. based on GAMs using $df=10$ (a, c) and $df=20$ (b, d). Bootstrapped confidence intervals are shown by grey lines. Acceleration in the rate of change (slope) in each year are shown by statistically significant second derivatives (f''), where black and white dots represent major downward- and upward trends, respectively. Vertical dashed lines mark the timing of the regime shift in the late 1980s.

Shiftograms

The shiftogram generally resulted in an early detection of regime changes well in advance of the regime shift. For *P. acuspes* both the Akaike's information criterion (AICC) and the p-joint significance test showed a gradual transition towards a local minimum (i.e., structural break point) 3-4 years before the regime shift (Fig. 8-5a), while for *Acartia* spp. an abrupt transition occurred only 2 years in advance (Fig. 8-5b). This was the case regardless of fitting to the entire time series or to the time-period preceding the regime shift. In both cases, the p-joint statistics decreased before the AICC and remained on low values over a longer time-period. In addition, performing tests on false positive and negative warnings using a slope F test based on the AICC (alertogram), shows that two years before the local minimum in 1987 was reached, the negative decrease towards a break becomes highly significant ($p < 0.05$) in terms of the estimated slopes (Fig. 8-5c). Thus, the year 1985 sharply marks the beginning of a gradual shift in *P. acuspes* with a clear alert signal. In addition, both type I and II errors exceed their upper significance limits before 1985 and after 1987, indicating that false positive and negative warnings occur outside the 1985-1987 period (Fig. 8-5c). In contrast, the *Acartia* spp. time series displayed a significant alert signal first in 1990 (Fig. 8-5d), despite a pronounced decrease in AICC and p-joint prior to the regime shift (Fig. 8-5b).

The shiftogram approach appeared to be promising in detecting structural breakpoints well in advance before the regime shift. However, the way these metrics approach a local minimum are influenced by the type of transition at hand in the time series. Sudden (pulse) transitions or more gradual changes strongly influence the shape (e.g., steepness and size) of the local minimum and hence the degree to which these transitions can be detected sufficiently in advance; a difference illustrated by the abrupt decrease in *Acartia* spp. (Fig. 8-5b) and the more gradual decline in *P. acuspes* (Fig. 8-5a). In addition, a local minimum of considerable width and little steepness may saturate the value and hence the reliability of the derived early-warning signal. However, the use of alertograms may compliment the shiftogram approach by adding valuable information for decision support, such as the strength of the negative slope of the AICC, as well as the significance (false positive signals) and the power (false negative signals) of this slope. Because the alertogram displays the false warning probabilities along with the false no-warning probabilities it aids in evaluating the urgency of potential management actions.

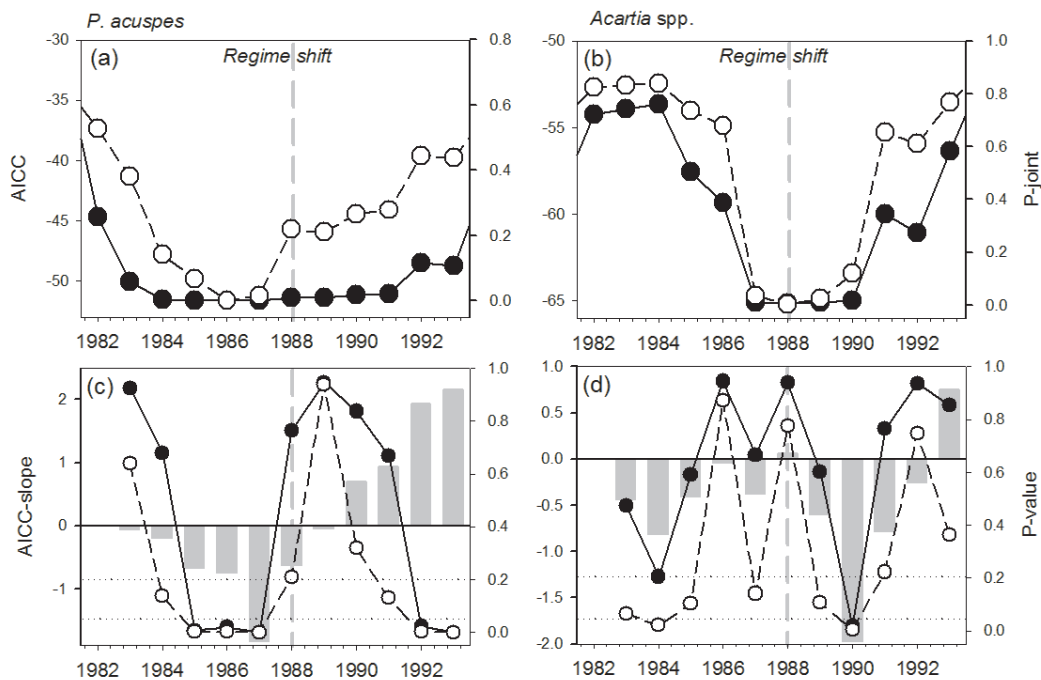


Figure 8-5: Shiftogram showing the transition towards a local minimum in the AICC (black) and p-joint (white) for *P. acuspes* (a) and *Acartia* spp. (b). In panel (c, d), an alertogram demonstrates the AICC slopes (vertical bars), the estimated probabilities (p-values) of false warnings (white) and false no warnings (i.e., the beta error, black) over a 5-year period before and after the regime shift. The two dotted horizontal lines represent the significance level ($p=0.05$) and the upper tolerance limits with regard to the probabilities of false detections (i.e., false alarm limit).

Table 8-1: Assessment of early-detection methods in terms of (i) the potential for detecting early-warnings signals in the selected time series, (ii) how far in advance early-warning signals could potentially be detected (i.e., in number of years before the regime shift), (iii) major associated methodological assumptions and drawbacks influencing early-warning detection and (iv) applicability to real ecosystem monitoring and management in terms of data needs.

