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Phenological shifts of three interacting zooplankton groups in relation to climate change

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Abstract:	Over the past decades, global warming has been linked to shifts in the distributions and abundances of species. In the southern North Sea, temperatures have increased in the last three decades and this will likely have consequences on the seasonality of marine organisms living in the area. Ctenophores such as *Beroe gracilis* and *Pleurobrachia pileus* could be particularly affected by changes in their phenology and that *of their prey, thus causing shifts in ecosystem function. Despite their global relevance, only a few long-term records of ctenophore abundance exist, and most of these records are semi-quantitative in nature. Therefore, our knowledge of the influence of environmental factors on their population development is limited. The long-term abundance dynamics of Beroe gracilis, Pleurobrachia pileus and their food calanoid copepods were analysed and special attention was focused on the response of these organisms to climate warming. Bayesian statistics showed that the phenology of the two ctenophores shifted in a step-like mode in the year 1987/88 to permanent earlier appearances. The seasonal change in the population blooms of Pleurobrachia pileus and Beroe gracilis correlated with a step-like increase in winter and spring sea surface temperatures. Possible explanations for the

	changes observed in these organisms could include higher reproductive rates, increased winter survival rates or both. Interannual variations in ctenophore abundances correlated well with the interannual changes in spring temperatures, although the impact of temperature on Beroe gracilis was less pronounced. The changes in copepods abundance were not consistent with changes in Pleurobrachia pileus and Beroe gracilis. Pleurobrachia pileus showed longer periods of high abundance after the permanent seasonal advancement. The longer periods were correlated with a decline in the average autumn abundance of copepods. The extended annual presence of Pleurobrachia pileus could have influenced fish stock decreases observed in the region.

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Phenological shifts of three interacting zooplankton groups in relation to climate change

M. H. Schlüter[1⋆], A. Merico [1], M. Reginatto [2], M. Boersma [3], K. H. Wiltshire [3] and W. Greve[4]

[1] *GKSS Research Centre, Institute for Coastal Research, Max-Planck-Str. 1, D-21502 Geesthacht, Germany*

[2] *Physikalisch–Technische Bundesanstalt, Bundesallee 100, D-38116 Braunschweig, Germany*

[3] *Biologisce Anstalt Helgoland, Alfred Wegener Institute for Polar and Marine Research, P.O. Box 180, D-27483 Helgoland, Germany*

[4] *Senckenberg Research Institute, Notkestr. 85, D-22607 Hamburg, Germany*

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ABSTRACT

Over the past several decades, global warming has been linked to shifts in the distributions and abundances of species. In the southern North Sea, temperatures have increased in the last three decades and this will likely have consequences on the seasonality of marine organisms living in the area. Ctenophores such as *Beroe gracilis* and *Pleurobrachia pileus* could be particularly affected by changes in their own phenology and that of their prey, thus causing shifts in ecosystem function. Despite their global relevance, only a few long–term records of ctenophore abundance exist, and most of these records are semi–quantitative in nature. Therefore, our knowledge of the influence of environmental factors on their population development is limited. In this study, the long–term abundance dynamics of *Beroe gracilis*, *Pleurobrachia pileus* and their food calanoid copepods were analysed for a highly temporally resolved time series in the German Bight at Helgoland Roads. Special attention was focused on the response of these organisms to climate warming. Bayesian statistics showed that the phenology of the two ctenophores shifted in a step–like mode in the year 1987/88 to permanent earlier appearances. The seasonal change in the population blooms of *Pleurobrachia pileus* and *Beroe gracilis* correlated with a step–like increase in winter and spring sea surface temperatures of the

southern North Sea. Possible explanations for the changes observed in these organisms could include higher reproductive rates, increased winter survival rates or both. Interannual variations in ctenophore abundances correlated well with the interannual changes in spring temperatures, although the impact of temperature on *Beroe gracilis* was less pronounced. The changes in copepods abundance were not consistent with changes in *Pleurobrachia pileus* and *Beroe gracilis*. *Pleurobrachia pileus* showed longer periods of high abundance after the permanent seasonal advancement. The longer periods were correlated with a decline in the average autumn abundance of copepods. The extended annual presence of *Pleurobrachia pileus* could have influenced fish stock decreases observed in the region.

Key words: *Pleurobrachia pileus*, phenology, regime shift, *Beroe gracilis*, copepods, Bayesian statistics, Helgoland Roads, North Sea

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1 INTRODUCTION

General scientific consensus is that Earth's climate is warming at an accelerated rate (IPCC 2007). Climate change will inevitably impact habitats, ecosystems and biological resources. The seasonality of species in coastal waters could be particularly sensitive to warming (Costello 2006; Sullivan et al. 2007).

A number of recently published works provide evidence for shifts in biotic variables in connection to climate change. For example, Root et al. (2003); Dose and Menzel (2006); Cleland et al. (2007) and Schleip et al. (2008), reported phenological changes in terrestrial plants and animals in boreal and temperate zones of the Northern Hemisphere. A growing body

* Corresponding author.

Merja Schlüter

tel: +49 4152 871561

fax: +49 4152 872020

e-mail: merja.schlueter@gkss.de

of evidence also shows that northern marine ecosystems have experienced regime shifts related to climate change, including the North Sea (Beaugrand 2004; Edwards and Richardson 2004; Schlüter et al. 2008; Wiltshire et al. 2008). Increases in the populations of gelatinous zooplankton have raised particular concern over the last decade, and their proliferation in coastal areas has been associated to warming trends (Hay 2006; Molinero et al. 2008; Purcell 2009).

Predation of zooplankton by gelatinous zooplankton and prey escape mechanisms depend on many factors; these include the abundance of the predator, spatial and temporal predator-prey match/mismatch (Cushing 1990), consumption rates (Greve 1972), food preferences (Baker and Reeve 1974; Greene et al. 1986), and physical and chemical variations of the aquatic medium. These complex factors vary with the life histories of organisms. They determine the different energy flow in foodwebs, and could influence the function of the entire aquatic ecosystem.

