Research

Cite this article: Boersma M, Grüner N, Tasso Signorelli N, Montoro González PE, Peck MA, Wiltshire KH. 2016 Projecting effects of climate change on marine systems: is the mean all that matters? *Proc. R. Soc. B* **283**: 20152274. <http://dx.doi.org/10.1098/rsob.2015.2274>

Received: 28 September 2015

Accepted: 16 December 2015

Subject Areas:

ecology

Keywords:

temperature optimum, distribution, North Sea, global change, Helgoland Roads, climate

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsob.2015.2274> or via <http://rsob.royalsocietypublishing.org>.

Projecting effects of climate change on marine systems: is the mean all that matters?

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Studies dealing with the effects of changing global temperatures on living organisms typically concentrate on annual mean temperatures. This, however, might not be the best approach in temperate systems with large seasonality where the mean annual temperature is actually not experienced very frequently. The mean annual temperature across a 50-year, daily time series of measurements at Helgoland Roads (54.2° N, 7.9° E) is 10.1°C while seasonal data are characterized by a clear, bimodal distribution; temperatures are around 6°C in winter and 15°C in summer with rapid transitions in spring and autumn. Across those 50 years, the temperature at which growth is maximal for each single bloom event for 115 phytoplankton species (more than 6000 estimates of optimal temperature) mirrors the bimodal distribution of the *in situ* temperatures. Moreover, independent laboratory data on temperature optima for growth of North Sea organisms yielded similar results: a deviance from the normal distribution, with a gap close to the mean annual temperature, and more optima either above or below this temperature. We conclude that organisms, particularly those that are short-lived, are either adapted to the prevailing winter or summer temperatures in temperate areas and that few species exist with thermal optima within the periods characterized by rapid spring warming and autumn cooling.

1. Introduction

As a result of the current changes in world-wide temperatures, thermal effects on physiology and vital rates, such as growth and reproduction of poikilothermic organisms have received a great deal of attention in recent years (e.g. [1–5]), including the potential consequences of shifts in global distribution [6–8]. In the context of global warming, meta-analyses are often the method of choice, and many of these focus on the changes in annual mean temperatures (e.g. [9–11]) or, when including more measurements per year, removing the seasonal temperature signal as one of the first steps in the analysis [12]. For example, the recent meta-analysis of Thomas *et al.* [3] focused on annual mean temperatures from different locations, showing a close correlation between those annual means and the reported temperature optima of different phytoplankton species collected from these locations. However, in most cases, the optimal temperature of the phytoplankton was 5–10°C higher than the annual mean temperatures at the respective location, especially at mid-latitudes (temperate regions). As an explanation, Thomas *et al.* [3] discussed the asymmetry of many temperature responses [13] such as steeper declines in growth at

warmer compared to colder than optimum temperatures and, hence, a higher (lower) cost of having optimum temperatures that are lower (higher) than ambient temperatures could select for optimum temperatures higher than the annual mean temperatures. This would also explain the observation of Thomas *et al.* [3] that, at the very high and very low latitudes, optimal temperatures are closer to the annual mean temperature simply because the variation in temperatures is lower than that in temperate latitudes.

Chen [5] elaborated on the analysis of Thomas *et al.* [3], extending their dataset and investigated the hypothesis that thermal breadth should increase with latitude, as the range of temperatures increases, especially in terrestrial environments [14]. Contrary to his predictions, Chen [5] observed no such change in niche breadth in phytoplankton and attributed this to the temperature buffering capacity of water, especially in marine systems. However, particularly in temperate environments, there may be an alternative explanation. In temperate seas which show a clear seasonality, the annual mean temperature may not be the best indicator of the prevailing temperatures that organisms experience. The North Sea with its relatively warm summers and cold winters is a typical example of such a temperate sea with strong seasonal fluctuations of high amplitude in temperature (i.e. from -3 to 21°C [12], figure 1*a*). The average water temperature over 50 years (1962–2011) of daily observations at the Helgoland Roads (54.2°N , 7.9°E) sampling site is 10.1°C [15] but, as a result of the clear seasonality, the temperature frequency distribution has a bimodal distribution with peaks at 5 – 6°C and 16 – 17°C (figure 1*b*). In fact, the temperatures most often measured over 50 years at Helgoland Roads were 4.6°C (128 times) and 16.6°C (146 times). These temperatures reflect the typical winter and summer conditions, between which, short and steep transitions occur. For example, the value of 11.7°C has only been measured 31 times in 50 years of daily observations, despite it being close to the grand mean of 10.1°C , which itself was observed 44 times in 50 years.