Method	i	ii	iii	iv
<i>1. Indicators of critical slowing down</i>				
A. Temporal variance	Low	0	Size of window, Length of time series	Long-term data, slow variables
B. Temporal AR(1)	Medium	1	Size of window, Length of time series	Long-term data, slow variables
C. Spatial variance	Medium	1	Uneven sampling (No. /distribution)	Spatial data, consistent design
D. Spatial r (Moran's I)	Medium	1	Uneven sampling (No. /distribution)	Spatial data, consistent design
<i>2. Trend analysis</i>				
A. Temporal GAM (I)	Low	(1)	Degrees of smoothers, "retrospective" (f'')	Recent trend, pressures/drivers
B. Temporal GAM (II)	Low	(1)	retrospective" analysis, f'' calculation (t+1)	Recent trend, pressures/drivers
<i>3. Shiftograms</i>				
A. Shiftogram (AICC)	High	2-4	Gradual/rapid decrease, global vs local minima	Time series, contrasts/variability
B. Shiftogram (p-joint)	High	2-4	Broad local minima, timing of shift	Time series, contrasts/variability
C. Alertogram	High	1	Slope, power, significance of shifts in AICC	Time series, contrasts/variability

Conclusions

The versatility of methods for early detection of regime shifts in ecological time series provide an important toolbox for scientists and ecosystem managers. As learned from our example, no 'one-size-fits all' solution to deriving and interpreting spatio-temporal patterns announcing critical transitions exists (Scheffer *et al.* 2009). Given by the type of transitions (i.e. sudden (pulse) transitions or more gradual changes) in the chosen ecological time series, some indicators and methods may result in clear early-warning signals, as demonstrated by the shiftogram and alertogram approaches, while other methods may have limited utility in informing ecosystem-based management, as they show no or weak (i.e. too late for a management measure to implement) early-warning potential (Tab. 8-1).

Hence, we suggest that a multiple method approach may provide a sound scientific basis for detecting and evaluating early-warning signals and thus provide timely advice for immediate management actions in the face of future ecosystem changes (Biggs *et al.* 2009). Such a multiple method approach should be based on (i) the availability and quality of monitoring data; (ii) a thorough sensitivity analysis of key methodological assumptions and potential sources of bias of a given methodology; and (iii) a scientifically sound interpretation of results based on the best available knowledge concerning the ecological variable in question. Eventually, early-warning systems, including suitable indicators and related methods, for detecting and preventing unwanted catastrophic changes must be tailored to the local ecosystem characteristics.

ACKNOWLEDGEMENTS

We wish to thank the Latvian Institute of Food Safety, Animal health and Environment (BIOR) for providing time series and maintaining long-term monitoring and data handling; an essential source of information necessary for scientific decision support and successful implementation of ecosystem-based management in general, and the Baltic Sea in particular. In addition, we would like to thank Rachel Fewster and Verena Trenkel for providing methods and guidance for trend analysis. This research is a contribution to the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea (WGIAB). VD was supported by an ERC grant awarded to M. Scheffer and SO by BONUS-AMBER.

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| **8 MANUSCRIPT 4**

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Supporting Information

SI text

The Baltic Sea is a large semi-enclosed sea (Fig. 8-S1), which due to its brackish nature is characterized by low species diversity, but high productivity. Climatic conditions since the late 1980s have significantly changed the living conditions for plant and animal populations inhabiting the area, caused by increasing temperatures and decreasing salinity and oxygen levels (Möllmann *et al.* 2008). In addition to climate forcing, anthropogenic impact from overfishing and eutrophication likely contributed to the abrupt regime shift, which included trophic cascading involving several trophic levels (Casini *et al.* 2009, Möllmann *et al.* 2009). The regime shift occurred during a transition period between 1988 and 2003, where all external drivers were on extreme levels (Möllmann *et al.* 2009). For the purpose of this study we assume the major changes to have happened already in 1988 (Fig. 8-1a).

We used *Pseudocalanus acuspes* and *Acartia* spp., two key zooplankton species in the Central Baltic Sea food web significantly contributing to the reorganisation of the ecosystem, as indicators for the regime shift (Möllmann *et al.* 2009). The population sizes of these zooplankton species changed drastically during the regime shift (Fig. 8-1b, c), which had strong implications for their major predators, such as larval cod (Hinrichsen *et al.* 2002, Voss *et al.* 2003, Möllmann *et al.* 2008), as well as the main planktivores in the ecosystem, i.e., herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Möllmann *et al.* 2005). Due to their pivotal role as mediators between lower trophic levels and the fish community (Möllmann *et al.* 2003), their rapid response to climate variability (high sensitivity to salinity and temperature, respectively), as well as availability of long-term temporally and spatially resolved monitoring programs (Möllmann *et al.* 2000), i.e., monthly coverage of sampling stations from 1959-2010, *P. acuspes* and *Acartia* spp. serve as suitable indicators for the ecosystem regime shift in the Central Baltic Sea.

In order to assess the ability to detect abrupt regime shifts sufficiently in advance for management, we applied a set of early-detection methods on spatially aggregated and disaggregated (by sampling stations) data set of *P. acuspes* and *Acartia* spp. biomass covering the period 1962-2008. We used data representing spring as this is the main reproductive season of the copepods (Hansen *et al.* 2006, Renz & Hirche 2006).

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Supporting tables and figures

Table 8-S1: Test results for recent trends and changes in trends over 3-year periods before the regime shift in 1988 using intersection–union test (IU, 11). P-values from a χ^2 goodness-of-fit test indicate whether the GAM fits satisfactory to the entire time series. Significant negative (-) or positive (+) time trends in the rate of change (f'), as well acceleration (+) or deceleration (-) of the current trend (f'') are shown. Hence, an increase in a rate of decline is indicated by negative f' and a positive f'' .