Only two major pathways of energy flow, however, were relevant to this work: one that transfers resources to higher trophic levels linked to humans, in a presumably healthy ecosystem, and the other that moves resources to "waste" (in the sense of lost fish production) in the case of a system dominated by gelatinous organisms. The relative dominance of these pathways determines the biogeochemical cycling of key elements, such as carbon. Important economical issues are at stake. For instance, blooms of ctenophore organisms, recently identified as the most basal known lineage of animals (Dunn et al. 2008), have the potential to damage the fish industry by consuming fish eggs and larvae (Purcell and Arai 2001).

The present study examines data collected in a survey of the marine holoplankton *Pleu-*

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robrachia pileus (O. F. Müller, 1776), the most abundant gelatinous zooplankton in the German Bight and an important carnivore in coastal waters (Bamstedt 1998). *P. pileus* has been found in many parts of the world ocean and is, therefore, of global relevance. This almost cosmopolitan organism shows marked seasonality, with peak abundances in the North Sea and adjacent areas appearing in early summer (van der Veer and Sadee 1984; Williams and Collins 1985) and autumn (Fraser 1970).

The preferential prey of *P. pileus* are mesozooplankter, and calanoid copepods (Greve and Reiners 1988; Frid et al. 1994) in particular. Ctenophores are capable of regulating the abundance of their prey and thus can influence the dynamics of copepod populations (Sullivan and Reeve 1982). *P. pileus* does not have many predators which are quantitatively important. In the coastal regions of the North Sea, only the ctenophore *Beroe gracilis* (C. Künne, 1939) can significantly graze down a *P. pileus* population. Greve and Reiners (1988) and Bamstedt (1998) proposed that *P. pileus* populations, observed in the North Sea, occur in cycles as they are restricted by the occurrence of *B. gracilis* as in a classical predator–prey relationship.

During the last three decades, the German Bight exhibited a warming trend with an average temperature increase of 1.7 °C (Schlüter et al. 2008; Wiltshire et al. 2008). The most substantial warming occurred during the winter and spring months. The present study focuses on understanding the impact of these climatic changes on the phenology of three interacting zooplankton groups (*B. gracilis*, *P. pileus* and copepods) at Helgoland Roads from 1975 to 2004 and on the possible consequences to their predator–prey interactions.

The analyses were conducted using Bayesian statistics. An advantage of the Bayesian ap-

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proach is that a coherent framework based on probability theory can be defined, allowing one to test multiple hypotheses concerning the characteristics of the time series under investigation.

2 MATERIALS AND METHODS

2.1 Data

The zooplankton data (which will be available under "Wulf Greve collection of Helgoland Roads zooplankton") analysed in this study were from samples collected at Helgoland Roads (54° 11'3" N, 7° 54'0" E) three times a week since 1975 (Greve et al. 2004). Sea surface temperature (SST) data were sampled every working day (Wiltshire et al. 2008).

The selected data included adult *P. pileus*, juvenile *P. pileus*, juvenile *B. gracilis* (one of *P. pileus* most important predator), and a group of five small calanoid copepods (*Paracalanus parvus* (Claus, 1863), *Pseudocalanus elongatus* (Boeck, 1872), *Centropages* spp., *Acartia* spp., *Temora longicornis* (O.F. Müller, 1785)), which are the most common copepods in the German Bight and represent the main food source for adult *P. pileus*. These copepods tended to co–occur each year, with some exceptional cases in which distinct succession patterns were noticeable. Periods of high *P. pileus* abundance tended to coincide with periods of high copepod abundance. Juvenile and adult *P. pileus* groups were analysed separately, although they are not independent from one another. From an ecological point of view, however, because of their size difference, they were decoupled into two distinct time series.

To evaluate the potential phenological changes in all these groups, two indices were defined: 1) the "Start of bloom" (SOB), i.e. the time at which organism populations began the

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build–up, associated with the week of the year during which the population reached a level corresponding to 15 % of the annual cumulative abundance, and 2) the "End of bloom" (EOB), associated with the week of the year during which the population reached a level corresponding to 85 % of the annual cumulative abundance. Sensitivity analysis indicated that these threshold levels were insensitive to variations of up to 30 % (results not shown). SST data were separated into multiple time series: one time series for each month, from January to June, over the period extending from 1975 to 2004. The monthly SSTs were also grouped into two main seasons, winter (from January to March) and spring (from April to June), to evaluate the different impacts of winter and spring temperatures on the organisms.

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2.2 Bayesian Approach

Bayesian theory was used to characterise potential changes and correlations in the three zooplankton groups under study relative to temperature. Bayesian statistical methods use observations to update the probability that a hypothesis (model) is true. This approach was first used to detect phenological shifts in terrestrial systems by Dose and Menzel (2004), as it permitted the discovery of changes in the time series of phenological data and correlated these changes with potential driving factors, such as temperature (Dose and Menzel 2006). This analysis also provided estimates of uncertainties, because all calculations were performed using full probability distributions.

Three models were considered: 1) a constant model (M1), which assumed that the time series under investigation had no trend; 2) a linear model (M2), which assumed that a linear trend was present (either increasing or decreasing); and 3) a change–point model (M3), which assumed that there were at least one and possibly more step–like shifts in the time

series.

The models were ranked using the Deviance Information Criterion (DIC), a Bayesian model comparison method. DIC ranked competing models based on a trade–off between the fit of the model to the data and the complexity of the model.

Bayesian correlation coefficients were estimated to identify possible coherences between the changes in temperature and the changes in the zooplankton phenological time series.

At the position in the time series at which a step–like shift was detected, the strength of the predator–prey relationship between juvenile *P. pileus* and *B. gracilis* was characterised by calculating the Bayesian probability for observing the difference between the time series of the SOB of *Beroe* and the time series of the EOB of *P. pileus* (diff = $\mathrm{SOB}_{B.gracilis}$ - $\mathrm{EOB}_{P.pileus}$), both during the period prior to the shift (the first regime, R1) and during the period after the shift (the second regime, R2).

