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

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Keywords:	phenology, regime shift, <i>Pleurobrachia pileus</i> , copepods, Bayesian statistics, <i>Beroe gracilis</i> , North Sea, Helgoland Roads
Abstract:	<p>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 <i>Beroe gracilis</i> and <i>Pleurobrachia pileus</i> 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 <i>Beroe gracilis</i>, <i>Pleurobrachia pileus</i> 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 <i>Pleurobrachia pileus</i> and <i>Beroe gracilis</i> correlated with a step-like increase in winter and spring sea surface temperatures. Possible explanations for the</p>

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.



For Review Only

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1 Phenological shifts of three interacting zooplankton 2 groups in relation to climate change

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1 March 2010

5 ABSTRACT

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

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

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

1 INTRODUCTION

30 General scientific consensus is that Earth's climate is warming at an accelerated rate (IPCC
31 2007). Climate change will inevitably impact habitats, ecosystems and biological resources.
32 The seasonality of species in coastal waters could be particularly sensitive to warming
33 (Costello 2006; Sullivan et al. 2007).

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

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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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6 64 *robrachia pileus* (O. F. Müller, 1776), the most abundant gelatinous zooplankton in the
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8 65 German Bight and an important carnivore in coastal waters (Bamstedt 1998). *P. pileus* has
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10 66 been found in many parts of the world ocean and is, therefore, of global relevance. This al-
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12 67 most cosmopolitan organism shows marked seasonality, with peak abundances in the North
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14 68 Sea and adjacent areas appearing in early summer (van der Veer and Sadee 1984; Williams
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16 69 and Collins 1985) and autumn (Fraser 1970).
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22 71 The preferential prey of *P. pileus* are mesozooplankton, and calanoid copepods (Greve and
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24 72 Reiners 1988; Frid et al. 1994) in particular. Ctenophores are capable of regulating the abun-
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26 73 dance of their prey and thus can influence the dynamics of copepod populations (Sullivan
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28 74 and Reeve 1982). *P. pileus* does not have many predators which are quantitatively impor-
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30 75 tant. In the coastal regions of the North Sea, only the ctenophore *Beroe gracilis* (C. Künne,
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32 76 1939) can significantly graze down a *P. pileus* population. Greve and Reiners (1988) and
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34 77 Bamstedt (1998) proposed that *P. pileus* populations, observed in the North Sea, occur in
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36 78 cycles as they are restricted by the occurrence of *B. gracilis* as in a classical predator-prey
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38 79 relationship.
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48 81 During the last three decades, the German Bight exhibited a warming trend with an average
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50 82 temperature increase of 1.7 °C (Schlüter et al. 2008; Wiltshire et al. 2008). The most sub-
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52 83 stantial warming occurred during the winter and spring months. The present study focuses
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54 84 on understanding the impact of these climatic changes on the phenology of three interacting
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56 85 zooplankton groups (*B. gracilis*, *P. pileus* and copepods) at Helgoland Roads from 1975 to
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58 86 2004 and on the possible consequences to their predator-prey interactions.
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88 The analyses were conducted using Bayesian statistics. An advantage of the Bayesian ap-

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 ($54^{\circ} 11'3''$ N, $7^{\circ} 54'0''$ 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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6 112 build-up, associated with the week of the year during which the population reached a level
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8 113 corresponding to 15% of the annual cumulative abundance, and 2) the “End of bloom”
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10 114 (EOB), associated with the week of the year during which the population reached a level
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12 115 corresponding to 85% of the annual cumulative abundance. Sensitivity analysis indicated
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14 116 that these threshold levels were insensitive to variations of up to 30% (results not shown).
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16 117 SST data were separated into multiple time series: one time series for each month, from
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18 118 January to June, over the period extending from 1975 to 2004. The monthly SSTs were also
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20 119 grouped into two main seasons, winter (from January to March) and spring (from April to
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22 120 June), to evaluate the different impacts of winter and spring temperatures on the organisms.
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31 2.2 Bayesian Approach

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34 122 Bayesian theory was used to characterise potential changes and correlations in the three
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36 123 zooplankton groups under study relative to temperature. Bayesian statistical methods use
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38 124 observations to update the probability that a hypothesis (model) is true. This approach was
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40 125 first used to detect phenological shifts in terrestrial systems by Dose and Menzel (2004),
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42 126 as it permitted the discovery of changes in the time series of phenological data and corre-
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44 127 lated these changes with potential driving factors, such as temperature (Dose and Menzel
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46 128 2006). This analysis also provided estimates of uncertainties, because all calculations were
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48 129 performed using full probability distributions.
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56 131 Three models were considered: 1) a constant model (M1), which assumed that the time
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58 132 series under investigation had no trend; 2) a linear model (M2), which assumed that a lin-
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60 133 ear trend was present (either increasing or decreasing); and 3) a change-point model (M3),
134 which assumed that there were at least one and possibly more step-like shifts in the time

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6 135 series.