Start year	End year	χ^2 (p-value)	Trend (f')	Change (f'')
<i>P. acuspes</i>				
1985		1987		<0.001
1984		1986		<0.001
<i>Acartia</i> spp.				
1985		1987		<0.001
1984		1986		<0.001

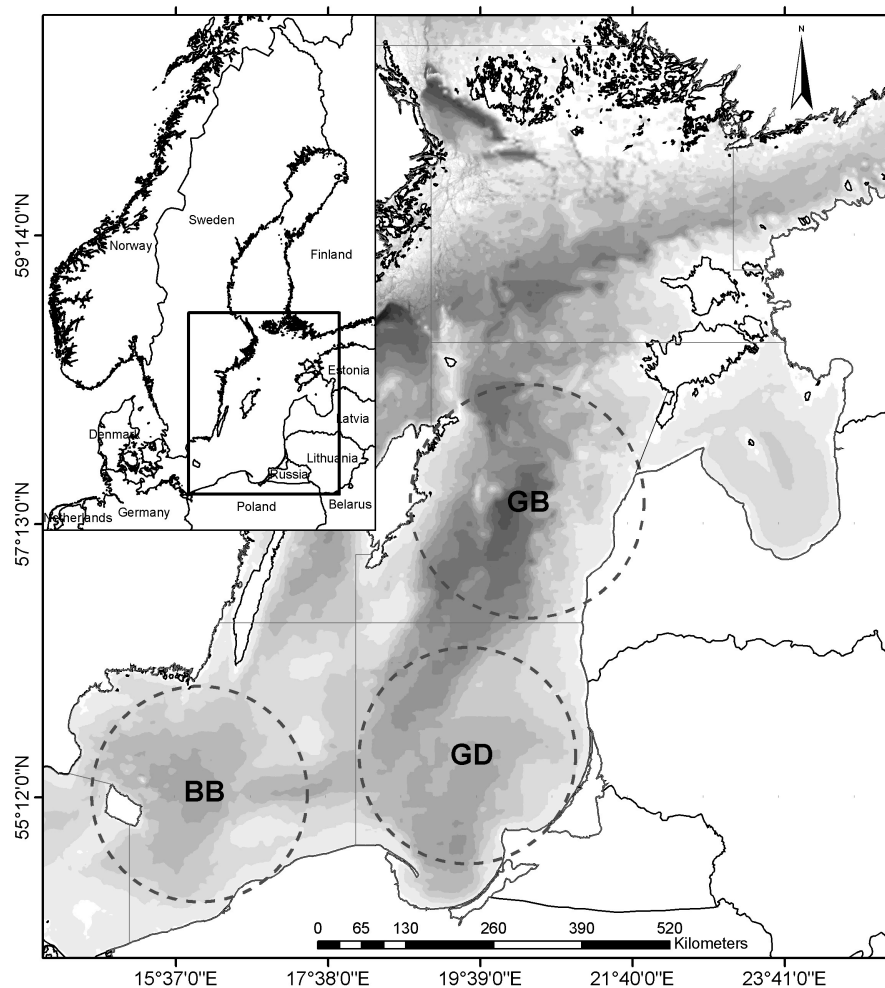


Figure 8-S1: Map of the Baltic Sea and its location within Northern Europe. The central part of the Baltic Sea encompasses three deep (< 70 m) basins important for marine biota, the Bornholm Basin (BB), the Gdansk Deep (GD) and the Gotland Basin (GB); largely corresponding to the *International Council for the Exploration of the Sea (ICES)* official sub-divisions 25, 25 and 28, respectively (thin lines). Furthermore, these basins are part of a long-term spatially and temporally disaggregated zooplankton monitoring program in the Baltic Sea.

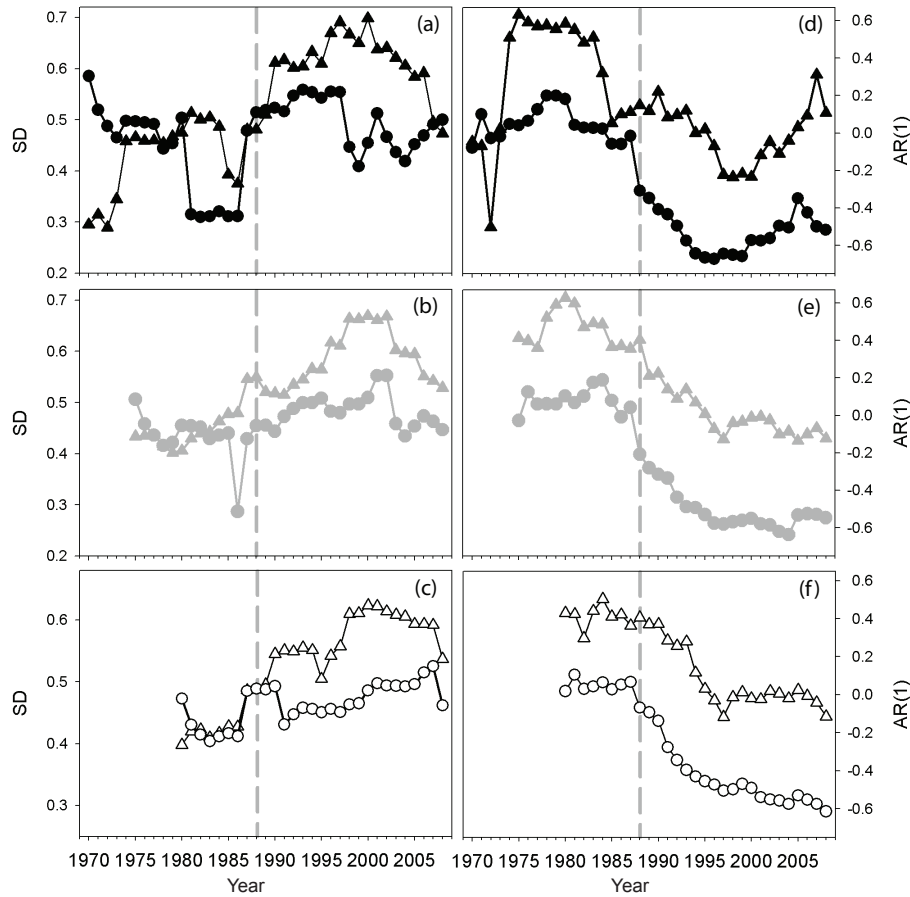


Figure 8-S2: Temporal variance of *P. acuspes* (circles) and *Acartia* spp. (triangles) estimated by standard deviations (SD) and the first-order autocorrelation coefficient (AR(1)) of detrended time series for a sliding window of 10 (a, d), 15 (b, e) and 20 (c, f) years. Vertical dashed bars mark the timing of the Central Baltic Sea regime shift in the late 1980s.