To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid copepods, two time series were constructed: one for the copepod total spring abundances (from April to June) and another for the copepod total autumn abundances (from October to December). The probability of observing the difference between the two regimes in each time series was calculated using the Bayesian approach.

A detailed description of the Bayesian models adopted is reported in the supporting online information.

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3 RESULTS

3.1 Model selection

The analyses based on the DIC indicated that the change–point model was best supported by the SOB data for the *P. pileus* juvenile, *P. pileus* adult and *B. gracilis* juvenile (see Table 1). The linear model was ranked second, and the constant model was ranked third in importance. The only exception was found in the copepod SOB time series, for which the linear model was ranked first, followed by the change–point model, then by the constant model in importance. It is important to note that all models, M1, M2, and M3, exhibited a similar DIC for the copepods, suggesting that all models were equivalent (although not identical) in this case.

Table 1

Figure 1 shows (in circles) the SOB data for the *P. pileus* juvenile, *P. pileus* adult, *B. gracilis* juvenile and copepods, the average functional behaviour of the data calculated using the change–point model (continuous line), and the corresponding 95 % credible intervals (dotted lines). The modelled evolution of the average SOBs showed a step toward earlier weeks within the years 1987-1989, leading to permanent advances in the timings of their phenological occurrence in the following years. The shift was less pronounced in the SOB data for copepods, for which a linear decreasing trend was determined to be most likely (see DIC values in Table 1). The step in the mean evolution of the SOBs was sharpest in the adult *P. pileus* data.

For the period 1975–1987, the mean SOB of *P. pileus* juvenile occurred around week 20

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(Figure 1a), the mean SOB of *P. pileus* adult occurred around week 21 (Figure 1b), and the mean SOB occurred around week 25 for *B. gracilis* juvenile (Figure 1c). For the period 1989-2004, the mean SOB shifted forward to week 14 for *P. pileus* juvenile, to week 11 for *P. pileus* adult, and to week 21 for *B. gracilis* juvenile. In contrast, the SOBs of the calanoid copepods were relatively stable (Figure 1d).

Figure 1

Based on the DIC the favoured model (see Table 2) appeared to be the change–point model in the monthly SST data as well. The linear model, however, was also supported by the data for January, March, April, and May. The constant model was ranked third. Figure 1 shows the modelled SST time series (from January to June, panels e–j, respectively), along with the corresponding 95 % credible intervals. Concomitant with the shift in the phenological data, a shift toward persisting higher mean temperatures occurred in the years between 1987 to 1989 in all time series, with the only exception being June annual SST, which showed a second step–like change in the year 1998. March and May annual values (Figures 1g and 1i) showed the steepest shifts.

Table 2

3.2 Change point analysis

Figure 2 shows the probability distribution of a single change point in the SOBs of the three zooplankton types and in the winter and spring SSTs. The highest probability for a change point in the week representing the SOB centred on the years 1988/89 both for *P. pileus* and *B. gracilis* (Figure 2a). The probability that the SOB of copepods changed in a

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step–like fashion was considerably smaller than the probability for step–like SOB changes in *P. pileus* and *B. gracilis* data and was centred around the years 1990/91. Low probabilities of additional step–like changes in the SOB time series of copepods were noticeable in the years 1997 and 2002.

Figure 2

The probability for a change point in SST winter and SST spring was highest in the years 1987–1989 (Figure 2b), which correspond to a concomitant change in the phenological time series of the ctenophores.

3.3 Correlation analysis

A Bayesian correlation (see Data and methods, and supporting online information, section S2.3, for details on the method used) between ctenophore abundance and SST winter indicated an advance in the timings of their phenological occurrence corresponding with a temperature rise ($r = -0.6$). This same correspondence pattern was especially strong for SST spring (Table 3). These analyses clearly indicated that changes in SST winter and SST spring are strongly correlated with the shifts to earlier times in the SOBs of *P. pileus* and *B. gracilis*. The correlations between the SOBs and SST spring were higher than the correlations between the SOBs and SST winter, suggesting a strong sensitivity of the gelatinous zooplankton to temperatures at the beginning of the bloom season. Changes in temperature appeared to have a minor impact on the SOBs of copepods (correlation coefficient of about -0.2, Table 3).

Table 3

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The importance of temperature as a determinant for the SOB of gelatinous zooplankton was deduced by the relation between the year–to–year changes in the SOBs (indicated by dSOB) and the year–to–year changes in winter and spring temperatures (indicated by dSST winter and dSST spring, see Figure 3. For example, dSOB of *P. pileus* could be advanced by up to eight weeks if dSST spring increased by approximately 1–2 °C (Figure 3a). The correlation analyses indicated that dSOB and dSST spring time series yielded the best correlation (results are summarised in Table 4). This was also confirmed by a linear regression analysis, shown in Figure 3.

Figure 3

Table 4

3.4 Changes in seasonal occurrence

Following the results of the change–point analysis, the zooplankton abundances were averaged over two different periods (Figure 4): one period, regime 1 (R1), was defined from 1975 to 1987, and another period, regime 2 (R2), was defined from 1988 to 2004.

Figure 4

In R1, *P. pileus* phenology was characterised by a unimodal distribution with peak abundance at around weeks 23–25 (Figure 4a, dashed lines). In R2, the phenology of *P. pileus* was different, and was characterised by a bimodal distribution with a minimum abundance around weeks 23–25 (Figure 4b, dashed lines). The spring increase in abundance advanced

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in time from mid–late June in R1 to April–May in R2. Also, the total annual abundance increased from about 7,200 individuals m^{-3} in R1 to about 9,800 individuals m^{-3} in R2.

In contrast, *B. gracilis* exhibited a single population maximum in both periods (R1 and R2 in Figure 4a–b, dotted line). The phenologies of *B. gracilis* differed somewhat between the two regimes, but they differed to a far lesser extent than the phenologies of *P. pileus*. The total annual abundance in R1 (8,700 individual m^{-3}) was greater than in R2 (3,200 individual m^{-3}). The populations of *B. gracilis* and *P. pileus*, however, showed a predator–prey like pattern in both periods (R1 and R2). The copepod data showed a single maximum in the organism population between weeks 20–35 in both regimes (Figure 4a–b, grey lines). The distribution width was somewhat narrower in R2 compared to the distribution width in R1.

