

The response of temperate aquatic ecosystems to global warming: novel insights from a multidisciplinary project

Ulrich Sommer, Rita Adrian, Barbara Bauer & Monika Winder

Marine Biology

International Journal on Life in Oceans and Coastal Waters

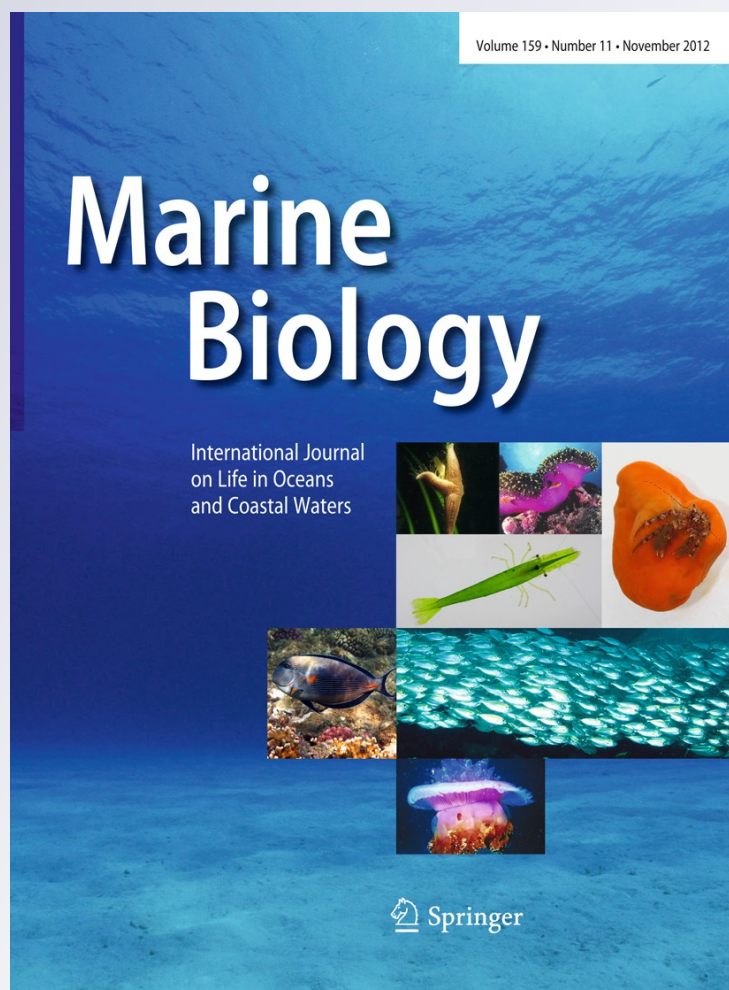
ISSN 0025-3162

Volume 159

Number 11

Mar Biol (2012) 159:2367-2377

DOI 10.1007/s00227-012-2085-4



Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

The response of temperate aquatic ecosystems to global warming: novel insights from a multidisciplinary project

Ulrich Sommer · Rita Adrian · Barbara Bauer ·
Monika Winder

Published online: 26 October 2012
© Springer-Verlag Berlin Heidelberg 2012

Abstract This article serves as an introduction to this special issue of *Marine Biology*, but also as a review of the key findings of the AQUASHIFT research program which is the source of the articles published in this issue. AQUASHIFT is an interdisciplinary research program targeted to analyze the response of temperate zone aquatic ecosystems (both marine and freshwater) to global warming. The main conclusions of AQUASHIFT relate to (a) shifts in geographic distribution, (b) shifts in seasonality, (c) temporal mismatch in food chains, (d) biomass responses to warming, (e) responses of body size, (f) harmful bloom intensity, (f), changes of biodiversity, and (g) the dependence of shifts to temperature changes during critical seasonal windows.

Keywords Aquatic ecosystems · Global change · Warming · Seas · Lakes · Rivers

Electronic supplementary material The online version of this article (doi:10.1007/s00227-012-2085-4) contains supplementary material, which is available to authorized users.

U. Sommer (✉) · B. Bauer
Helmholtz Centre for Ocean Research (GEOMAR),
DüsternbrookerWeg 20, 24105 Kiel, Germany
e-mail: usommer@geomar.de

B. Bauer
e-mail: bbauer@geomar.de

R. Adrian
Leibniz-Institute of Freshwater Ecology and Inland Fisheries
(IGB), 12587 Berlin, Germany
e-mail: adrian@igb-berlin.de

M. Winder
Department of Systems Ecology, University of Stockholm,
10691 Stockholm, Sweden
e-mail: mwinder@ecology.su.se

Introduction

Ecological responses to climate change are evident across systems and latitudes. Still, our ability to predict climatic effects at the ecosystem level is limited due to the complexity of direct and indirect interactions and the difficulty to account for possible compensations as well as phenotypic and (micro) evolutionary adaptations at all levels. Moreover, study programs covering diverse habitats, such as freshwater lakes, rivers and marine environments, and the whole range of responses at the genetic, physiological, and ecological level are rare.

Understanding the patterns and mechanisms of climate change impacts across ecosystems and different hierarchical levels was the focus of the DFG (Deutsche Forschungsgemeinschaft = German Research Council) funded priority program 1162 AQUASHIFT: “The impact of climate variability on aquatic ecosystems: Match and mismatch resulting from shifts in seasonality and distribution.” The AQUASHIFT projects have been distributed all over Germany covering marine and freshwater organisms and communities and investigating responses to climate warming at various hierarchical levels by using a broad range of methodological approaches. The research program lasted from 2005 to 2012 and is the subject of this special issue in *Marine Biology*. This special issue represents a series of focused summaries of the individual projects and selected highlights resulting from the projects. The only article outside the AQUASHIFT community is the review by Russell and Connell (2012) emphasizing the importance of spatial and temporal scale and interaction of climate warming with other environmental stressors.