We hypothesize that, especially short-lived species, such as microalgae, other unicellular organisms or zooplankters (or life stages) with a clear seasonal window and with only a few active generations per year (and subsequent resting stages or cysts), will not be adapted to the annual mean temperature in highly seasonal environments, but rather to the most frequently measured temperatures, i.e. the typical winter and summer temperatures. Thus, these organisms typically experience only fairly short time windows, with restricted temperature regimes, and as a result, have no adaptive need for a broad thermal window. In fact, exactly this was observed for the microalgal data set by Chen [5]: no latitudinal differences in thermal breadth in microalgae. This approach is the temporal equivalent of the study by Potter *et al.* [16], who argued that microclimates are very important in a larger spatial area. For the North Sea, we expect to find many optimum temperatures for organisms to be at around 5 – 6°C or 16 – 17°C , and not many in between these temperatures. We investigated this hypothesis, using three approaches: first, we investigated the temperatures at which maximal growth rates of algal species were observed in field data; second, we re-analysed the dataset of Chen; and third, we compiled independent literature data on the optimum growth of other organisms residing in (or close to) the North Sea. Furthermore, we used an independent temperature dataset for the South Pacific to test whether the

bimodal temperature distribution that we observe for the North Sea can also be observed in other geographical areas.

2. Material and methods

(a) Analysis of the time series

The Helgoland Roads time series was used as the database for the analyses in this study [17]. Work-daily (Monday–Friday) temperature measurements were available for the years 1962–2011. These measurements were made with an accuracy of 0.1°C , directly after sampling using a hand-held thermometer in a bucket of freshly sampled water. The available temperature data were binned in 1°C bins and the frequency table of the different temperatures was computed. For the computation of the maximum growth rates of microalgae in the Helgoland Roads dataset, we selected 115 phytoplankton taxa [18]. The density estimates of the microalgae were based on work-daily counts at this sampling spot. The original data were first pre-treated using a smoothing spline algorithm [19], which also dealt with missing values in the dataset. Subsequently, we used these data to establish the temperature where population growth of the different algal species was maximal. For this, we computed the inflection points of the ascending part of the smoothed abundance curves of every bloom, using the method described by Grüner *et al.* [20]. Net population growth rates are highest at this inflection point, thus, we propose that the growing conditions for the taxon are optimal on this day. This might not be completely accurate as a variety of factors, such as nutrient availability, light conditions and predation, influence growth of phytoplankton, but there is no *a priori* reason to assume that the estimate is biased. The measured temperature at the day of these inflection points was noted, and we assume that this temperature represents the optimal temperature for this given bloom. Subsequently, we generated a frequency distribution of the computed optimal temperatures. To correct for the potential inflation of the likelihood of finding inflection points at temperatures that occurred more frequently, we divided the frequency distribution of the inflection points by the frequency distribution of the temperatures. This yielded an unbiased distribution of the occurrence of the highest relative growth rates per bloom for any given temperature. Furthermore, to assess whether the actual temperature distribution was different from the distribution of the inflection points, we generated a set ($n = 999$) of random distributions from the measured temperature distribution with the same sample size as the number of inflection points. We averaged the different frequencies sampled for the different temperatures and computed a standard deviation based on these 999 random sets, and the 99.9% confidence interval based on the computed mean and standard deviation. This distribution was then compared to the actual distribution of the inflection points.

(b) Collecting independent data

First, we re-analysed the most complete global database on the temperature response of microalgae obtained from different areas [5], including the few more cases that we found (table S1, electronic supplementary material), and investigated whether we could find differences in distributions of optimal temperatures in different latitudes, as we argued that the clear seasonality of temperatures should be visible mostly in temperate regions. For this we used all of the marine algae from the database by Chen [5], added some more studies that evaded the previous collection efforts from the literature (table S1, electronic supplementary material) and compared the distribution of optimal growth temperatures over 10° latitude sections, expecting to find higher variation for the temperate latitudes, expressed as deviations from normal distribution combined with a platykurticity of the distributions at temperate latitudes