3.5 Predator–prey relationships

The strength of the predator–prey relationship between *P. pileus* and *B. gracilis* was investigated by calculating the probability of the difference between two phenophases, in this case the difference was between $\mathrm{EOB}_{P.pileusjuvenile}$ and $\mathrm{SOB}_{B.gracilisjuvenile}$ (the method is described in detail in Data and methods, and in supporting online information, section S.2.4). The time overlap of about four weeks between $\mathrm{SOB}_{B.gracilisjuvenile}$ and $\mathrm{EOB}_{P.pileusjuvenile}$ suggested a strong predator–prey relationship (see Figure 5a) in R1, whereas a probability maximum centred on positive values (two weeks) supported a weaker predator–prey relationship in R2 (Figure 5b).

Figure 5

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To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid copepods, the probability of observing the difference between the two regimes in the copepods‘ spring and autumn abundance time series was calculated using the Bayesian approach. The copepod spring abundance (from April to June) was reduced to about 500 individuals m^3 from R1 to R2. Note, however, that the evidence for such a change remained small because the 95 % credible interval (−1717.0 to +1066.0) included zero. The difference in abundance relative to the autumn period (from October to December) was more pronounced (see Figure 5b), with a reduction in R2 to about 1275 individuals m^3.

4 DISCUSSION AND CONCLUSIONS

The analysis of the timings of phenological occurrences of the three zooplankton groups provided an effective method for the detection of ecological changes in the populations of organisms related to climate change. Bayesian statistics provided a mathematically rigorous framework for testing hypotheses (or models), and permitted the quantitative expression of results in terms of probabilities.

This study used the DIC criterion to evaluate three different models for the potential patterns in the phenological time series: 1) no change, 2) linear change, and 3) step–like change. In general, bloom timings of *P. pileus* (Figure 1a and 1b), *B. gracilis* (Figure 1c) and annual SSTs (Figure 1e–j) followed a similar pattern of change that, in general, was best represented by a step–like shift. A linear increasing or decreasing trend was found to be less likely, with the only exception being the phenological time series of copepods (Table 1). The constant model was ranked the least probable for all organisms, although for copepods the differences among the models were small (see Tables 1 and 2).

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The highest probability for a step–like change in the SOBs of *P. pileus* and *B. gracilis* was obtained in the year 1988/89 (Figure 2a) coincident with the step–like changes in SST winter and SST spring (Figure 2b). The timing of this step–change agreed with the timing of a regime shift, described by Beaugrand (2004) and Schlüter et al. (2008), in biological and hydrometeorological variables of the southern North Sea and German Bight. In line with previous findings (Greve et al. 2004), the change–point analysis showed good correlation between the SOB of *P. pileus* and SST winter. The correlation, however, improved when SST spring was considered, suggesting that the timing of the blooms were sensitive to the temperature conditions occurring in the bloom season.

The relatively high correlation between the spring bloom timings of ctenophores and SST winter (Table 3) and the higher winter densities of *P. pileus* of the second regime (Figure 4) support the hypothesis (Purcell et al. 2001; Sullivan et al. 2001) of an effect of warm winter conditions on the survival and success of overwintering adults. The higher correlation found between the spring abundances and SST spring (Table 3) suggested a cause–effect relationship between warmer temperatures and the earlier ctenophore appearance during R2 via impacts on metabolic processes (Molinero et al. 2008) and ovule production. In fact, the year–to–year changes in winter and spring temperatures were linearly related to the year–to–year changes in the SOB of the ctenophores. The steeper slopes obtained from SST spring (Figure 3) confirmed that variations in spring bloom timings were more sensitive to spring SST than to winter SST.

This study also highlighted the differential impact of temperature on two different but adjacent trophic levels (copepods and their predator *P. pileus*), possibly through different temperature tolerances. Only relatively modest changes in copepod phenology (Figure 1d

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and 2a) were detected, suggesting that a step–like shift toward warmer conditions had little influence on the whole group of these five copepods due to complex life history traits, e.g. diapause, larval development and dissimilarities in food requirements for the different life stages. When considered individually, these five copepods tended to co–occur each year, with some exceptional cases in which distinct succession patterns were noticeable. Generally, periods of high *P. pileus* abundances occurred during periods of high copepod abundance (see Figure 4). Ctenophores, nevertheless, are capable of causing marked decreases in copepods (Greve and Reiners 1988; Kuipers et al. 1990; Purcell and Decker 2005). The present study indicated a weak predator–prey like pattern between copepods and *P. pileus* in the spring (Figure 5c). The appearance of a second reproductive phase of *P. pileus* during R2, however, had an impact on the copepod group (Figure 5d), related to a reduction in the average autumn biomass (compare also Figure 4a with Figure 4b).

This study showed a remarkably robust predator–prey relationship between *B. gracilis* and *P. pileus*, during R1 (Figure 5a). Such a feature was less pronounced during R2 (Figure 5b), when *P. pileus* was characterised by two distinct reproductive phases. Although *B. gracilis* appeared to drive the decline of the first peak in *P. pileus* abundance, this seemed less likely for the decline of the second peak. The lower abundances of *B. gracilis* during R2 could be caused by a detrimental effect of warming conditions on this organism, an interpretation supported by the narrow thermal tolerance of *B. gracilis* (Purcell 2005). The increase in mean temperature during the second regime made a second reproductive phase of *P. pileus* possible after *B. gracilis* had declined. This mismatch appeared responsible for the all–season presence of *P. pileus* in the plankton community of the German Bight.

However, the three interacting groups investigated in this study represented only a crosssec-

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tion of the more complex ecosystem, and the importance of other factors cannot be excluded. Transport processes, for example, are among those aspects that contribute to the intricacies of the system (Williams and Collins 1985; Greve and Reiners 1988; Wang et al. 1995). Aggregation (Graham et al. 2001), complex life histories (Schneider 1987; Greve et al. 1996) and adaptation are other processes that complicate the system, but these factors could not be considered here because of the difficulties associated with their quantification.