The AQUASHIFT program contained projects devoted to three types of aquatic habitats including running waters, lakes, and marine environments. Focal functional groups

were benthos, plankton, and fish. The spectrum of methodology comprised:

- Single-species culture experiments
- microcosm experiments, that is, experiments with small, artificial communities assembled from cultures
- mesocosm experiments, that is, experiments with natural communities
- analysis of field data, in particular long-term studies
- modeling studies

We briefly summarize here some of the highlights of this project, while a detailed description of the individual studies can be found in the original publications of the AQUASHIFT program (Table 1), including the articles contained in this special issue of MARINE BIOLOGY. An extended version of Table 1 is available as an Electronic Supplement 1 and contains all publications resulting from the AQUASHIFT program. It can also be used as a “guide” to the scientific literature resulting from the AQUASHIFT program. We conclude with key results and with a discussion of how overarching projects across ecosystems contribute to our understanding on the effects of global change impacts.

The diversity of methods, focal ecosystems, subsystems and organisms, and research questions precludes a statistical meta-analysis across ecosystems, although results were combined and contrasted to identify general patterns if possible (e.g., Winder et al. 2012). Here, we highlight a selection of the most important findings from studies of this special issue and from AQUASHIFT articles published elsewhere. The corresponding authors of this volume and the principal investigators of the AQUASHIFT projects have agreed on the interpretation of the selected highlights.

Major findings

Range shifts

Poleward shifts in geographic ranges belong to the most expected and most often reported biological responses to climate warming (Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2002). A well-studied aquatic example is the northward range expansion of the invasive cyanobacterium *Cylindrospermopsis raciborskii* (Wiedner et al. 2007). Biogeographic studies within the AQUASHIFT consortium were focussed on dragonflies, snails, and ciliates. The dragonfly studies showed both direct range shifts as well as latitudinal shifts of life cycles, for example, in voltinism, which likely cause range shifts (Braune et al. 2008; Flenner et al. 2010; Söndgerath et al. 2012). A modeling study on the distribution of NW European freshwater pulmonate snails (Burgmer et al. 2007;

Cordellier et al. 2012; Pfenninger et al. 2011) predicted range shifts based on present-day temperature niches of snails. Areal range losses in the South are expected to be bigger than range gains in the North, even under unlimited dispersal. In an experimental study using European populations of the freshwater ciliate *Paramecium* (Krenek et al. 2012), it became obvious that all high-latitude *Paramecium* genotypes may benefit from increasing temperatures by an enhanced population growth, while only certain genotypes at the warm edge of their current geographic range (Europe) would be sensitive to climate warming. Similar to most bioclimatic envelope studies, evolutionary changes of the temperature niche were not accounted in these studies, but local adaptation to a tropical temperature regime were apparent in one *Paramecium* strain (Krenek et al. 2012). A further example for local temperature adaptation comes from a comparative study of populations of the sea grass *Zostera marina* originating from a latitudinal gradient from Norway to the Mediterranean Sea. They were exposed to a heat wave in a common garden experiment. Surprisingly, southern and northern populations lost shoots and showed damage due to heat to a similar extent (Bergmann et al. 2010; Winters et al. 2011). This was consistent with stress gene expression measurements during the acute heat stress. However, when the global gene expression profile was examined using next-generation RNAseq technology, southern population returned much faster to normal, control group gene expression patterns, thus revealed “transcriptomic resilience” (Franssen et al. 2011).

A comparison of the ecology of small, pelagic fish from German lakes (small *Coregonus* spp.) and the North and Baltic Seas (herring and sprat) indicates that these cold- or cool-water species are at risk under future warming because of suboptimal water temperatures. A substitution by trophodynamically equivalent, warm-water fish species (e.g., sardines and anchovies for herring and sprat) was not found, but cannot be excluded for the future. A somewhat contradicting result was found by Haslob et al. (2012) who predicted maximal population growth rates of sprat at moderate warming (4 °C above present), while 6 °C warming would have adverse effects. Besides continuous range shifts, invasions of non-native species change biogeographic distributions of species. Though primarily caused by man-made vectors, Weitere et al. (2009) demonstrated that the establishment of invasive species can be facilitated by warming.

Shifts in seasonality

Similar to range shifts, an earlier onset of biological spring events belongs to the most expected responses to global warming and has frequently been reported from aquatic ecosystems (Weyhenmeyer et al. 1999; Gerten and Adrian

Table 1 Scientific articles resulting from the AQUASHIFT program sorted by basic methodology and focal functional groups (“benthos” includes also insects with benthic larval stages)

Basic methodology	Focal functional group	Publications
Single-species experiments	Freshwater benthos	Viergutz et al. (2012)*
		Weitere et al. (2008)
	Freshwater plankton	Dziallas and Grossart (2011a)
		Dziallas and Grossart (2011b)
		Dziallas and Grossart (2012)*
		Dziallas et al. (2011)
	Marine plankton	Krenek et al. (2012)
		Dieckmann et al. (2012)*
		Holste and Peck (2006)
		Holste et al. (2009)
Microcosms	Fish	Isla et al. (2008)
	Freshwater benthos	Petereit et al. (2008)
		Hillebrand (2011)
	Freshwater plankton	Hillebrand et al. (2012)*
		Burgmer and Hillebrand (2011)
		Hillebrand et al. (2012)*
		Nomdedeu et al. (2012)*
		Norf and Weitere (2010)
		Viergutz et al. (2007)
	Mesocosms	Marine plankton
Freshwater benthos		Wohlers-Zöllner et al. (2011)
		Schlief and Mutz (2009)
Marine benthos		Bergmann et al. (2010)
		Franssen et al. (2011)
		Winters et al. (2011)
		Wohlers-Zöllner et al. (2011)
Freshwater plankton		Berger et al. (2007)
		Berger et al. (2010)
		Sebastian et al. (2012)*
	Winder et al. (2012)*	
	Marine plankton	Aberle et al. (2007)
		Aberle et al. (2012)*
		Engel et al. (2011)
		Hoppe et al. (2008)
		Klauschies et al. (2012)*
		Lewandowska et al. (2012)
Analysis of field data	Freshwater benthos	Sommer and Lengfellner (2008)
		Sommer and Lewandowska (2011)
	Freshwater plankton	Sommer et al. (2007)
		Sommer et al. (2012)*
		Winder et al. (2012)*
		Wohlers et al. (2009)
		Wohlers-Zöllner et al. (2012)*
		Burgmer et al. (2007)
		Cordellier et al. (2012)*
		Adrian et al. (2012)*
Huber et al. (2010)		
Huber et al. (2012)		
Hülsmann et al. (2012)		
Rolinski et al. (2007)		
Seebens et al. (2009)		