Figure 1. (a) Mean weekly temperatures measured at the Helgoland Roads sampling site for the period of 1990–1999 [15]. (b) The frequency distribution of the daily temperature measurements at the Helgoland Roads long-term station. A bi-modal distribution is observed with maxima at 5–6°C and 16–17°C. (c) The frequency distribution of the number of inflection points (defined in the text) of 115 phytoplankton measured over 50 years (1962–2012) from the Helgoland dataset; (d) the average number of inflection points corrected for the difference in distribution of the temperatures; and (e) top panel, grey bars: average and standard deviation of the distribution of 6561 randomly sampled temperatures from the total temperature distribution, compared to the real distribution of the inflection points (data from figure 1c), the dotted lines indicate the 99.9% confidence interval of the randomly sampled temperatures, the bottom panel shows the difference between the two distributions, showing the same pattern as figure 1d. Coloured bars indicate that this difference was significant at a significance level of $p < 0.001$. (Online version in colour.)

relative to the leptokurticity at lower and higher latitudes. Second, we collected data from published studies on temperature responses of organisms inhabiting the North Sea or adjacent seas, investigating the hypothesis that the group of organisms

obtained from this region also display a bimodal distribution of optimum temperatures, mirroring the field results. Here, we excluded microalgae as this group was already examined in the aforementioned analysis. Using different databases, we searched

for data on the temperature-dependent performance of North Sea species, employing a range of different keyword combinations including, for example, *temperature*, *growth*, *optim**, *response*, and at times specific species names for which we had not found data yet, but which are so common that we assumed that these data must be available. Studies were included that either directly or indirectly provided an estimate of the optimal temperature for growth. The analysis only included studies employing at least three temperatures and where growth rate (or any other response/performance variable) displayed a clear optimum on one of the experimental temperatures. In cases where the original study did not yield a maximal response in the middle of the temperature range, it was not possible to estimate the optimal temperature, and these studies were excluded from the analysis. In total, our search yielded a dataset including both poikilothermic animals and macroalgae. Since the response factor of interest was simply the temperature of maximal growth, it was not necessary to do a formal meta-analysis as all of the units were identical: temperature of optimal performance. Rather, we investigated the frequency of occurrence of all of the optimum temperatures.

(c) Time series of sea surface temperatures

In order to investigate the global importance in the temperature distributions, we also investigated seasonal temperatures on a global scale. For this, a time series of sea surface temperatures (Reynolds-SST-v2) data was downloaded from the site Integrated Climate Data Center (http://icdc.zmaw.de/sst_reynolds.html?&L=1), with a spatial resolution of 0.25° . To investigate the effects of seasonal dynamics, we selected the 145.5° W longitude in the South Pacific, as this transect is far away from any continent, and hence is not influenced by local upwelling processes in coastal areas. Furthermore, the influence of North–South currents, with potential effects on sea surface temperatures is small. Close to the Equator, the South Equatorial Counter Current transports water from east to west and below 60° latitude, the Antarctic Circumpolar Current transports water in the other direction. Mean monthly SST temperatures were used and averaged over 1° latitude, thus yielding a database of 80 (degrees latitude) $\times$ 32 (years) $\times$ 12 (months) temperature measurements. The frequency of observations was plotted after subtracting the mean value for each latitude, and the frequency of observations of these anomalies was plotted in 0.5°C bins (see also [21]).

(d) Temperature change

A changing bimodal distribution could have unexpected consequences for the frequency of individual measurements. To analyse this, we divided the Helgoland Roads dataset into two parts, before and after 1989, the year of a ‘major regime’ shift in the North Sea [10], and plotted the temperature distributions for these two periods. Furthermore, we correlated the relative frequency of each temperature with year as the independent variable to investigate which temperatures have increased in frequency and which have decreased. Thus, a negative correlation coefficient indicates a gradual decrease of the observed frequency of this temperature over the whole time period.