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11 137 The models were ranked using the Deviance Information Criterion (DIC), a Bayesian model
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13 138 comparison method. DIC ranked competing models based on a trade-off between the fit of
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15 139 the model to the data and the complexity of the model.
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21 141 Bayesian correlation coefficients were estimated to identify possible coherences between the
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23 142 changes in temperature and the changes in the zooplankton phenological time series.
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28 144 At the position in the time series at which a step-like shift was detected, the strength of
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30 145 the predator-prey relationship between juvenile *P. pileus* and *B. gracilis* was characterised
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32 146 by calculating the Bayesian probability for observing the difference between the time series
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34 147 of the SOB of *Beroe* and the time series of the EOB of *P. pileus* ($\text{diff} = \text{SOB}_{B.gracilis} -$
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36 148 $\text{EOB}_{P.pileus}$), both during the period prior to the shift (the first regime, R1) and during the
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38 149 period after the shift (the second regime, R2).
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46 151 To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid
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48 152 copepods, two time series were constructed: one for the copepod total spring abundances
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50 153 (from April to June) and another for the copepod total autumn abundances (from October
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52 154 to December). The probability of observing the difference between the two regimes in each
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54 155 time series was calculated using the Bayesian approach.
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60 157 A detailed description of the Bayesian models adopted is reported in the supporting online
158 information.

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6 159 **3 RESULTS**

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10 160 **3.1 Model selection**

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13 161 The analyses based on the DIC indicated that the change–point model was best supported
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15 162 by the SOB data for the *P. pileus* juvenile, *P. pileus* adult and *B. gracilis* juvenile (see
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17 163 Table 1). The linear model was ranked second, and the constant model was ranked third in
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19 164 importance. The only exception was found in the copepod SOB time series, for which the
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21 165 linear model was ranked first, followed by the change–point model, then by the constant
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23 166 model in importance. It is important to note that all models, M1, M2, and M3, exhibited
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25 167 a similar DIC for the copepods, suggesting that all models were equivalent (although not
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27 168 identical) in this case.
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34 170 Table 1

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39 172 Figure 1 shows (in circles) the SOB data for the *P. pileus* juvenile, *P. pileus* adult, *B.*
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41 173 *gracilis* juvenile and copepods, the average functional behaviour of the data calculated us-
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43 174 ing the change–point model (continuous line), and the corresponding 95% credible intervals
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45 175 (dotted lines). The modelled evolution of the average SOBs showed a step toward earlier
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47 176 weeks within the years 1987–1989, leading to permanent advances in the timings of their
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49 177 phenological occurrence in the following years. The shift was less pronounced in the SOB
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51 178 data for copepods, for which a linear decreasing trend was determined to be most likely (see
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53 179 DIC values in Table 1). The step in the mean evolution of the SOBs was sharpest in the
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55 180 adult *P. pileus* data.
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182 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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6 207 step-like fashion was considerably smaller than the probability for step-like SOB changes in
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8 208 *P. pileus* and *B. gracilis* data and was centred around the years 1990/91. Low probabilities
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10 209 of additional step-like changes in the SOB time series of copepods were noticeable in the
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18 212 Figure 2

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22 214 The probability for a change point in SST winter and SST spring was highest in the years
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24 215 1987–1989 (Figure 2b), which correspond to a concomitant change in the phenological time
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26 216 series of the ctenophores.

27 28 29 30 31 217 **3.3 Correlation analysis**

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34 218 A Bayesian correlation (see Data and methods, and supporting online information, section
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36 219 S2.3, for details on the method used) between ctenophore abundance and SST winter in-
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38 220 dicated an advance in the timings of their phenological occurrence corresponding with a
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40 221 temperature rise ($r = -0.6$). This same correspondence pattern was especially strong for
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42 222 SST spring (Table 3). These analyses clearly indicated that changes in SST winter and SST
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44 223 spring are strongly correlated with the shifts to earlier times in the SOBs of *P. pileus* and
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46 224 *B. gracilis*. The correlations between the SOBs and SST spring were higher than the corre-
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48 225 lations between the SOBs and SST winter, suggesting a strong sensitivity of the gelatinous
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50 226 zooplankton to temperatures at the beginning of the bloom season. Changes in temperature
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52 227 appeared to have a minor impact on the SOBs of copepods (correlation coefficient of about
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54 228 -0.2 , Table 3).

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

240

241 Figure 3

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243 Table 4

244 3.4 Changes in seasonal occurrence

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

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249 Figure 4

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

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6 255 in time from mid–late June in R1 to April–May in R2. Also, the total annual abundance
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8 256 increased from about 7,200 individuals m^{-3} in R1 to about 9,800 individuals m^{-3} in R2.