The fact that *P. pileus* extended its annual presence may lead to diverse consequences through various other top–down (increased predation on fish eggs and larvae) and bottom–up processes that could not be considered in this study but may ultimately cause ecosystem–wide disruptions (Hay 2006). North Sea fish stocks, for example, are presently in an alarming state of decline (ICES 2008). Gelatinous zooplankton outbreaks could potentially exacerbate this situation and may lead to trophic dead ends by channelling the flow of energy to “waste” (in the sense of lost fish production).

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Table 1. Ranking of different models using DIC: comparison of the constant, linear, and change–point model for the SOB of *Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *B. gracilis* juvenile and copepods at Helgoland Roads.

Species	Model	DIC	Best ranked model
P. pileus juvenile	Constant	182.15	Step
	Linear	178.82	
	Step	171.82	
P. pileus adult	Constant	195.39	Step
	Linear	167.1	
	Step	143.71	
B. gracilis juvenile	Constant	189.1	Step
	Linear	183.53	
	Step	178.24	
Copepods	Constant	142.68	Linear/step
	Linear	138.92	
	Step	141.27	

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Table 2. Ranking of different models using DIC: comparison of the constant, linear, and change–point model for monthly mean SST at Helgoland Roads.

Month	Model	DIC	Best ranked model
SST January	Constant	136.24	Step
	Linear	133.33	
	Step	130.22	
SST February	Constant	161.26	Step
	Linear	158.17	
	Step	153.18	
SST March	Constant	160.3	Step
	Linear	152.96	
	Step	149.17	
SST April	Constant	147.17	Step
	Linear	137.79	
	Step	134.75	
SST May	Constant	126.07	Step
	Linear	117.14	
	Step	113.69	
SST June	Constant	108.15	Step
	Linear	102.16	
	Step	95.28	

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Table 3. Median of the posterior distribution of the correlation coefficient for seasonal mean winter and spring SST and the SOB of the zooplankton groups (*Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *B. gracilis* juvenile and copepods), along with the 95 % credible interval.

	P. pileus juvenile	*P. pileus* adult	*B. gracilis* juvenile	Copepods
SST winter	−0.59 (−0.79,−0.3)	−0.65 (−0.82,−0.37)	−0.53 (−0.75,−0.21)	−0.11 (−0.46,0.25)
SST spring	−0.69 (−0.81,−0.36)	−0.77 (−0.89,−0.57)	−0.59 (−0.79,−0.27)	−0.2 (−0.53, 0.16)

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Table 4. Median of the posterior distribution of the correlation coefficient for the change rate of seasonal mean winter and spring SST and the change rate of the SOB of the zooplankton groups (*Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *B. gracilis* juvenile and copepods), along with the 95 % credible interval.

	d*P. pileus* juvenile	d*P. pileus* adult	d*B. gracilis* juvenile	dCopepods
dSST winter	−0.61 (−0.8,−0.3)	−0.74 (−0.87,−0.5)	−0.35 (−0.63,0.02)	−0.26 (−0.58,0.11)
dSST spring	−0.66 (−0.83, −0.4)	−0.76 (−0.88,−0.54)	−0.5 (−0.74,−0.17)	−0.38 (−0.66,−0.02)

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Figure 1: SOB (in circles) of the respective zooplankton groups at Helgoland Roads, in terms of weeks after the beginning of the year, together with the mean evolution of the phenological time series of the zooplankton data (line) calculated using the change–point model and the corresponding 95 % credible interval (dotted line) from 1975 to 2004: a) SOB of *Pleurobrachia pileus* juvenile, b) SOB of *Pleurobrachia pileus* adult, c) SOB of *Beroe gracilis* juvenile, d) SOB of copepods. Monthly mean SST at Helgoland Roads (open circles) from 1975 to 2004, together with the calculated evolution of the mean temperature using the change–point model (black line) and its 95 % credible interval (dotted line) for: e) SST of January, f) SST of February, g) SST of March, h) SST of April, i) SST of May, j) SST of June.

Figure 2: a) Probability for a change–point in the SOB of *Pleurobrachia pileus* juvenile (continuous line), the SOB of *Pleurobrachia pileus* adult (dashed line), the SOB of *Beroe gracilis* juvenile (dashed dotted line), the SOB of copepods (dotted line) from 1975 to 2004 and b) the probability for a change–point in the seasonal mean SST from 1975 to 2004: SST winter (dashed line) and SST spring (continuous line).

Figure 3: Annual change rate of seasonal mean winter SST versus the annual change rate of SOB (open squares) of a) *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult, c) *Beroe gracilis* juvenile and d) copepods, and the slope of the relationship calculated using the Bayesian model (grey line) for the time period from 1975 to 2004. Annual change rate of seasonal mean spring SST versus the annual change rate of SOB (full squares) of a) *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult, c) *Beroe gracilis* juvenile and d) copepods, and the slope of the relationship calculated using the Bayesian model (black line) for the time period from 1975 to 2004. The R^2 was calculated for the best estimate of the parameters from the Bayesian analysis.

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Figure 4: Two seasonal mean abundances of *Pleurobrachia pileus* juvenile (continuous line), *Beroe gracilis* juvenile (dashed line) and copepods (grey line), a) for regime 1 (R1; from 1975 to 1987) and b) for regime 2 (R2; from 1988 to 2004).

Figure 5: Probability density function for the difference between the SOB in the annual abundance of *Beroe gracilis* juvenile and the EOB of the first peak in the annual abundance of *Pleurobrachia pileus* juvenile for a) R1 (1975–1987) and b) R2 (1988–2004). Probability density function of c) the difference between the time series of copepods total spring abundance in R1 (1975–1987) and in R2 (1988–2004), and d) the difference between the time series of copepods total autumn abundance in R1 (1975–1987) and in R2 (1988–2004).