3. Results

Based on the distribution of the temperatures in the North Sea (figure 1), we hypothesized that resident species should have optimal thermal performance (in terms of vital rates and physiology) at either the typical winter or the summer temperature, but not at the overall annual mean. Using the long-term series of phytoplankton data collected at Helgoland Roads, we obtained a database with 6561 observations, or roughly one bloom per species and year over the 50-year period. Not surprisingly, the temperature frequency distribution of maximum

Figure 2. Top panel: frequency distribution of optimum temperatures for growth for microalgae from [5] and table S1, electronic supplementary material. The data were sorted over 10° latitude, so 5 represents $0\text{--}10^\circ$ N and S, and so on. Within these latitudes, we standardized the data by subtracting the mean annual temperature from the location the algae were isolated from, and binned these in 2°C bins. The curves represent the expected normal distributions per latitude, different colours represent the significance of the deviation from normality following a Shapiro–Wilk W -test (red, solid $p < 0.01$; orange, dashed $0.01 < p < 0.05$; blue, dotted $p > 0.05$). Bottom panel: kurtosis of the distributions at the different latitudes. It can be seen that at the lower latitudes, the distributions are more leptokurtic than the normal distribution, whereas the opposite is true for the temperate latitudes. (Online version in colour.)

growth was very similar to the *in situ* temperature frequency distribution (figure 1c). However, even after we corrected for the difference in the number of observations of the specific temperatures, we observed the same pattern (figure 1d): more instances of maximal growth at $6\text{--}7^\circ\text{C}$ and $17\text{--}18^\circ\text{C}$ than at the other temperatures, indicating that the phytoplankton species are adapted to the two most common, small ranges in temperatures at Helgoland Roads, or at least to temperatures close to these. The comparison of the actual distribution of the inflection points with the distributions of temperatures generated by the 999 random samplings (figure 1e) shows the same pattern. The incidence of the temperatures at inflection points was clearly not a random sample from the temperature distribution. In fact, the frequency of only a few temperatures was not significantly different from random at $p < 0.001$ (white bars in figure 1e, bottom panel).

Considering all of the algal species collected over all latitudes from the Chen [5] dataset, plus the ones we added, and collating those into 10° absolute latitude groups, we observed a clear change in distributions of optimal temperatures over the latitudinal gradient. Where the optimal temperatures were normally distributed and strongly leptokurtic at lower latitudes (figure 2), the opposite was the case for the temperate latitudes, where the distributions were strongly platykurtic. In fact, especially for the $50\text{--}60^\circ$ latitudes, there were many optima for growth higher than the mean, but also a few instances of species with optima lower than the annual mean, with a gap in between, thus suggesting that the species occurring here were adapted either to the summer or to the winter temperatures.

Using the collection of the independent measurements on optimal temperatures (summarized in table S1, electronic supplementary material), we observed (figure 3) that the distribution of these published values has a similar shape to the one for the microalgae from figure 2 at 55° . The distribution is

Figure 3. Frequency distribution of reported published values of optimum temperatures for organisms in the North Sea with the normal distribution in black (see also table S1, electronic supplementary material, for a complete list of organisms and the appropriate references). Many species have temperature optima clearly above the highest temperature measured around Helgoland (figure 1b), and even though this database includes a range of taxonomic groups from bacteria to long-lived species such as fish, we can observe a gap in the frequency of the optimum temperatures in the middle range of around 12°C, close to those temperatures with low frequencies of observation in the Helgoland Roads sampling site. (Online version in colour.)

also platykurtic (kurtosis = -0.67), and significantly deviating from normal with a p -value of 0.06 (Shapiro–Wilk’s $W = 0.97$; $n = 77$), and that many of the species have optimal temperatures higher than the highest reported values for daily temperature for the North Sea. Moreover, we observed a gap in optimal temperatures in the middle of the temperature range, as was to be expected from the frequency distribution of the temperatures. This was considerably less clear than in the Helgoland Roads phytoplankton dataset. On the one hand, this was caused by the fact that much less data were available for temperature responses based on experimental approaches from the North Sea and, on the other hand, because the taxonomic range in selected organisms from the North Sea was much larger. We observed no significant differences in the mean optimal temperature between the two major groups animals and macroalgae ($t_{72} = 1.77$; $p = 0.08$).

The North Sea shows a very large seasonal variability in temperatures, but the phenomenon observed here is not unique to the North Sea. In a completely unrelated dataset (South Pacific), a similar pattern can be observed for the temperate latitudes. Even though this signal is less clear because monthly averages of temperature were used, a clear lack of observations close to the mean (figure 4a) in the temperate regions was still observed, and the modes of the distributions on either side of the mean were several degrees Celsius away from the mean (figure 4b).