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13 258 In contrast, *B. gracilis* exhibited a single population maximum in both periods (R1 and
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15 259 R2 in Figure 4a–b, dotted line). The phenologies of *B. gracilis* differed somewhat between
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17 260 the two regimes, but they differed to a far lesser extent than the phenologies of *P. pileus*.
18
19 261 The total annual abundance in R1 (8,700 individual m^{-3}) was greater than in R2 (3,200
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21 262 individual m^{-3}). The populations of *B. gracilis* and *P. pileus*, however, showed a predator–
22
23 263 prey like pattern in both periods (R1 and R2). The copepod data showed a single maximum
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25 264 in the organism population between weeks 20–35 in both regimes (Figure 4a–b, grey lines).
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27 265 The distribution width was somewhat narrower in R2 compared to the distribution width
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29 266 in R1.

30 31 32 33 34 35 36 267 **3.5 Predator–prey relationships**

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39 268 The strength of the predator–prey relationship between *P. pileus* and *B. gracilis* was investi-
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41 269 gated by calculating the probability of the difference between two phenophases, in this case
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43 270 the difference was between $\text{EOB}_{P.pileusjuvenile}$ and $\text{SOB}_{B.gracilisjuvenile}$ (the method is described
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45 271 in detail in Data and methods, and in supporting online information, section S.2.4). The time
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47 272 overlap of about four weeks between $\text{SOB}_{B.gracilisjuvenile}$ and $\text{EOB}_{P.pileusjuvenile}$ suggested a
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49 273 strong predator–prey relationship (see Figure 5a) in R1, whereas a probability maximum
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51 274 centred on positive values (two weeks) supported a weaker predator–prey relationship in R2
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53 275 (Figure 5b).

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6 279 To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid
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9 280 copepods, the probability of observing the difference between the two regimes in the cope-
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11 281 pods' spring and autumn abundance time series was calculated using the Bayesian approach.
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13 282 The copepod spring abundance (from April to June) was reduced to about 500 individu-
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15 283 als m³ from R1 to R2. Note, however, that the evidence for such a change remained small
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17 284 because the 95 % credible interval (−1717.0 to +1066.0) included zero. The difference in
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20 285 abundance relative to the autumn period (from October to December) was more pronounced
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22 286 (see Figure 5b), with a reduction in R2 to about 1275 individuals m³.

27 287 4 DISCUSSION AND CONCLUSIONS

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30 288 The analysis of the timings of phenological occurrences of the three zooplankton groups
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32 289 provided an effective method for the detection of ecological changes in the populations of
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34 290 organisms related to climate change. Bayesian statistics provided a mathematically rigorous
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36 291 framework for testing hypotheses (or models), and permitted the quantitative expression of
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38 292 results in terms of probabilities.

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44 294 This study used the DIC criterion to evaluate three different models for the potential pat-
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46 295 terns in the phenological time series: 1) no change, 2) linear change, and 3) step-like change.

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48
49 296 In general, bloom timings of *P. pileus* (Figure 1a and 1b), *B. gracilis* (Figure 1c) and annual
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51 297 SSTs (Figure 1e–j) followed a similar pattern of change that, in general, was best represented
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53 298 by a step-like shift. A linear increasing or decreasing trend was found to be less likely, with
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55
56 299 the only exception being the phenological time series of copepods (Table 1). The constant
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58 300 model was ranked the least probable for all organisms, although for copepods the differences
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60 301 among the models were small (see Tables 1 and 2).

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6 303 The highest probability for a step-like change in the SOB of *P. pileus* and *B. gracilis* was
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8 304 obtained in the year 1988/89 (Figure 2a) coincident with the step-like changes in SST winter
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10 305 and SST spring (Figure 2b). The timing of this step-change agreed with the timing of a
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12 306 regime shift, described by Beaugrand (2004) and Schlüter et al. (2008), in biological and
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14 307 hydrometeorological variables of the southern North Sea and German Bight. In line with
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16 308 previous findings (Greve et al. 2004), the change-point analysis showed good correlation
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18 309 between the SOB of *P. pileus* and SST winter. The correlation, however, improved when
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20 310 SST spring was considered, suggesting that the timing of the blooms were sensitive to the
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22 311 temperature conditions occurring in the bloom season.
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30 313 The relatively high correlation between the spring bloom timings of ctenophores and SST
31
32 314 winter (Table 3) and the higher winter densities of *P. pileus* of the second regime (Figure 4)
33
34 315 support the hypothesis (Purcell et al. 2001; Sullivan et al. 2001) of an effect of warm win-
35
36 316 ter conditions on the survival and success of overwintering adults. The higher correlation
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38 317 found between the spring abundances and SST spring (Table 3) suggested a cause-effect
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40 318 relationship between warmer temperatures and the earlier ctenophore appearance during
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42 319 R2 via impacts on metabolic processes (Molinero et al. 2008) and ovule production. In fact,
43
44 320 the year-to-year changes in winter and spring temperatures were linearly related to the
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46 321 year-to-year changes in the SOB of the ctenophores. The steeper slopes obtained from SST
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48 322 spring (Figure 3) confirmed that variations in spring bloom timings were more sensitive to
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50 323 spring SST than to winter SST.
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58 325 This study also highlighted the differential impact of temperature on two different but ad-
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60 326 jacent trophic levels (copepods and their predator *P. pileus*), possibly through different
327 temperature tolerances. Only relatively modest changes in copepod phenology (Figure 1d