Table 1 continued

Basic methodology	Focal functional group	Publications
		Straille et al. (2010)
		Tirok and Gaedke (2007a, b)
		Wagner and Benndorf (2007)
		Wagner and Adrian (2011)
		Wagner et al. (2012a)*
	Marine plankton	Freund et al. (2012)*
		Lohmann and Wiltshire (2012)*
		Wiltshire et al. (2008)
		Wiltshire et al. (2010)
	Cross-system analysis	Wagner et al. (2012a)*
Analysis of field and experimental data	Freshwater plankton	Paul et al. (2012)
		Pinkhaus et al. (2007)
		Wagner and Benndorf (2007)
		Zeis et al. (2010)
	Fish	Mehner et al. (2012)*
	Across functional groups	Daufresne et al. (2009)
Modeling	Freshwater benthos	Braune et al. (2008)
		De SenerpontDomis et al. (2007)
		Flenner et al. (2010)
		Kupisch et al. (2012)
		Moenickes et al. (2012)*
		Richter et al. (2008)
	Freshwater plankton	Diehl (2007)
		Huber et al. (2008)
		Nomdedeu et al. (2012)*
		Peeters et al. (2007a)
		Peeters et al. (2007b)
		Schalau et al. (2008)
		Tirok and Gaedke (2006, 2007a, b)
	Marine plankton	Gaedke et al. (2010)
		Klauschies et al. (2012)*
	Fish	Haslob et al. (2012)*

* Articles in this volume of Marine Biology

2000; Wehenmeyer 2001; Edwards et al. 2002; Stenseth et al. 2002), often concentrating on the timing of plankton spring blooms. While a general trend toward earlier timing of seasonal blooms at warmer temperature was observed in marine and freshwater mesocosm experimental studies (Tirok and Gaedke 2007a, b; Winder et al. 2012), this pattern is not consistent across ecosystems. For example, retardation by warming (Wiltshire and Manly 2004) or the absence of a response (Wiltshire et al. 2008) was reported for the Helgoland time series, German Bight, North Sea. A further extension of the analysis (Lohmann and Wiltshire 2012) showed a rather complex pattern, influenced by the intrusion of clearer water from the Atlantic Ocean. Under clear-water conditions, warming accelerates the spring bloom, while under turbid conditions, growth rates of algae

become light-limited, and thus, temperature-enhanced grazing can delay the bloom. The fundamental importance of light for the timing of phytoplankton blooms has also been shown by the Baltic Sea mesocosm experiments (Sommer et al. 2012) and the limnetic mesocosm experiments in Brunsee (Berger et al. 2007, 2010). Both increasing light and warming were shown to advance the phytoplankton spring bloom (Klauschies et al. 2012; Winder et al. 2012).

While surface irradiance and turbidity dominate the effective light climate for phytoplankton growth in shallow water bodies, this role is taken by turbulent mixing and the seasonal shift between thermal winter mixing and summer stratification in deep systems (Peeters et al. 2007a, b). Here, the onset of stratification leads to a step-wise

increase in the light availability for phytoplankton (“light switch”). Thus, the seasonal advancement of thermal stratification under climate warming will also lead to an earlier increase in light availability. In freezing water bodies also ice melt can lead to a sudden change in light (Rolinski et al. 2007). The interplay between temperature, stratification, and light was also the focus of the limnetic mesocosm experiments on Brunsee (Sebastian et al. 2012), highlighting the role of thermal stratification as light switch.

Phenological shifts in zooplankton key species and fish larvae have also been demonstrated in field studies (Hülsmann et al. 2012; Wagner et al. 2012b). The spring increase in the grazing pressure by herbivorous zooplankton is not necessarily a numerical response to elevated food levels. It may be dominated by a temperature-induced increase in the activity of overwintering zooplankton “which are already there” (marine copepods: Wiltshire and Manly 2004; Sommer and Lewandowska 2011) or it may be a temperature-triggered population increase relatively independent of food conditions (*Daphnia* in Lake Constance: Schalaus et al. 2008; Straile et al. 2010). In the case of the Saldenbach reservoir, *Daphnia* phenological patterns were found to be independent of winter conditions (Hülsmann et al. 2012). Rather, they depended on warming during early stratification, which was also the critical period for hatching and early growth of fish (Wagner and Benndorf 2007; Wagner et al. 2012b).

Temperature effects on the timing of biological events can be quite variable between different groups of organisms, even if other factors (e.g., light) are kept constant or eliminated mathematically. While the spring bloom of phytoplankton was only advanced by ca. 1 day per °C of warming (Sommer et al. 2012), emergence of dragonflies was advanced by 6–7 days (Richter et al. 2008) and the hatching of copepod nauplii by 9 days per °C of warming (Sommer et al. 2007).