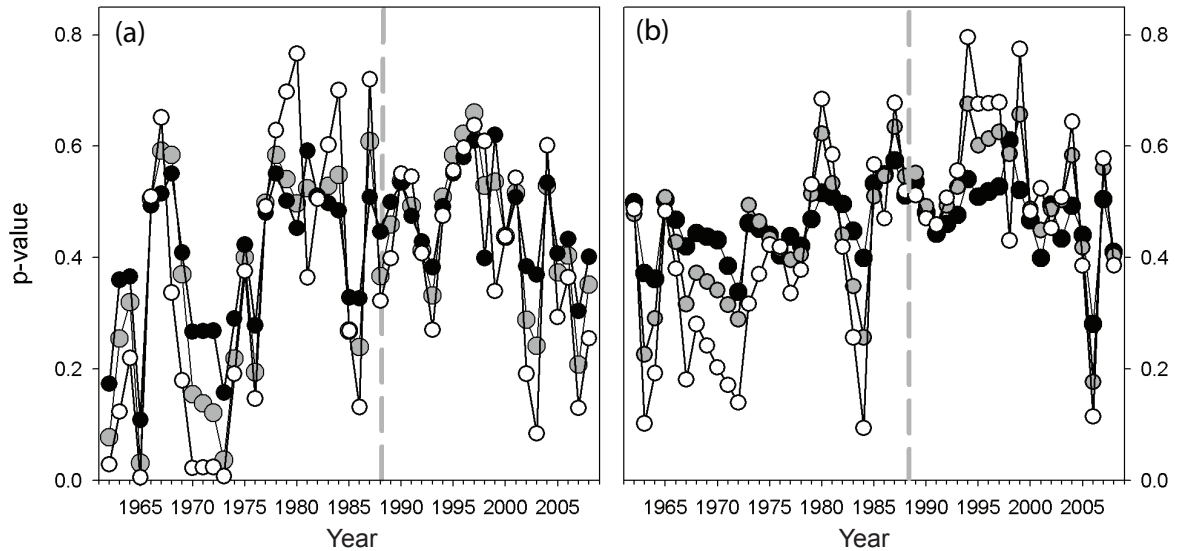


Figure 8-S3: The degree of spatial correlation for *P. acuspes* (a) and *Acartia* spp. (b) estimated as the mean significance (p-value) of spatial correlation coefficients derived from a Moran's I test across 6 (black), 8 (grey) and 10 (white) randomly assigned stations (after 1000 resamples). Vertical dashed bars mark the timing of the Central Baltic Sea regime shift in the late 1980.

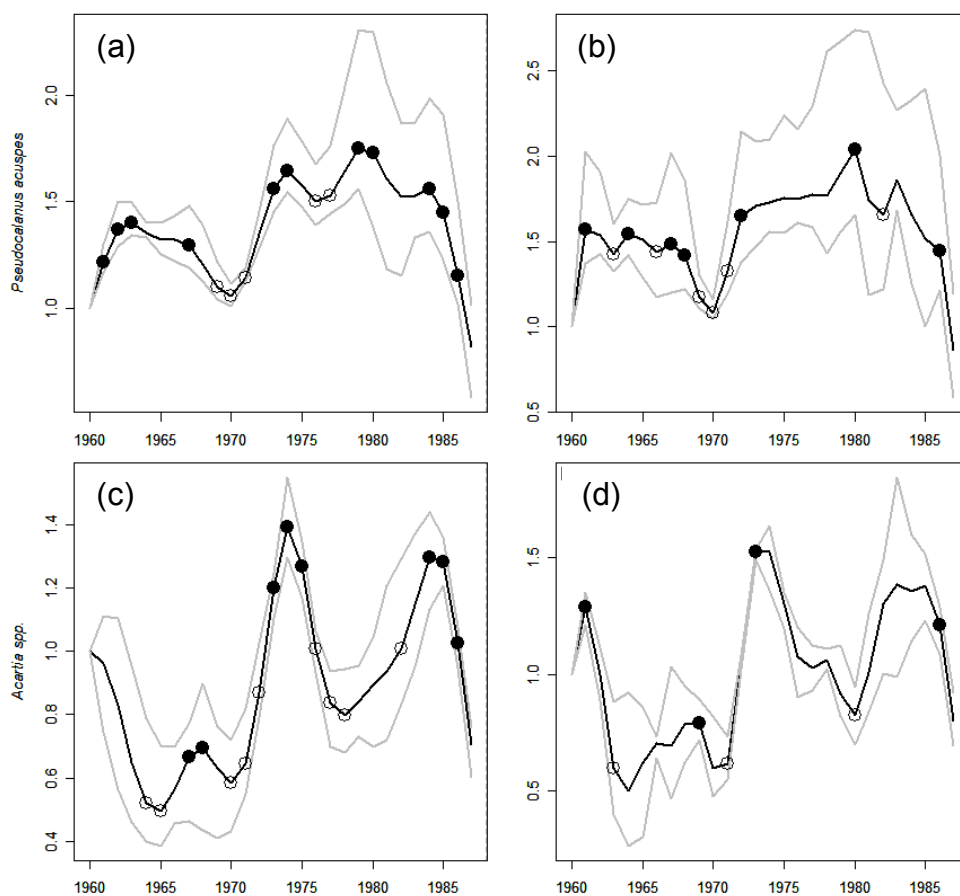


Figure 8-S4: Smoothed indicator time series of *P. acuspes* and *Acartia* spp. with GAM $df=10$ (a, b) and $df=20$ (c, d) from 1960-1987. Bootstrapped confidence intervals are shown by grey lines. Acceleration in the rate of change (slope) in each year are shown by statistically significant second derivatives (f''), where black and white dots represent major downward- and upward trends, respectively.