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6 328 and 2a) were detected, suggesting that a step-like shift toward warmer conditions had lit-
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9 329 tle influence on the whole group of these five copepods due to complex life history traits,
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11 330 e.g. diapause, larval development and dissimilarities in food requirements for the different
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13 331 life stages. When considered individually, these five copepods tended to co-occur each year,
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15 332 with some exceptional cases in which distinct succession patterns were noticeable. Generally,
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17 333 periods of high *P. pileus* abundances occurred during periods of high copepod abundance
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19 334 (see Figure 4). Ctenophores, nevertheless, are capable of causing marked decreases in cope-
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21 335 pods (Greve and Reiners 1988; Kuipers et al. 1990; Purcell and Decker 2005). The present
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23 336 study indicated a weak predator-prey like pattern between copepods and *P. pileus* in the
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25 337 spring (Figure 5c). The appearance of a second reproductive phase of *P. pileus* during R2,
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27 338 however, had an impact on the copepod group (Figure 5d), related to a reduction in the
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29 339 average autumn biomass (compare also Figure 4a with Figure 4b).
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341 This study showed a remarkably robust predator-prey relationship between *B. gracilis* and
342 *P. pileus*, during R1 (Figure 5a). Such a feature was less pronounced during R2 (Figure 5b),
343 when *P. pileus* was characterised by two distinct reproductive phases. Although *B. gracilis*
344 appeared to drive the decline of the first peak in *P. pileus* abundance, this seemed less likely
345 for the decline of the second peak. The lower abundances of *B. gracilis* during R2 could be
346 caused by a detrimental effect of warming conditions on this organism, an interpretation
347 supported by the narrow thermal tolerance of *B. gracilis* (Purcell 2005). The increase in
348 mean temperature during the second regime made a second reproductive phase of *P. pileus*
349 possible after *B. gracilis* had declined. This mismatch appeared responsible for the all-season
350 presence of *P. pileus* in the plankton community of the German Bight.
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352 However, the three interacting groups investigated in this study represented only a crossec-

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6 353 tion of the more complex ecosystem, and the importance of other factors cannot be excluded.

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8 354 Transport processes, for example, are among those aspects that contribute to the intricacies

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10 355 of the system (Williams and Collins 1985; Greve and Reiners 1988; Wang et al. 1995). Ag-

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12 356 gregation (Graham et al. 2001), complex life histories (Schneider 1987; Greve et al. 1996)

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15 357 and adaptation are other processes that complicate the system, but these factors could not

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18 358 be considered here because of the difficulties associated with their quantification.

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21
22 360 The fact that *P. pileus* extended its annual presence may lead to diverse consequences

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24 361 through various other top-down (increased predation on fish eggs and larvae) and bottom-

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27 362 up processes that could not be considered in this study but may ultimately cause ecosystem-

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30 363 wide disruptions (Hay 2006). North Sea fish stocks, for example, are presently in an alarming

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32 364 state of decline (ICES 2008). Gelatinous zooplankton outbreaks could potentially exacerbate

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34 365 this situation and may lead to trophic dead ends by channelling the flow of energy to “waste”

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37 366 (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
<i>P. pileus</i> juvenile	Constant	182.15	Step
	Linear	178.82	
	Step	171.82	
<i>P. pileus</i> adult	Constant	195.39	Step
	Linear	167.1	
	Step	143.71	
<i>B. gracilis</i> juvenile	Constant	189.1	Step
	Linear	183.53	
	Step	178.24	
Copepods	Constant	142.68	Linear/step
	Linear	138.92	
	Step	141.27	

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.