Mismatch in food chains

A temporal mismatch between supply and demand in food chains (Cushing 1990) has frequently been mentioned as a potentially adverse effect of climate change (Visser et al. 1998; Edwards and Richardson 2004; Durant et al. 2007; Thackeray et al. 2010). In fact, a mismatch between seasonal maxima of food availability and food demand can be expected if the seasonal development of both the producer and consumer respond differently to warming or if only one of both responds to temperature, while the other responds to light (Winder and Schindler 2004). Assuming that the phenology of consumers is evolutionarily tuned to the present-day seasonality of food availability, the expectation of an increasing risk of mismatch under a

changing climate seems highly plausible. Far reaching effects of a trophic mismatch can be expected when sensitive life cycle stages (nauplius larvae of copepods, fish larvae; Cushing 1990) starve because their food organisms bloom too early or too late. The subtitle of the AQUASHIFT program indicates a strong motivation to look out for such cases, both in the analysis of field data and in community level mesocosm experiments, but clear-cut cases of such a mismatch were pinpointed only rarely. A mismatch between copepod nauplii and phytoplankton reported from the first Baltic Sea mesocosm experiments under low light—high temperature and high light—low temperature combinations (Sommer et al. 2007) was not confirmed by the subsequent experiments (Sommer et al. 2012). Warming could even increase the synchrony between phytoplankton and copepod nauplii under high light conditions (Klauschies et al. 2012). Similarly, detailed field studies suggest the presence of highly efficient life cycle strategies in a freshwater copepod to tackle the phenology of its food source, that is, the phytoplankton spring bloom (Seebens et al. 2009). In the case of the phytoplankton–heterotrophic protist link, warming increased the temporal synchrony between both trophic levels as well (Aberle et al. 2012; Tirok and Gaedke 2007a).

The lake mesocosm experiments (Berger et al. 2010; Sebastian et al. 2012; Winder et al. 2012) did not report cases of mismatch. In contrast, increased (light-dependent) algal production and increased (temperature-dependent) *Daphnia* growth both speeded up successional dynamics as shown in coupled *Daphnia*–phytoplankton models (Diehl 2007). For the *Daphnia*–phytoplankton interaction, modeling studies suggest that a mismatch is only likely to occur under extreme warming and a strong reliance of *Daphnia* dynamics on recruitment from resting eggs, triggered by day length (De SenerpontDomis et al. 2007). In the Saldenbach Reservoir study, climate-driven phenology shifts of the participant species led to a switch between invertebrate and fish predation on the herbivorous zooplankton (Wagner and Benndorf 2007; Wagner et al. 2012b). Simulations based on field and laboratory data showed that an increase of environmental temperature has the potential to cause a decoupling of the life cycle of *Gammarus pulex* and the availability of its food resource leaf litter in temperate streams (Moenickes et al. 2012; Kupisch et al. 2012).

Changes in biomass

The metabolic theory of ecology (Allen et al. 2002; Brown et al. 2004) predicts that at a constant supply rate of the limiting basal resource (light or nutrient), biomass declines with increasing temperature because of increasing metabolic demands per unit biomass. This effect is enhanced at the primary producer level if heterotrophic processes are

more strongly accelerated by warming than photosynthesis, as shown by an overview of Q_{10} -data in Sommer and Lengfellner (2008). This prediction was supported by the mesocosm experiments by Müren et al. (2005) and O'Connor et al. (2009). Within AQUASHIFT, the Baltic Sea mesocosm experiments (Klauschies et al. 2012; Sommer et al. 2012; Winder et al. 2012), the microcosm experiments of Burgmer and Hillebrand (2011), and modeling Lake Constance phytoplankton (Tirok and Gaedke 2007b) also showed a declining phytoplankton biomass, while the lake mesocosms did not show a decline of phytoplankton biomass under warmer conditions (Sebastian et al. 2012; Winder et al. 2012). However, both freshwater and marine mesocosm experiments agreed in demonstrating a dominant role of light for the determination of bloom biomass (Klauschies et al. 2012). Climate-induced changes in thermal stratification regime rather than direct temperature effects positively affected cyanobacteria biomass during summer (Wagner and Adrian 2009b). Zooplankton species with high thermal tolerances such as thermophilic cyclopid copepods became more abundant (Wagner and Adrian 2011).

For freshwater benthos, the decline in biomass was tested at the level of macrofauna populations and on the level of open biofilm communities in mesocosm experiments. The clam *Corbicula fluminea* showed pronounced decreases in the individual body mass with temperature increase (Weitere et al. 2009). Also the total biomass of riverine benthic ciliate communities showed significant decreases with warming in summer as hypothesized (Norf and Weitere 2010). However, biomass increases with warming were measured in winter.

Changes of body size

Based on the data partially obtained from the AQUASHIFT projects, Daufresne et al. (2009) claimed that a reduction in body size should be considered the third universal response to global warming after shifts in range and seasonality. While the generality of this claim is still under debate (Gardner et al. 2011), supporting evidence is cumulating from mesocosm experiments (e.g., Yvon-Durocher et al. 2011), analyses of long-term data series (e.g., Winder et al. 2009), and even from the paleontological record (e.g., Finkel et al. 2007). Shifts toward smaller body size may be brought about by species replacements, increase in the share of juveniles, and size changes at defined developmental stages, for example, maturity. The AQUASHIFT projects found examples for shifts between differently sized species in phytoplankton (Klauschies et al. 2012; Sommer et al. 2012) and for a reduced size at maturity in zooplankton (Isla et al. 2008; Sebastian et al. 2012). Changes in age structure, however, were highly variable

and depended on sampling time, because experimental populations were not in demographic equilibrium (Sebastian et al. 2012).

In rivers, where benthic filter feeders are able to control plankton passing by, episodic temperature changes can significantly alter plankton size structure. Mesocosm experiments by Viergutz et al. (2007) showed that summer heat waves enhance nanoplankton (<20 μm) abundances due to differential temperature responses of the plankton growth rates and the grazing rates by filter feeders. The increased abundance of nanoplankton leads to an increased grazing pressure on bacteria (usually <2 μm) and thus to shifts in plankton size structure (Weitere et al. 2008).