9 General Discussion

Ecosystems provide various kinds of services for human societies, which have to be soundly protected and managed in light of climate fluctuations and changes as well as increasing direct human pressures (e.g. fishery, shipping traffic, input of nutrients). Profound knowledge of key ecosystem species serves as a basis in integrated management approaches such as the Ecosystem Approach to Management (EAM) framework. The analysis of key species has the advantage of providing detailed information on causal processes and species-environment relationships (Lindenmayer *et al.* 2007). Hence, quantifying the relative importance of each species and identifying the key species is an important step within the EAM framework. Another, similarly important step is the identification of the critical life stages within the key species (Geist 2010), which has rarely been applied (Russell *et al.* 2012). Despite the holistic approach, the focus is often set to species with a high economic value such as fishes in marine ecosystems. Instead, zooplankton is rather underrepresented although several studies could demonstrate its key role in the ecosystems (e.g. Alheit *et al.* 2005, Hays *et al.* 2005, Möllmann *et al.* 2008) and its suitability as indicator for climatic changes/effects (e.g. Fromentin & Planque 1996, Beaugrand 2003, Chiba *et al.* 2006).

To gain more insights into the long-term dynamics of copepods, the dominant zooplankton species in the marine realm, and to assess various potentials in future ecosystem research the following studies were conducted within the present thesis:

First, the long-term developments of the three major copepods *Acartia* spp., *Temora longicornis*, and *Pseudocalanus acuspes* in the Central Baltic (CBS) were assessed within the context of the habitat characteristics and their environmental niches (**manuscript 1**). The CBS features a strong vertical and horizontal gradient in temperature and salinity; species are therefore likely to differ stronger in their physiological adaptations (i.e. their fundamental niches) as well as species interactions. Under environmental changes such as climate or food web changes, the single species within the community are likely to display different population trajectories in space and time, which eventually may change the community structure over time. And indeed, comparing the long-term trends of the three study species and their main drivers, both seasonally and spatially (i.e. basin-specific), indicates that the effects of climate depended strongly on species-specific habitat utilization. Direct climate effects were more pronounced at the upper water layers, shifting the potential thermal niche of *Acartia* spp. and *T. longicornis* further into the optimal part of their fundamental niche. *Acartia* spp. displayed furthermore significant differences in their spatial distribution, which is probably caused by multiple indirect climate effects. Predation was additionally important, indicating that predation may have reduced the size of the

9 GENERAL DISCUSSION

realized niche, in particular for *P. acuspes* experiencing the largest vertical overlap with predators.

After the main drivers of the long-term overall population dynamics were identified (**manuscript 1**), their contribution to the seasonal life stage abundances of *P. acuspes* in combination with internal density effects were further assessed to improve the understanding of the life cycle dynamics of *P. acuspes* (**manuscript 2**). For this, GAMs were applied within a discrete stage-structured population modelling approach. In addition, GAMs were extended by including threshold formulations (TGAMs) to test for changes between bottom-up and top-down trophic regulation under contrasting predation regimes. The integrative analysis revealed a complex interplay of linear density and predation effects and non-linear hydro-climate effects, the latter being stage- and season-specific. In general, younger stages (nauplii (N), copepodite I-III (C13)) were more affected by temperature and the BSI, while older stages (copepodite IV-V (C45), females (F)) were influenced by salinity, except in winter. Predation had a significant, negative effect on older stages throughout the year and controlled the bottom-up effects (i.e. density and salinity) mainly in summer and autumn on the C45. Based on the findings of this analysis, the major peak in abundances observed for all stages across the seasons in the 1970s/1980s can be better understood as our results suggests a combination of various biotic and abiotic conditions.

Based on the empirically derived relationships of internal and external drivers on the individual life history stages of *P. acuspes*, a single life cycle model was developed. This model was then used to simulate past long-term dynamics under observed and alternative environmental conditions and to project future dynamics (**manuscript 3**). Two major aims were addressed. First, to identify key critical life stages within the life history of a key ecosystem species and the propagation of indirect effects. This was assessed by simulating how individual stages would have developed under alternative, past environmental conditions. Here, C45 in winter and F in spring were identified as the most sensitive stages to direct and indirect effects of salinity and predation. Secondly, potential futures of *P. acuspes* were investigated by conducting stochastic projections of the population's response to one climate and a number of fisheries management and eutrophication scenarios. The results show that under a potential climate-induced freshening of the Baltic Sea, salinity may more strongly control the biomass of *P. acuspes* independently of the predation level. The projected salinity drop to levels historically unreported caused a collapse of *P. acuspes* population size in all scenarios. The model output further indicates that density-dependence plays a role but cannot compensate for this collapse.