	<i>P. pileus</i> juvenile	<i>P. pileus</i> adult	<i>B. gracilis</i> 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)

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 <i>P. pileus</i> juvenile	d <i>P. pileus</i> adult	d <i>B. gracilis</i> 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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6 469 Figure 1: SOB (in circles) of the respective zooplankton groups at Helgoland Roads, in terms
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8 470 of weeks after the beginning of the year, together with the mean evolution of the pheno-
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10 471 logical time series of the zooplankton data (line) calculated using the change–point model
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12 472 and the corresponding 95 % credible interval (dotted line) from 1975 to 2004: a) SOB of
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14 473 *Pleurobrachia pileus* juvenile, b) SOB of *Pleurobrachia pileus* adult, c) SOB of *Beroe gracilis*
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16 474 juvenile, d) SOB of copepods. Monthly mean SST at Helgoland Roads (open circles) from
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18 475 1975 to 2004, together with the calculated evolution of the mean temperature using the
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20 476 change–point model (black line) and its 95 % credible interval (dotted line) for: e) SST of
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22 477 January, f) SST of February, g) SST of March, h) SST of April, i) SST of May, j) SST of June.
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30 479 Figure 2: a) Probability for a change–point in the SOB of *Pleurobrachia pileus* juvenile
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32 480 (continuous line), the SOB of *Pleurobrachia pileus* adult (dashed line), the SOB of *Beroe*
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34 481 *gracilis* juvenile (dashed dotted line), the SOB of copepods (dotted line) from 1975 to 2004
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36 482 and b) the probability for a change–point in the seasonal mean SST from 1975 to 2004: SST
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38 483 winter (dashed line) and SST spring (continuous line).
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44 485 Figure 3: Annual change rate of seasonal mean winter SST versus the annual change rate
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46 486 of SOB (open squares) of a) *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult,
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48 487 c) *Beroe gracilis* juvenile and d) copepods, and the slope of the relationship calculated us-
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50 488 ing the Bayesian model (grey line) for the time period from 1975 to 2004. Annual change
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52 489 rate of seasonal mean spring SST versus the annual change rate of SOB (full squares) of a)
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54 490 *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult, c) *Beroe gracilis* juvenile and d)
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56 491 copepods, and the slope of the relationship calculated using the Bayesian model (black line)
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58 492 for the time period from 1975 to 2004. The R^2 was calculated for the best estimate of the
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60 493 parameters from the Bayesian analysis.

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

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

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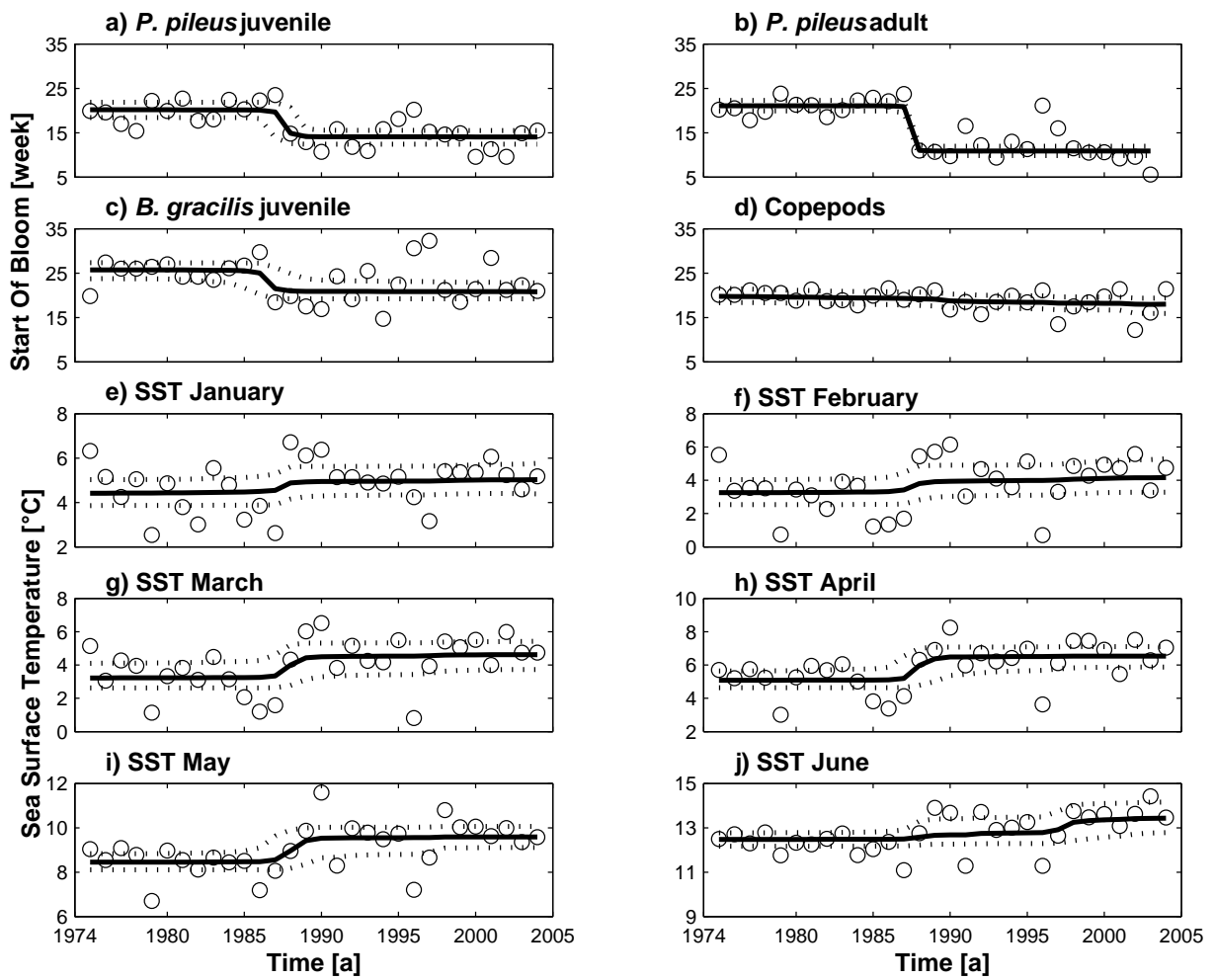