Dividing the frequency distribution of the temperatures in the North Sea into two (figure 5, before and after the major regime shift of 1989) shows that investigating changes in the annual mean temperature does not give the full picture. Previous studies (e.g. [22]) have highlighted the fact that colder temperatures have become less frequent (temperatures less than 4°C have become rare), thus, those organisms with their optimal performance at those temperatures are expected

to have suffered, and as a result cold, stenothermic species should have disappeared. However, continued warming will increase the frequencies of temperatures that were previously fairly uncommon, even in the middle of the temperature spectrum (6–10°C in figure 5), whereas other, warmer temperatures will continue to decrease in frequency (13–16°C). This becomes even clearer from the correlation analysis, where we correlated the number of observations of temperatures per year with time. Figure 5b shows the correlation coefficients, indicating that temperatures less than 5°C as well as those between 13 and 16°C have declined in frequency while those between 6 and 12°C and above 17°C have increased in frequency.

4. Discussion

Many studies on the effects of changing temperatures on species distributions have been carried out in the context of changing annual means (e.g. [23,24]), with typically the first step in the analysis being a correction for seasonal cycles (e.g. [12]). This is an approach that ignores the seasonal variation present especially in temperate systems (but see [21]). In fact, the most parsimonious explanation for the observation of Thomas *et al.* [3] that the optimum temperatures of algae collected from temperate latitudes are higher than the annual mean temperatures from these sites, is that these microalgal species are adapted to the ambient summer temperatures, which are higher than the annual mean temperatures. Based on the North Sea temperature dataset as well as the dataset from the South Pacific, it can be seen that the typical summer temperatures of temperate latitudes are somewhere in the order of 3–5°C higher than the annual mean temperature measured at the sites, which is similar to the difference that Thomas *et al.* [3] reported between the optimum temperatures of the temperate species and the annual mean temperatures. Still, this would mean that in the study of Thomas *et al.* [3] mainly species with optima for growth in the summer were considered, and not those with winter optima. Furthermore, using the seasonal dynamics, we can also explain the observations made by Chen [5] and to some extent by Sunday *et al.* [21] that the niche breadth does not get much wider at temperate latitudes, as many species (especially the microalgae from the Chen dataset) are specialized to certain seasons.

In our analysis of the Helgoland Roads algal dataset, we observed that there is a clear bimodal distribution in the optimal temperatures. We do not know whether the environmental conditions at the day of maximum growth in a bloom really represent the optimal conditions (temperatures) of a given species, but it is the best approximation as the net growth rate is highest at that moment for any given bloom, and it is certainly much better than taking the days of maximum densities, where net growth is essentially zero (cf. [19,25,26]). Furthermore, it is difficult to imagine that environmental conditions can be better on days with lower growth rates. The approach of Gruner *et al.* [20] used more than one environmental variable, and of course, it could be the case that not all of the environmental variables are optimal at the point of highest population growth, however, there is no real way to correct for this.

In contrast to Chen [5] and Thomas *et al.* [3], we observed just as many ‘winter’ as ‘summer’ species in the Helgoland dataset, most likely as a result of the high intensity of the Helgoland sampling. As samples were taken on a daily

Figure 4. (a) Frequency distribution of the monthly sea surface temperature measurements taken from the Reynolds-SST-v2 dataset at a transect of 145° W through the Southern Pacific Ocean; (b) the modes of anomalies of all the values above the mean (red) and those below the mean (blue). (Online version in colour.)

Figure 5. Frequency distribution of the daily temperature measurements at the Helgoland Roads long-term station separated into two time periods, one before 1989 and one after this. Inset gives the correlation coefficients between year and the percentage of occurrence of the different temperatures. It can be seen that despite warming the temperatures between 13 and 16°C have decreased in frequency. (Online version in colour.)

basis, we also have detected small winter blooms, which might be more difficult to detect in more remote areas which can only be accessed by ship. We do not know when the algae from the datasets were isolated, but as many ship-board expeditions have their main focus on the growing season, it could well be that this created a bias. Our Helgoland data suggest the lack of selective pressures leading to the need for optimal temperatures at temperatures with very low frequency of occurrence, and hence the relative paucity of species with an optimum at the in-between temperatures [27]. It remains to be seen whether the changes in phytoplankton community composition at Helgoland [28] can be linked to the changes in the relative frequency of certain temperatures (figure 5), or whether other factors such as for example the changes in nutrients are more important [17].