Harmful blooms

Warming is often expected to enhance harmful algal blooms because the prototypes of such blooms, dinoflagellate red tides in the sea, and cyanobacterial blooms in lakes are favored under stratified, warm summer conditions. Warming increases the strength of thermal stratification and thereby the separation between a light-rich and nutrient-poor surface layer and a light-poor but nutrient-rich layer below, a separation which provides a selective advantage for large, vertically motile phytoplankton. While no AQUASHIFT project dealt with red tides, an increased tendency toward cyanobacterial blooms during summers with elevated stability of vertical stratification and phosphorus richness was shown for Müggelsee (Wagner and Adrian 2009a, b). Contrary to stratification effects, direct temperature effects were unimportant in promoting dominance of cyanobacteria. Some cyanobacterial species (*Anabaena* sp.) benefitted directly from stable water column conditions, whereas for example, *Planktothrix* sp. took advantage of stratification-induced internal nutrient loading (Huber et al. 2012, Wagner and Adrian 2011). Within a single cyanobacterial taxon (*Microcystis aeruginosa*), warming favors toxic strains (Dziallas and Grossart 2011b) but the toxicity is modulated by the interaction with associated bacterial communities, which themselves respond to temperature changes and other abiotic variables (Dziallas et al. 2011; Dziallas and Grossart 2012).

Changes in biodiversity

Model experiments with phytoplankton and periphyton microcosms showed faster competitive exclusion at higher temperatures (Burgmer and Hillebrand 2011, Hillebrand 2011), an effect that could be reversed by the presence of herbivores (Burgmer and Hillebrand 2011). Independent of the response of species richness, species replacements in time become faster under warmer temperatures (Burgmer

and Hillebrand 2011; Hillebrand et al. 2010, 2012). Thus, temporal species turnover is enhanced and species persistence reduced in warmed communities, both plankton and benthos. These shifts in biodiversity have consequences for functional performance of the communities. Lower richness translates into lower resource use efficiency (biomass production per unit resource) and the accelerated species replacements increased the temporal variability of biomass production.

Genetic diversity might also be influenced by warming. In cold-winter years, genetic diversity of *Daphnia* increased significantly during spring, presumably due to a higher contribution of emergence from resting eggs to population growth (Hülsmann et al. 2012). In addition, the genetic composition of the population differed substantially between cold- and warm winter years (Zeis et al. 2010). This will affect physiological capabilities of the spring population to cope with high temperature and/or low oxygen (Pinkhaus et al. 2007; Paul et al. 2012), life history strategies, and potentially also the inducibility of defense strategies against predators (Hülsmann and Wagner 2007).

Changes in biogeochemical cycles

The effect of changed community composition on the dynamics of biogeochemical cycles was studied in the Baltic Sea mesocosms. While phytoplankton production decreased or only slightly increased with warming (Lewandowska et al. 2012), bacterial production and respiration increased strongly with warming (Hoppe et al. 2008). As a result, particulate organic carbon and particulate organic phosphorus accumulated more strongly under colder conditions, while dissolved organic carbon accumulated more strongly under warmer conditions (Wohlers-Zöllner et al. 2012). The effect on gas exchange with the atmosphere consists of a reduced drawdown of DIC in the water and, therefore, a reduced CO₂ uptake from the atmosphere and thus a weakening of the biological carbon pump (Wohlers et al. 2009).

Dependence of warming responses on critical time windows

Many biological responses cannot be explained by an increase in long-term average temperature but by critical, sometimes quite short periods during the annual climatic and hydrographic cycle (Adrian et al. 2012). The conditions during such critical time windows might have consequences in biomass and compositional patterns several months later. It has, for example, been shown for Bautzen Reservoir that May temperatures >14 °C result in a summer depression of the dominant herbivorous zooplankton *Daphnia galeata*, because only under such conditions, the

mid-season minimum of phytoplankton biomass (“clear-water phase”) coincides with maximal predation by the predatory zooplankton *Leptodora kindtii* and juvenile perch (Wagner and Benndorf 2007). Similarly, interannual variability of lake summer crustacean plankton responded more strongly to temperatures around the clear-water phase than to summer temperatures (Huber et al. 2010). However, such critical time windows often cannot be defined by certain calendar months or weeks but by the hydrographic cycle or important cardinal events such as the timing of ice-off or the timing of the clear-water phase (Wagner and Adrian 2009a). To account for such dependencies and to provide a framework for comparison across ecosystems, Wagner et al. (2012a) propose a classification scheme which combines hydrographically defined periods of the year with a cold–warm classification based on long-term temperature records.

Conclusions

The AQUASHIFT projects reported in part quite complex response patterns to climate warming which go beyond the easily expected ones, such as poleward distribution changes, earlier start of the growth season, and increased metabolic rates. Present-day biogeography, latitudinal clines in phenology, and physiological temperature response curves are necessary ingredients to understand and predict the future state of ecosystems, but they are not sufficient. Interactions of temperature with other features of the physical environment and biotic interactions may overrule direct temperature effects. Thermal stratification and its consequences for light and nutrient supply in the surface layer of stratified lakes and oceans is the most prominent indirect physical effect of warming (Peeters et al. 2007a, b). In shallow water bodies, water level changes due to enhanced evaporation and their consequences on the sediment–water nutrient flux have to be considered.

Biotic interactions as modulators of climate change effects have been reported from several AQUASHIFT projects (Burgmer and Hillebrand 2011; Dziallas and Grossart 2012; Gaedke et al. 2010; Klauschies et al. 2012; Sommer and Lewandowska 2011; Wagner and Benndorf 2007; Wagner et al. 2012b) as well as from terrestrial ecosystems (Suttle et al. 2007). For two-link food chains, it is easy to predict an increasing disadvantage for the prey, if the predator profits more strongly from warming than the prey. Predictions become already less straightforward for tritrophic interactions with an intermediate consumer, which competes with the predator for prey but is also consumed by the predator (e.g., phytoplankton—heterotrophic protists—crustacean zooplankton, Aberle et al. 2012) and will be still more difficult for complete food

webs. Responses might be highly context-dependent, and it remains a challenge for future research to identify when and under which circumstances, trophic and non-trophic interactions act as shock absorbers or amplifiers of climate impacts.