Figure 1.

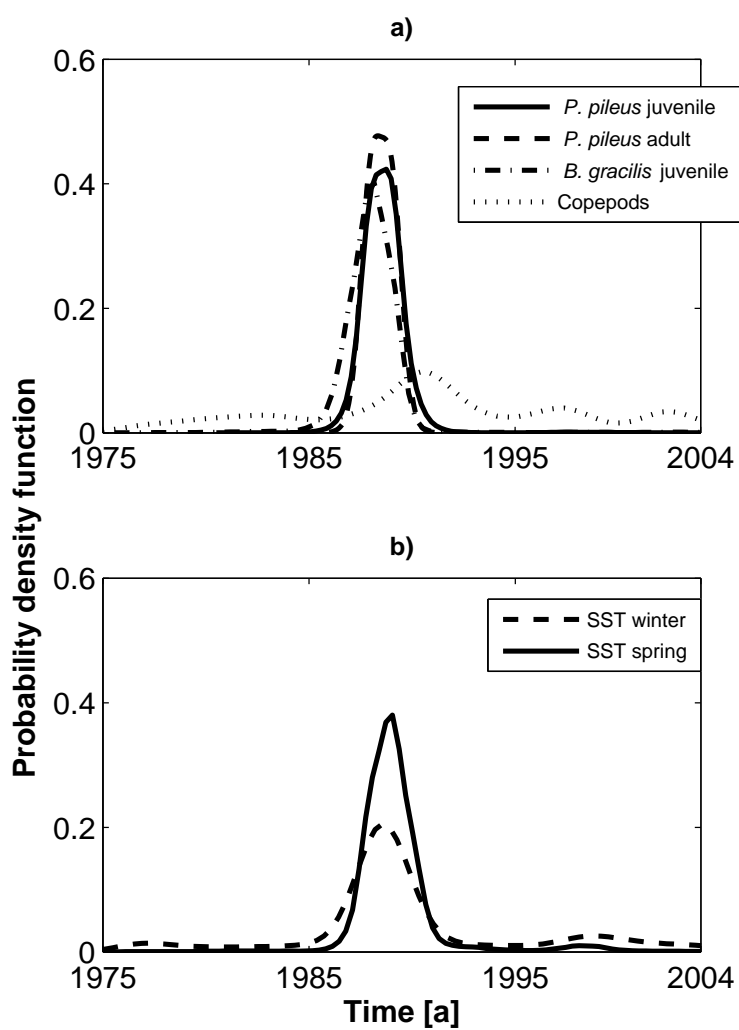


Figure 2.