Lastly, to detect regime shifts in marine systems in advance for short-term management efforts to maintain key ecosystem goods and services, a set of early-warning indicator methods based on zooplankton key species dynamics were evaluated (**manuscript 4**). Using the Baltic Sea key species *Acartia* spp. and *P. acuspes* exemplarily, the practical use of temporal and spatial indicators of critical slowing down, trend analysis and the shiftogram were compared. This

comparison revealed different strengths and disadvantages of the various methods. The temporal indicators of critical slowing down were rather limited due to several constraints. In contrast, the spatial indicators performed better in the sense that both methods (i.e. variance and autocorrelation of spatially disaggregated data) yielded similar results, i.e. detected the shift mostly a year in advance, and were quite robust to the applied random resampling of monitoring stations. However, due to the natural spatial variability in the dynamics of copepods, there is the likelihood of early-warning signals being potential false alarms. The other two approaches were originally developed to identify recent trends and change points in ecological time series. Here, the shiftogram seems most promising. Particularly when used in combination with the alertogram. Limitations here are given in the type of transition (e.g. gradual change or a sudden shift), which can influence the degree of detecting the transition sufficiently in advance. Therefore, a multiple approach is eventually suggested to provide a sound scientific basis for evaluating early-warning signals in the management process.

Overall, this study of copepod long-term dynamics using different theoretical perspectives that represent the fundamentals of contemporary ecology, i.e. habitat role and niche space, demographic dynamics, multi-species interactions, and ecological thresholds in trophodynamics and regime shifts (Real & Levin 1991, Turchin 2003, Andersen *et al.* 2009), helped to gain important insights into internal processes of the key zooplankton species and their interactions with ecosystem components in the Baltic Sea.

The first study shows clearly that the CBS represents a heterogeneous habitat, particularly in the vertical. Hence, species with strong differences in their physiological requirements (represented by their fundamental niches FN), such as *Acartia* spp., *T. longicornis*, and *P. acuspes*, can easily co-exist by occupying different depth ranges. But a vertical habitat separation is not always given. The mesozooplankton community in the CBS comprises of various other species like cladocerans (*Evadne nordmannii*, *Podon* spp. *Bosmina* spp.), rotifers (*Synchaeta* spp., *Keratella* spp.), appendicularians (*Frittilaria borealis*) or chaetognaths and meroplanktic larvae of e.g. polychaetes, bivalves, gastropods, bryozoans, and echinoderms. They are mostly abundant in spring or summer and often inhabit the upper water column. Consequently, they are likely to overlap to some degree in their potential niches, i.e. the part of the FN that is realized in the habitat, which increases competition (Hutchinson 1957, Jackson & Overpeck 2000). The eminent role of intra- and interspecific competition in the population dynamics of zooplankton species has recently been shown by Twombly *et al.* (2007). The growth rates of the two investigated freshwater copepods were more influenced by the internal population density and the density of other copepods and cladocerans than by the predatory dipteran larvae and abiotic conditions. A major factor for competition in the pelagic zone is food supply. Oceanic copepod population have generally been suggested to be food-limited at certain times (Huntley & Boyd 1984). Several studies have confirmed this for single species and areas, e.g. for *T. longicornis* in the Long Island Sound (Peterson 1985) or *Acartia tonsa* in Narangasett Bay (Durbin *et al.* 1983). Other studies

found factors such as predation or temperature more important (Ohman 1985, Huntley & Lopez 1992). In the CBS, food-limitation could be also an important factor. Strong indications exist for *P. acuspes* (Renz *et al.*, submitted) with implications mainly for the level of intra-specific competition (i.e. density dependence; **manuscript 3**) due to the low spatial overlap with other zooplankton species. However, *P. acuspes* shows an ontogenetic vertical distribution with nauplii living near the surface as *Acartia* spp., and C13 in mid-depth water like *T. longicornis*. Food conditions could affect here also the level of inter-specific competition. Similarly, this interaction could be relevant in the long-term dynamics of *Acartia* spp. or *T. longicornis*, as they depend strongly on the dynamics of primary production (**manuscript 1**, Koski & Kuosa 1999, Dutz *et al.* 2010, Dzierzbicka-Glowacka *et al.* 2010). This type of biotic interaction therefore deserves further attention.

Biotic interactions in long-term studies of zooplankton populations, however, have so far been limited to a few studies (but see Kornilovs *et al.* 2001, Möllmann *et al.* 2003, Casini *et al.* 2009, Plourde *et al.* 2009). The present studies filled here an important gap by including predation as an additional driver to climate in the models. The strong role of predation on the long-term development of Baltic copepods becomes especially pronounced in *P. acuspes* (**manuscript 1,2**, Möllmann & Köster 2002), which shows the strongest overlap with the major predator sprat. Intermittent and usually seasonal predators such as chaetognaths, mysids or scyphozoans are often difficult to quantify (Mauchline 1998) but can present the main cause of mortality for some species and systems (Sameoto 1973, Ohman 1985, Tönneson & Tiselius 2005). In the CBS, pelagic invertebrate predators have only a limited impact on the zooplankton community (Barz 2006). The most dominant scyphozoan *Aurelia aurita*, which preys on zooplankton and fish eggs and larvae, is only abundant between June and September and inhabits mainly the upper 20m of the water column (Barz & Hirche 2005). Their daily feeding rates are relatively high but due to their observed low abundance in comparison to the zooplankton stock, the overall impact of *A. aurita* is suggested to be minor (Barz & Hirche 2005). *Cyanea capillata*, another scyphozoan, lives in the intermediate water layer and halocline but in small numbers. Higher numbers occur only after major influxes of saline water similar to the carnivorous hydrozoan *Euphysa aurata* (Telesh *et al.* 2009). The carnivorous ctenophore *Pleurobrachia pileus*, which occurs mainly in spring, is likely to prey on copepods but their low numbers will have little effect on the inter-annual population dynamics. Also the ctenophore *Mnemiopsis leidyi*, one of the most recent invaders to the Baltic Sea, will have little effect on copepods in the CBS. Due to the low salinity they have been only observed below the halocline and here only in low numbers (Kube *et al.* 2007). The brackish environment is also the reason, why other potential predators such as the chaetognaths *Sagitta elegans* and *S. setosa* are rather rare in the CBS and restricted to advection with inflow events. They probably do not reproduce and grow in the region (Maciejewska & Margonski, 2001). In spring, late autumn, and winter, the two dominant mysid species *Mysis mixta* and *Neomysis integer* feed strongly on *P. acuspes* and *T. longicornis* (Barz

& Hirche 2009). Nevertheless, the general low numbers and their occurrence in swarms in shallower areas suggest only a local negative impact (Barz 2006). For this reason, accounting for the fish density as a level of predation intensity has been an adequate measure to identify the role of predation in copepod long-term dynamics.