Acknowledgments We gratefully acknowledge funding of the priority program AQUASHIFT by the DFG. The content of the manuscript has been checked by all co-authors of this special issue and all PIs of the AQUASHIFT projects.

References

- Aberle N, Lengfellner K, Sommer U (2007) Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming. *Oecologia* 150:668–681
- Aberle N, Bauer B, Lewandowska A, Gaedke U, Sommer U (2012) Warming induces shifts in micro zooplankton phenology and reduces time-lags between phytoplankton and protozoan production. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1947-0
- Adrian R, Gerten D, Huber V, Wagner C, Schmidt S (2012) Windows of change: temporal scale of analysis is decisive to detect ecosystem responses to climate change. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1938-1
- Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–1548
- Berger SA, Diehl S, Stibor H, Trommer G, Ruhlenstroth M, Jäger C, Striebel M (2007) Water temperature and mixing depth affect timing and intensity of events during spring succession of the plankton. *Oecologia* 150:643–654
- Berger SA, Diehl S, Stibor H, Trommer G, Ruhlenstroth M (2010) Water temperature and stratification depth independently shift cardinal events during plankton spring succession. *Glob Change Biol* 7:1954–1965
- Bergmann N, Winters G, Rauch G, Eizaguirre C, Gu J, Nelle P, Fricke B, Reusch TBH (2010) Population-specificity of heat stress gene induction in northern and southern eelgrass *Zostera marina* populations under simulated global warming. *Mol Ecol* 19:2870–2883
- Braune E, Richter O, Söndgerath D, Suhling F (2008) Voltinism flexibility of a riverine dragonfly along thermal gradients. *Glob Change Biol* 14:470–482
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:771–1789
- Burgmer T, Hillebrand H (2011) Temperature mean and variance alter phytoplankton biomass and biodiversity in a long-term microcosm experiment. *Oikos* 120:920–933
- Burgmer T, Hillebrand H, Pfenninger M (2007) Effects of climate-driven temperature changes on the diversity of freshwater macro invertebrates. *Oecologia* 151:91–103
- Cordellier M, Pfenninger A, Streit B, Pfenninger M (2012) Assessing the effects of climate change on the distribution of pulmonate freshwater snail biodiversity. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1894-9
- Cushing DH (1990) Plankton production and year-class strength in fish populations—an update of the match-mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *Proc Nat Acad Sci* 106:12788–12793
- De SenerpontDomis LN, Mooij WM, Hülsmann S, van Nes EH, Scheffer M (2007) Can overwintering versus diapausing strategy in *Daphnia* determine match-mismatch events in zooplankton-algae interactions? *Oecologia* 150:682–698
- Dieckmann ABS, Clemmesen C, St John MA, Paulsen M, Peck MY (2012) Environmental cues and constraints affecting the seasonality of dominant calanoid copepods in brackish, coastal waters: a case study of *Acartia*, *Temora* and *Eurytemora* species in the south-west Baltic. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1955-0
- Diehl S (2007) Paradoxes of enrichment: effects of increased light versus nutrient supply on pelagic producer-grazer systems. *Am Nat* 169:E171–E191
- Durant JM, Hjermandt DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res* 33:271–283
- Dziallas C, Grossart H-P (2011a) Temperature and biotic factors influence bacterial communities associated with *Microcystis* sp. (cyanobacteria). *Environ Microbiol* 13:1632–1641
- Dziallas C, Grossart H-P (2011b) Increasing oxygen radicals and water temperature select for toxic *Microcystis* sp. *PLoS One* 6(9):e25569
- Dziallas C, Grossart HP (2012) Microbial interactions with the cyanobacterium *Microcystis aeruginosa* and their dependence on temperature. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1927-4
- Dziallas C, Pinnow S, Grossart HP (2011) Detection and quantification of toxigenic and toxic cyanobacterial cells using recognition of individual gens fluorescence in situ hybridization (RING-FISH) and flow cytometry. *Limnol Oceanogr Methods* 9(2011):67–73
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Edwards M, Beaugrand G, Reid PC, Rowden A, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar Ecol Progr Ser* 239:1–10
- Engel A, Händel N, Wohlers J, Lunau M, Grossart HP, Sommer U, Riebesell U (2011) Effects of sea surface warming on the production and composition of dissolved organic matter during phytoplankton blooms: results from a mesocosm study. *J Plankt Res* 33:357–372
- Finkel ZV, Sebbo J, Feist-Burkhardt S et al (2007) A universal driver of macroevolutionary change in the size of marine phytoplankton over the Cenozoic. *Proc Nat Acad Sci* 104:20416–20420
- Flenner I, Richter O, Suhling F (2010) Latitudinal variations in development in dragonfly populations and effects of rising temperatures. *Freshw Biol* 55:397–410
- Franssen SU, Gu J, Bergmann N, Winters G, Klostermeier UC, Rosenstiel P, Bornberg-Bauer E, Reusch TBH (2011) Transcriptional resilience to global warming in the seagrass *Zostera marina*, a marine foundation species. *Proc Nat Acad Sci* 108:19276–19281
- Freund JA, Grüner N, Brüse S, Wiltshire KH (2012) Changes in the phytoplankton community at Helgoland, North Sea: lessons from single spot time series analyses. *Mar Biol* (in this issue). doi:10.1007/s00227-012-2013-7
- Gaedke U, Ruhlenstroth-Bauer M, Wiegand I, Tirok K, Aberle N, Breithaupt P, Lengfellner K, Wohlers J, Sommer U (2010) Biotic interactions may overrule direct climate effects on spring phytoplankton dynamics. *Glob Change Biol* 16:1122
- Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third universal response to warming? *Trends Ecol Evol* 26:285–291
- Gerten D, Adrian R (2000) Climate driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnol Oceanogr* 45:1058–1066