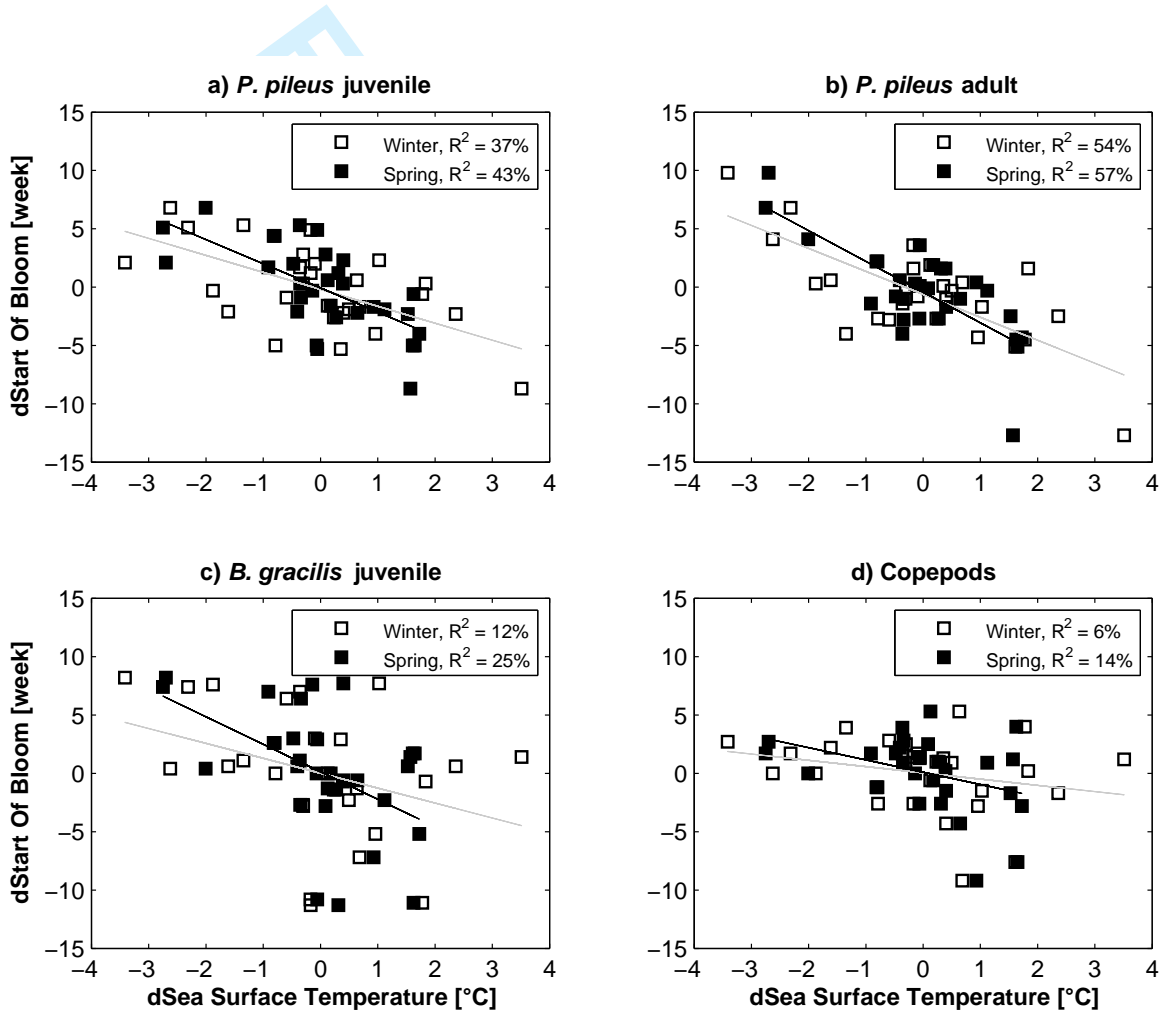


Figure 3.