Population dynamics of animal species are the results of a complex interplay of abiotic and biotic ecosystem components. They can act multiplicatively, leading to an increase or decrease across all stages and seasons as seen for *P. acuspes* (**manuscript 2**) and generating stable limit cycles as seen for the seed beetle (Shimada & Tuda 1996), or counteract each other (Sunding & Zivin 2000). In addition, direct environmental effects can involve time lags. While the metabolism of the ovary can be directly affected by changing food regimes, the effects itself becomes later apparent in the rate of laying eggs (Mauchline 1998). Direct effects can be also amplified by life cycle mediated indirect effects (**manuscript 3**), although this has rarely been quantified so far. It underlies the crucial importance of considering population dynamics not only by looking at one stage group, e.g. adults, or total biomass or abundances clearer picture. The strong negative predation effect found in spring for total biomass (**manuscript 1**, Kornilovs *et al.* 2001, Möllmann *et al.* 2008) is not singly the result of higher F mortalities due to predation but also of lower survival rates from overwintering C45, which are most vulnerable to predation. In fact, when looking at the F dynamics alone, the density of C45 in winter explains the inter-annual variability of F better than predation itself (**manuscript 2**).

In the same line it is important when modelling population dynamics to account for non-linear functional relationships, particularly for abiotic forcing (Stenseth *et al.* 2006, Zhou *et al.* 2008, Llope *et al.* 2009). The strong implication of the asymptotic, threshold-like salinity effect on F in spring (**manuscript 2**) on the overall population dynamics is illustrated in the projected stock collapse (**manuscript 3**); when salinity decreases to levels below this threshold, a sudden shift from a predation or top-down regulated dynamic to a bottom-up (i.e. salinity) control is induced. A linear model applied here would have failed to capture this key mechanism. Models designed to particularly identify non-additive effects, i.e. thresholds in functional relationships, like SETAR, nCPA or TGAM (Tong 1990, King & Richardson 2003, Ciannelli *et al.* 2004), are relatively new. Their applications have proven to be useful in gaining a better mechanistic understanding (Grenfell *et al.* 1998, Stenseth *et al.* 2004, Ciannelli *et al.* 2005, Llope *et al.* 2009), particularly in the trophodynamical flows (Casini *et al.* 2009, Llope *et al.* 2011). Findings here have shed some light into the hot debate whether zooplankton is bottom-up or top-down controlled, which was fueled with evidences on both sides (see for overview Mackas & Beaugrand 2010). The new evidences based on threshold models indicate both processes being important at certain times, depending on the level of predation (Casini *et al.* 2009, Llope *et al.* 2011, Stige *et al.* 2009). For instance, it was suggested that *P. acuspes* in the Baltic changed from a state controlled by hydro-climatic variables to a top-down regulation by planktivorous fish populations. This was supported in the present study, however, only for some stages and not throughout the year

(**manuscript 2**). In addition, the direction of the control is not only determined by top-down processes but can be also bottom-up induced (**manuscript 3**) which is in line with findings from other taxonomic groups (Litzow & Ciannelli 2007).

In summary, oscillatory patterns occur not only in the direction of the trophic control (Litzow & Ciannelli 2007) but also for the trigger of these switches, which has strong implications for past and future dynamics of the key species itself as well as for the community via interactive pathways. The application of GAMs and TGAMs as basis to relate copepod dynamics in terms of total biomass or stage abundance has been shown to be adequately and necessary as non-linearity and non-additivity were identified in various models. One of the constraints of using GAMs, however, is the interpretability of the coefficients. They need to be estimated graphically through the predicted or fitted values in the regression rather than allowing others to extract the coefficients directly from the function as in linear or non-linear regressions. This narrows its transferability on other datasets. Here lies a great advantage of non-linear regressions or polynomial terms included in linear regression as they allow for parameterization (Venables & Ripley 2002).

The development of a stochastic life cycle model based on coupled discrete, stage-structured GAMs is a novel approach and has demonstrated a good performance and robustness, which is an important criterion when serving to predict future dynamics. Discrete stage- or age-structured population models in zooplankton ecology belong mainly to the group of matrix models (Carlotti *et al.* 2000). Matrix models can be linear or non-linear, deterministic or stochastic (Caswell 2001). The inclusion of stochastic variation, i.e. "white noise", in discrete models can be done by including a random variable ϵ_t , adding a random value to the population N_t , or randomize the model parameter (Turchin 2003). However, in zooplankton population models (including matrix models but also numerical models based on differential equations) the inclusion of stochasticity are seldomly applied (Carlotti *et al.* 2000); Furthermore, most of the matrix models are built on linear relationships (e.g. Twombly *et al.* 2007, Torres-Sorando *et al.* 2003). The great advantage in our modelling approach lies in the fact that we considered stage-specificities while accounting also for relationships other than linear and included noise in the form adding resampled residuals to the modelled stage abundances to account for stochasticity.