- Haslob H, Hauss H, Peterleit C, Clemmesen C, Krau G, Peck MA (2012) Temperature effects on vital rates of different life stages and implications for population growth of Baltic sprat. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1933-6](https://doi.org/10.1007/s00227-012-1933-6)
- Hillebrand H (2011) Temperature mediates competitive exclusion and diversity in benthic microalgae under different N:P stoichiometry. *Ecol Res* 26:533–539
- Hillebrand H, Soininen J, Snoeijs P (2010) Warming leads to higher species turnover in a coastal ecosystem. *Glob Change Biol* 16:1181–1193
- Hillebrand H, Burgmer T, Biermann E (2012) Running to stand still: temperature effects on species richness, species turnover, and functional community dynamics. *Mar Biol* (in this issue). doi:[10.1007/s00227-011-1827-z](https://doi.org/10.1007/s00227-011-1827-z)
- Holste L, Peck MA (2006) The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. *Mar Biol* 148:1061–1070
- Holste L, St John MA, Peck MA (2009) The effects of temperature and salinity on reproductive success of *Temora longicornis* in the Baltic Sea: a copepod coping with a tough situation. *Mar Biol* 156:527–540
- Hoppe HG, Breithaupt P, Walther K, Koppe R, Bleck S, Sommer U, Jürgens K (2008) Climate warming in winter affects the coupling between phytoplankton and bacteria during the spring bloom. *Aquat Microbial Ecol* 51:105–115
- Huber V, Adrian R, Gerten D (2008) Phytoplankton response to climate warming modified by trophic state. *Limnol Oceanogr* 53:1–13
- Huber V, Adrian R, Gerten D (2010) A matter of timing: heat wave impact on crustacean zooplankton. *Freshw Biol* 55:1769–1779
- Huber V, Wagner C, Gerten D, Adrian R (2012) To bloom or not to bloom: contrasting responses of cyanobacteria to recent heat waves explained by critical thresholds of abiotic drivers. *Oecologia* 169:245–256
- Hülsmann S, Wagner A (2007) Multiple defence strategies of *Daphnia galeata* against predation in a weakly stratified reservoir. *Hydrobiologia* 594:187–199
- Hülsmann S, Wagner A, Pitsch M, Horn W, Paul RJ, Rother A, Zeis B (2012) Effects of winter conditions on *Daphnia* dynamics and genetic diversity in a dimictic temperate reservoir. *Freshw Biol* 57:1458
- Isla A, Lengfellner K, Sommer U (2008) Physiological response of the copepod *Pseudocalanus* sp. in the Baltic Sea at different thermal scenarios. *Glob Change Biol* 14:895–906
- Klauschieh T, Bauer B, Aberle N, Sommer U, Gaedke U (2012) Climate change effects on phytoplankton depend on cell size and food web structure. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1904-y](https://doi.org/10.1007/s00227-012-1904-y)
- Krenek S, Petzoldt T, Berendonk TU (2012) Coping with temperature at the warm edge—patterns of thermal adaptation in the microbial eukaryote *Paramecium caudatum*. *PLoS One* 7:e30598
- Kupisch M, Moenickes S, Schlieff J, Frassl M, Richter O (2012). Temperature dependent consumer-resource dynamics: a coupled structured model for *Gammarus pulex* (L.) and leaf litter. *Ecol Model*. doi:[10.1016/j.ecolmodel.2012.07.037](https://doi.org/10.1016/j.ecolmodel.2012.07.037)
- Lewandowska A, Breithaupt P, Hillebrand H, Hoppe HG, Jürgens K, Sommer U (2012) Responses of primary productivity to increased temperature and phytoplankton diversity. *J Sea Res*. doi:[10.1016/j.seares.2011.10.003](https://doi.org/10.1016/j.seares.2011.10.003)
- Lohmann G, Wiltshire KH (2012) Winter atmospheric circulation signature for the timing of the spring bloom of diatoms in the North Sea. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1993-7](https://doi.org/10.1007/s00227-012-1993-7)
- Mehner T, Busch S, Clemmesen C, Helland IP, Hölker F, Ohlberger J, Peck MA (2012) Ecological commonalities among pelagic fishes: comparison of freshwater ciscoes and marine herring and sprat. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1922-9](https://doi.org/10.1007/s00227-012-1922-9)
- Moenickes S, Frassl M, Schlieff J, Mutz M, Suhling F, Richter O (2012) Temporal patterns of populations in a warming world: a modelling framework. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1996-4](https://doi.org/10.1007/s00227-012-1996-4)
- Müren U, Berglund J, Samuelsson K, Andersson A (2005) Potential effects of elevated sea-water temperature on pelagic food webs. *Hydrobiologia* 545:153–166
- Nomdedeu MM, Willen C, Schieffer A, Arndt H (2012) Temperature-dependent ranges of coexistence in a model of a two-prey-one-predator microbial food web. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1966-x](https://doi.org/10.1007/s00227-012-1966-x)
- Norf H, Weitere M (2010) Resource quantity and seasonal background alter warming effects on communities of biofilm ciliates. *FEMS Microb Ecol* 74:361–370
- O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. *PLoS Biol* 7:e1000178
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Paul RJ, Mertenskötter A, Pinkhaus O, Pirow R, Gigengack U, Buchen I, Koch M, Horn W, Zeis B (2012) Seasonal and interannual changes in water temperature affect the genetic structure of a *Daphnia* assemblage (*D. longispina* complex) through genotype-specific thermal tolerances. *Limnol Oceanogr* 57:619–633
- Peeters F, Straile D, Lorke A, Livingstone DM (2007a) Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Glob Change Biol* 13:1898–1909
- Peeters F, Straile D, Lorke A, Ollinger D (2007b) Turbulent mixing and phytoplankton spring bloom development in a deep lake. *Limnol Oceanogr* 52:286–298
- Peterleit C, Haslob H, Kraus G, Clemmesen C (2008) The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae. *Mar Biol* 154:295–306
- Pfenninger M, Salinger M, Haun T, Feldmeyer B (2011) Factors and processes shaping the population structure and distribution of genetic variation across the species range of the freshwater snail *Radix balthica* (Pulmonata, Basommatophora). *BMC Evol Biol* 11:135
- Pinkhaus O, Schwerin S, Pirow R, Zeis B, Buchen I, Gigengack U, Koch M, Horn W, Paul RJ (2007) Temporal environmental change, clonal physiology and the genetic structure of a *Daphnia* assemblage (*D. galeata-hyalina* hybrid species complex). *Freshw Biol* 52:1537–1554
- Richter O, Suhling F, Müller O, Kern D (2008) A model for predicting the emergence of dragonflies in a changing climate. *Freshw Biol* 53:1868–1880
- Rolinski S, Horn H, Petzoldt T, Paul L (2007) Identifying cardinal dates in phytoplankton time series to enable the analysis of long-term trends. *Oecologia* 153:997–1008
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Russell BD, Connell SD (2012) Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. *Mar Biol* (in this issue). doi:[10.1007/s00227-011-1863-8](https://doi.org/10.1007/s00227-011-1863-8)
- Schalau K, Rinke K, Straile D, Peeters F (2008) Temperature is the key factor explaining interannual variability of *Daphnia* development in spring—a modelling study. *Oecologia* 157:531–543
- Schlieff J, Mutz M (2009) Effect of sudden flow reduction on the decomposition of alder leaves (*Alnus glutinosa* [L.] Gaertn.) in a temperate lowland stream: a mesocosm study. *Hydrobiologia* 624:205–217