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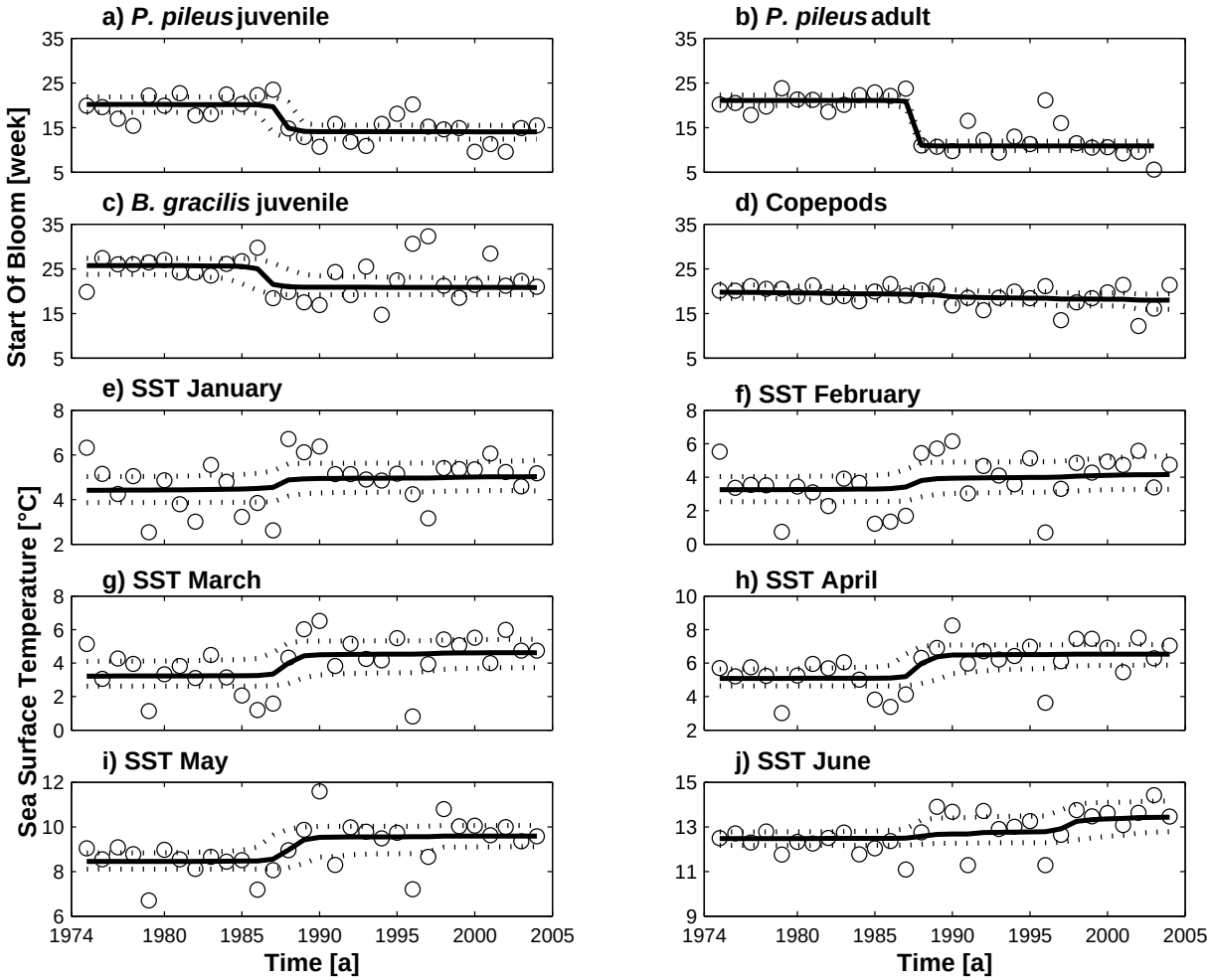
a) P. pileus juvenile
b) P. pileus adult
c) B. gracilis juvenile
d) Copepods
e) SST January
f) SST February
g) SST March
h) SST April
i) SST May
j) SST June
Start Of Bloom [week]
Sea Surface Temperature [°C]
Time [a]
Time [a]

Figure 1.

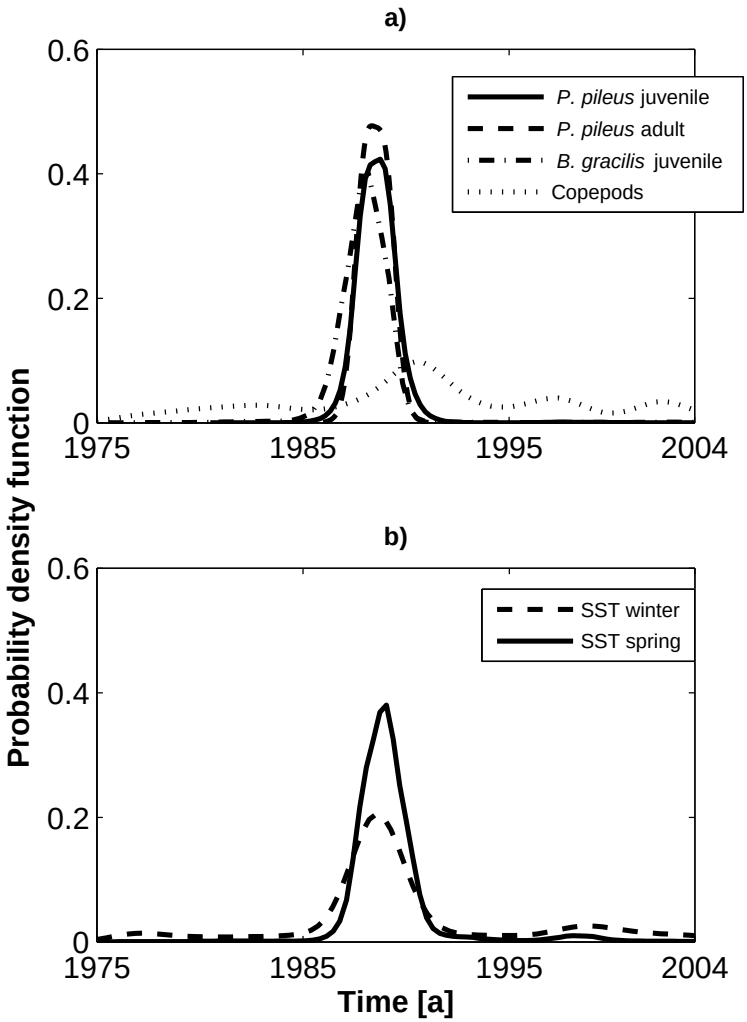
a)
0.6
0.4
0.2
0
1975
1985
1995
2004
P. pileus juvenile
P. pileus adult
B. gracilis juvenile
Copepods
b)
0.6
0.4
0.2
0
1975
1985
1995
2004
SST winter
SST spring
Probability density function
Time [a]