The independent database including a variety of taxa, yields a similar, albeit less clear, picture to the phytoplankton data from the Helgoland Roads. Even though recently three large meta-analysis type studies on the dependence of growth on temperature have been published [3,4,29], there is a remarkable lack of laboratory studies on the temperature dependence of organisms, particularly related to seasonally dynamic temperature regimes. In fact, we could not extract any data from the Boyd *et al.* [4] study as this study did not include any organisms from the North Sea. As a result, while our database may be representative for what is available in the literature, it is certainly not representative for what lives in the North Sea. Having said this, it is clear that very few temperature optima (figure 3) occur at 12°C, which is close to the minimum of the temperature frequency distribution of the Helgoland Roads dataset. The result is consistent with that stemming from the algal data from the Helgoland Roads. The independent dataset also includes longer lived organisms such as fish. The selective pressures on those organisms are different as they will typically experience both winter and summer, and this may result in a type of compromise in terms of selective pressure towards the annual mean temperature. Interestingly, however, many of the fish species seem to have optimal temperatures substantially higher than the annual mean temperature or even the average summer temperature. Also here, the explanation of Thomas *et al.* [3] regarding the shape of the response curve and the insurance against very high temperatures seems implausible. These high temperatures have never been measured in the southern North Sea in recent times. This could reflect a stronger selective pressure to higher temperatures in the evolutionary history of the species, or the fact that many of the nursery areas of juveniles included in our dataset are in the shallower Wadden Sea which experiences warmer summer temperatures [30]. Not only do different life stages, or age classes of many organisms react differently to temperature, different processes also show different temperature dependences. Hence, especially in more complex organisms with different thermal windows for growth,

reproduction and other processes [31] establishing optimal temperatures is difficult. Nevertheless, despite all these caveats, a bimodality of optimal temperatures was also apparent for this independent dataset. We did observe, though, that the distribution was more clearly bimodal in the Chen algal dataset which included only shorter lived (unicellular) organisms.

One of the big issues in current studies on reactions of organisms to temperature change are changes in species distributions (e.g. [32,33]). Interestingly, several of these studies reported that the velocity of climate change and seasonal shifts in ocean areas often deviate from simple pole-ward migrations and earlier springs/late autumns [7,34]. One of the potential explanations for this is that, even though the annual mean temperatures have increased as a consequence of global warming, this might not be the case for the frequency of observations for certain temperatures, and our analysis of the Helgoland Roads dataset helps demonstrate this: the incidence of temperatures between 6 and 12°C has increased, but that of 13–17°C has actually decreased. Thus, if species were to track their optimal temperatures, then some species might actually have to migrate in the direction of the equator to follow their optimal temperature [35], and this might reflect the approximately 20% of changes in distribution that were inconsistent with the predictions in the meta-analysis of Poloczanska *et al.* [7]. Obviously, temperature responses of organisms do not only depend on the optimum temperature, but also on the breadth of the thermal window [21,32], and it is unknown whether selective pressures acting to maximizing performance to the most often experienced temperature are independent from those acting to adjust thermal boundaries. Nevertheless, we argue that more robust projections of the impacts of warming on the distribution and productivity of marine poikilotherms can be derived by considering the relative frequency of temperatures, especially in temperate areas characterized by clear seasonal cycles.

Data accessibility. All data used in this study are accessible: the global algal data from the Chen [5] study in the supporting material of that publication, the collected data for our analysis in table S1, electronic supplementary material, and the data on the temperature and algal distributions around Helgoland from the Pangaea database (www.pangaea.de).

Authors' contributions. M.B. and K.H.W. conceived and designed the study. N.G. analysed the Helgoland Roads plankton data, N.T.S., M.A.P. and P.E.M.G. collected and analysed the temperature data. All authors collected data, drafted the manuscript and gave final approval for publication.

Competing interests. The authors declare no competing interests.

Funding. This study was supported by the German Federal Ministry for Education and Research (B.M.B.F.) [03F0609A, 03F0603C] to M.B. and K.H.W., the German Science Foundation, and by the Nippon Foundation, through POGO to N.T.S. and P.E.M.G.

Acknowledgements. We thank our colleagues Mirco Scharfe and Peter Lemke for helpful discussions and three anonymous reviewers for valuable comments and suggestions on how to improve the manuscript.

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