Conclusion

The analysis of copepod population dynamics on various temporal, spatial and demographical scales revealed versatile complexities of multiple drivers that influence the single species, and eventually the community structure, in manifold functional ways, i.e. linear, non-linear asymptotic, parabolic or threshold-like. The deeper understanding of these processes and their interplay helped building a model for simulation purposes on past and future dynamics of *P. acuspes*, which in turn furthered the mechanistic understanding. The novel approach of the life cycle model for *P. acuspes* has demonstrated its outstanding suitability in simulations for future

research but also underlines the great potential of projections of ecological systems not only for management, but also for a better understanding of ecological dynamics (Coreau *et al.* 2009). This model can serve as a modelling tool for modern ecosystem-based management of the Baltic Sea, where *P. acuspes* is a key species and affecting strongly the overall food web dynamics (Möllmann *et al.* 2008). Under the assumed freshening of the Baltic Sea (Meier *et al.* 2006), the originally arctic marine species will be endangered with strong implications for the pelagic community structure. As zooplankton is still underappreciated as an indicator for the management of marine ecosystems, it is suggested to develop similar models of key zooplankton species for other areas of the world ocean. Zooplankton species can be further useful indicators for present or short-term future ecosystem states. Due to some limitations in current early-warning indicator methods, however, a multiple method approach is here suggested to provide a sound scientific basis, urgently needed to maintain key ecosystem services.

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11 Annex

List of figures

Fig. 4-1:	The Baltic Sea	11
Fig. 5-1:	Study concept	24
Fig. 5-2:	Observed and predicted long-term trends	30
Fig. 5-3:	Statistical model results of <i>Acartia</i> spp.	33
Fig. 5-4:	Statistical model results of <i>T. longicornis</i>	33
Fig. 5-5:	Statistical model results of <i>P. acuspes</i>	34
Fig. 5-S1:	Partial plot from the BSI effect in the alternative spring model of <i>Acartia</i> spp.	47
Fig. 5-S2:	Basin-specific time series of hydrography	48
Fig. 5-S3:	Main trends of the hydrography within the Central Baltic Sea (CBS).	49
Fig. 5-S4:	Time series of BSI and PI	50
Fig. 6-1:	Seasonal stage distribution and inter-annual stage dynamics of <i>Pseudocalanus acuspes</i>	59
Fig. 6-2:	Time series of the hydroclimatic variables and the predation index (PI) showing significant effects in the statistical models	60
Fig. 6-3:	Results of the statistical modelling: Partial plots from the final GAMs showing the effect of each covariate	62
Fig. 6-4:	Statistical threshold models (TGAM) that performed better than the corresponding GAM	63
Fig. 6-5:	Conceptual diagramme of the annual life cycle of <i>Pseudocalanus acuspes</i>	68
Fig. 6-S1:	Baltic Sea and <i>Pseudocalanus acuspes</i>	79
Fig. 6-S2:	Diagnostic plots of the final GAM or TGAM formulations	80
Fig. 7-1:	Conceptual diagram of the study design	92
Fig. 7-2:	Predicted hindcast of seasonal stage abundances from our coupled life cycle model	95
Fig. 7-3:	Direct and indirect effects of changes in environmental conditions	96
Fig. 7-4:	Future projections of total biomass in the main production period (spring-summer)	99
Fig. 7-5:	Projected temporal developments of production rates in spring (N/F) and survival rates from winter to spring (F/C45)	101
Fig. 7-6:	Relationships between survival from C45 to F and environmental drivers salinity and predation	102
Fig. 7-S1:	Evaluation of model robustness	110

Fig. 7-S2.1-10:	Simulation of past stage dynamics under bootstrapped environmental conditions	111
Fig. 7-S3.1-4:	Projected future long-term stage dynamics	116
Fig. 7-S4:	Projected future dynamics of the environmental drivers	118
Fig. 8-1:	Ecosystem dynamics of the Central Baltic Sea illustrated by the first principle component of a principle component analysis of biotic time series	121
Fig. 8-2:	Temporal variance (estimated as standard deviations, SD) and the first-order autocorrelation coefficient (AR(1)) for <i>P. acuspes</i> (a,c) and <i>Acartia</i> spp. (b, d)	125
Fig. 8-3:	The coefficient of variation (CV) and degree of spatial correlation for <i>P. acuspes</i> (a, c) and <i>Acartia</i> spp. (b, d)	126
Fig. 8-4:	Smoothed time series of <i>P. acuspes</i> and <i>Acartia</i> spp. based on GAMs	128
Fig. 8-5:	Shiftoqram showing the transition towards a local minimum in the AICC (black) and pjoint (white) for <i>P. acuspes</i> (a) and <i>Acartia</i> spp. (b)	129
Fig. 8-S1:	Map of the Baltic Sea and its location within Northern Europe	138
Fig. 8-S2:	Temporal variance of <i>P. acuspes</i> (circles) and <i>Acartia</i> spp. (triangles)	139
Fig. 8-S3:	The degree of spatial correlation for <i>P. acuspes</i> (a) and <i>Acartia</i> spp. (b)	139
Fig. 8-S4:	Smoothed indicator time series of <i>P. acuspes</i> and <i>Acartia</i> spp.	140

List of tables

Tab. 5-1:	Summary of the F-ratio tests	30
Tab. 5-2:	Generalized Additive Model (GAM) results for the three copepods in spring and summer	32
Tab. 5-S1:	List of environmental variables used as covariates in the GAM analyses	46
Tab. 5-S2:	Generalized Additive Mixed Model (GAMM) result of the alternative spring model of <i>Acartia</i> spp.	47
Tab. 6-1:	Summary results of the final Generalized Additive Models (GAM) and the alternative threshold formulations (TGAMs) used to describe <i>P. acuspes</i> stage abundances in each season	61
Tab. 6-S1:	Number of samplings per year	76
Tab. 6-S2:	List of variables used in the GAM and TGAM analyses with their definition and data source	77
Tab. 6-S3:	Overview of covariates included in the full GAM and TGAM	78
Tab. 7-1:	Overview of the final Generalized Additive Models (GAM) and the alternative threshold formulations (TGAMs) we selected for our simulation	91
Tab. 8-1:	Assessment of early-detection methods in terms	130
Tab. 8-S1:	Test results for recent trends and changes in trends over 3-year periods before the regime shift in 1988 using intersection–union test (IU, 11)	137

12 Eidesstattliche Versicherung *Declaration on oath*

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, den 05. Juni 2012