Figure 2.

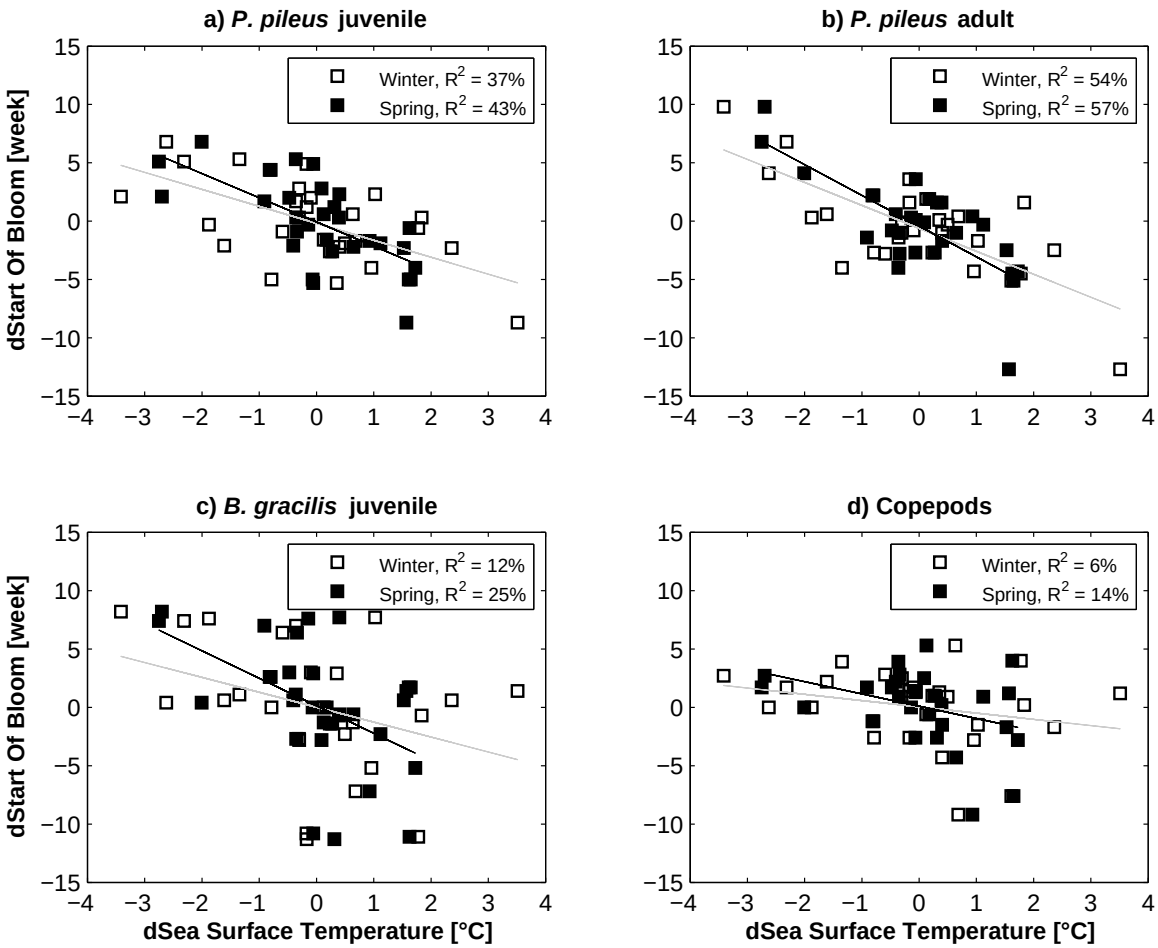
a) P. pileus juvenile
Winter, R2 = 37%
Spring, R2 = 43%
b) P. pileus adult
Winter, R2 = 54%
Spring, R2 = 57%
c) B. gracilis juvenile
Winter, R2 = 12%
Spring, R2 = 25%
d) Copepods
Winter, R2 = 6%
Spring, R2 = 14%
dStart Of Bloom [week]
dSea Surface Temperature [°C]

Figure 3.