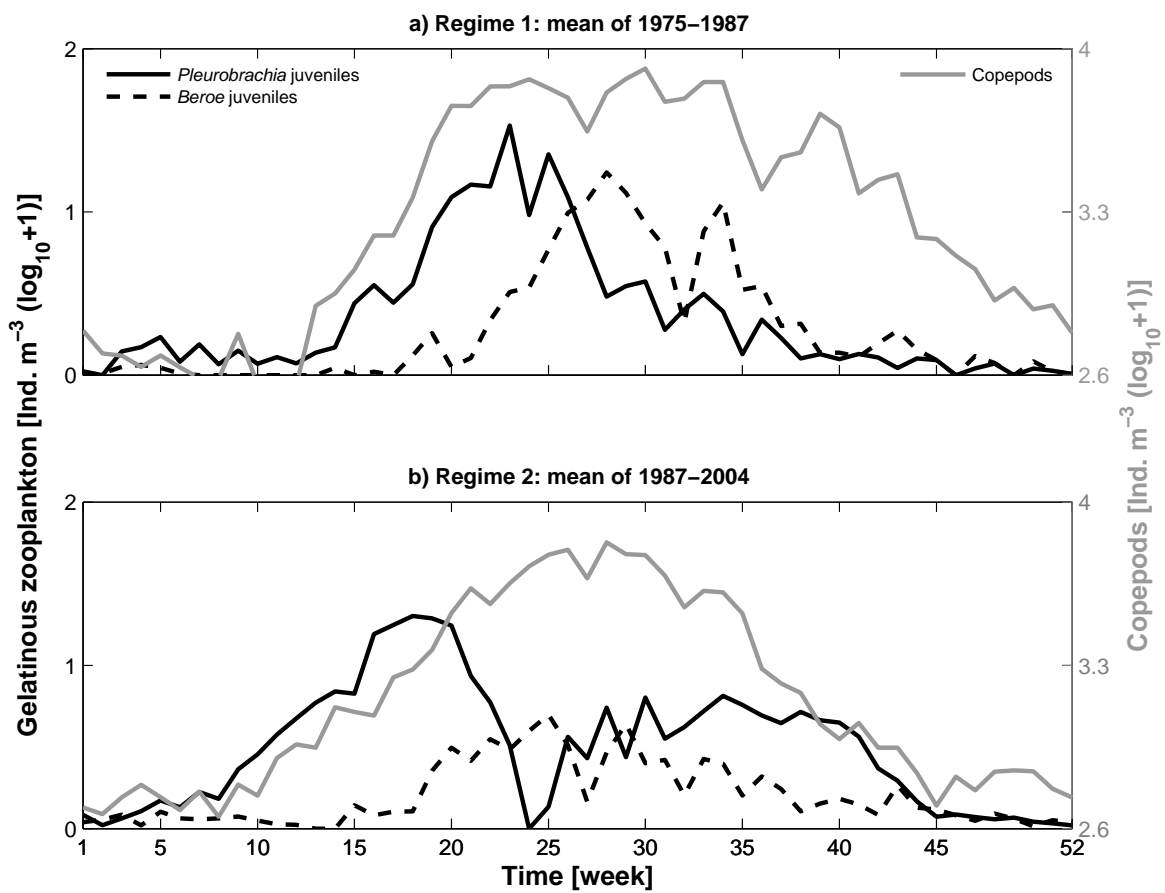


Figure 4.

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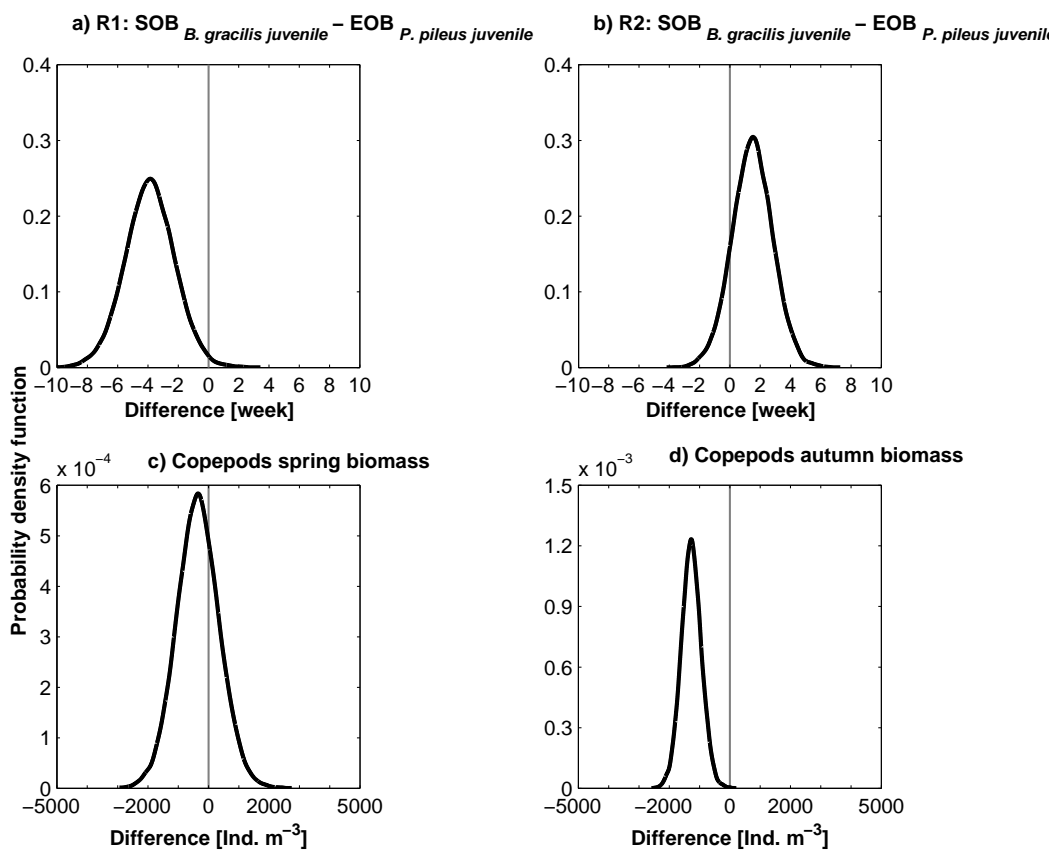


Figure 5.