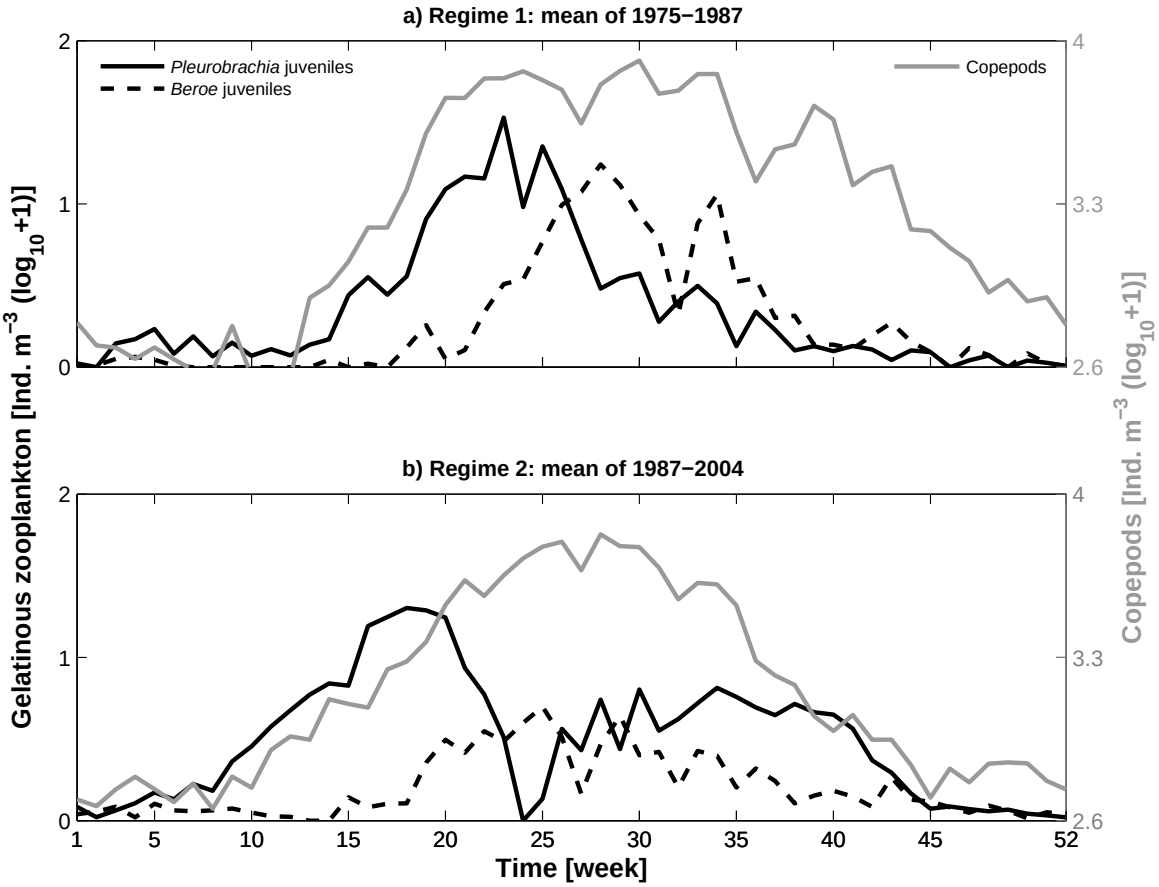
a) Regime 1: mean of 1975−1987
b) Regime 2: mean of 1987−2004
Pleurobrachia juveniles
Beroe juveniles
Copepods
Gelatinous zooplankton [Ind. m−3 (log10+1)]
Copepods [Ind. m−3 (log10+1)]
Time [week]
0
1
2
2.6
3.3
4
1
5
10
15
20
25
30
35
40
45
52

Figure 4.

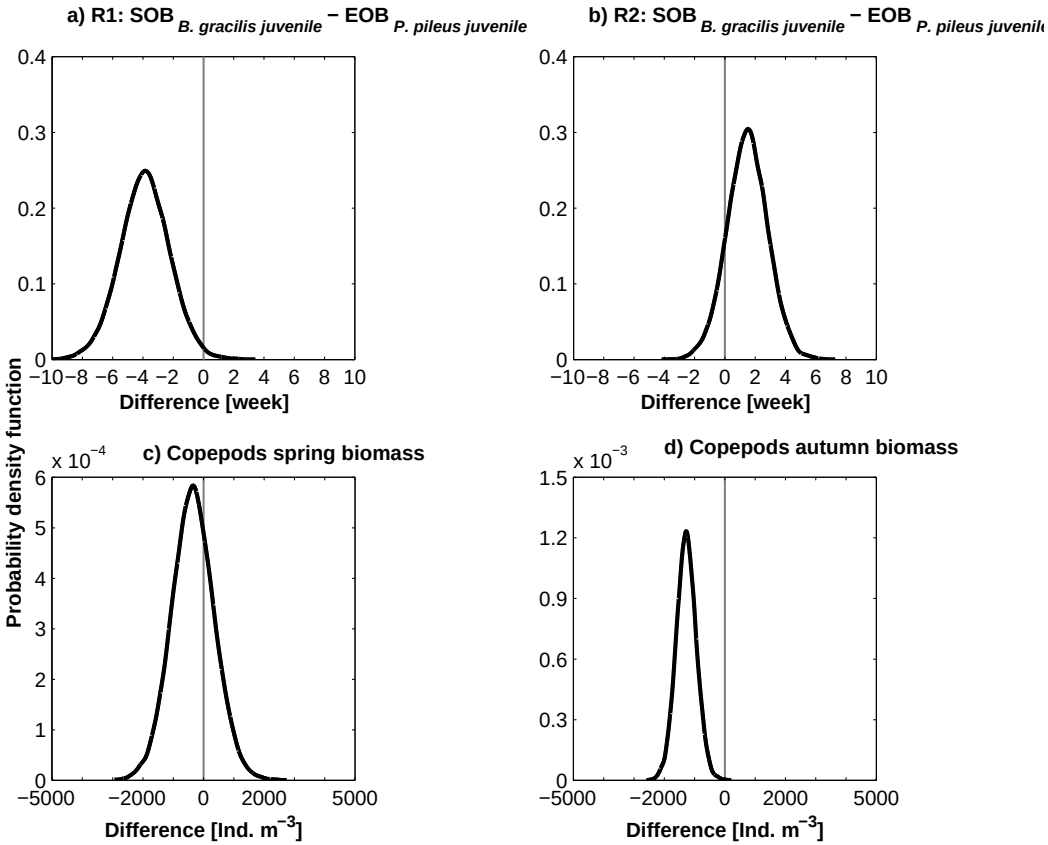
a) R1: SOB B. gracilis juvenile − EOB P. pileus juvenile
b) R2: SOB B. gracilis juvenile − EOB P. pileus juvenile
c) Copepods spring biomass
d) Copepods autumn biomass
Probability density function
Difference [week]
Difference [Ind. m−3]
x 10−4
x 10−3

Figure 5.