- Sebastian P, Stibor H, Berger SA, Diehl S (2012) Effects of water temperature and mixed layer depth on zooplankton body size. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1931-8
- Seebens H, Einsle U, Straile D (2009) Copepod life cycle adaptations and success in response to phytoplankton spring bloom phenology. *Glob Change Biol* 15:1394–1404
- Sommer U, Lengfellner K (2008) Climate change and the timing, magnitude and composition of the phytoplankton spring bloom. *Glob Change Biol* 14:1199–1208
- Sommer U, Lewandowska A (2011) Climate change and the phytoplankton spring bloom: warming and overwintering zooplankton have similar effects on phytoplankton. *Glob Change Biol* 17:154–162
- Sommer U, Aberle N, Engel A, Hansen T, Lengfellner K, Sandow M, Wohlers J, Zöllner U, Riebesell U (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia* 150:655–667
- Sommer U, Aberle N, Lengfellner K, Lewandowska A (2012) The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1897-6
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Straile D, Kerimoglu O, Peeters F, Jochimsen MC, Kümmerlin R, Rinke K, Rothhaupt KO (2010) Effects of a half a millennium winter on a deep lake—a shape of things to come? *Glob Change Biol* 10:2844–2856
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science* 315:604–642
- Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob Change Biol* 16:3304–3313
- Tirok K, Gaedke U (2006) Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *J Plankton Res* 28:361–373
- Tirok K, Gaedke U (2007a) a) Regulation of planktonic ciliate dynamics and functional composition during spring in Lake Constance. *Aquat Microb Ecol* 49:87–100
- Tirok K, Gaedke U (2007b) The effect of irradiance, vertical mixing and temperature on spring phytoplankton dynamics under climate change—long-term observations and models. *Oecologia* 150:625–642
- Viergutz C, Kathol M, Norf H, Arndt H, Weitere M (2007) Control of microbial communities by the macrofauna: a sensitive interaction in the context of extreme summer temperatures? *Oecologia* 151:115–124
- Viergutz C, Linn C, Weitere M (2012) Intra- and interannual variability surpasses direct temperature effects on the clearance rates of the invasive clam *Corbicula fluminea*. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1902-0
- Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc Lond Ser B* 265:1867–1870
- Wagner C, Adrian R (2009a) Exploring lake ecosystems: hierarchy responses to long-term change? *Glob Change Biol* 15:1104–1115
- Wagner C, Adrian R (2009b) Cyanobacteria dominance—quantifying the effects of climate change. *Limnol Oceanogr* 54:2460–2468
- Wagner C, Adrian R (2011) Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. *Freshw Biol* 56:1949–1961
- Wagner A, Benndorf J (2007) Climate-driven warming during spring destabilises a *Daphnia* population: a mechanistic food web approach. *Oecologia* 151:351–364
- Wagner A, Hülsmann S, Paul L, Paul RJ, Petzoldt T, Sachse R, Schiller T, Zeis B, Benndorf J, Berendonk TU (2012a) A phenomenological approach shows a high coherence of warming patterns in dimictic aquatic systems across latitude. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1934-5
- Wagner A, Hülsmann S, Horn W, Schiller T, Schulze T, Volkmann S, Benndorf J (2012b) Climate warming stabilizes a planktonic keystone herbivore by changes in trophic match. *Freshw Biol*. doi:10.1111/j.1365-2427.2012.02809.x
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:89–395
- Weyhenmeyer GA, Blenckner T, Pettersson K (1999) Changes of the plankton spring outburst related to the North Atlantic oscillation. *Limnol Oceanogr* 44:1788–1792
- Wehenmeyer GA (2001) Warmer winters: are planktonic populations in Sweden's largest lake affected? *Ambio* 30:565–571
- Weitere M, Dahlmann J, Viergutz C, Arndt H (2008) Differential grazer-mediated effects of high summer temperatures on pico- and nanoplankton communities. *Limnol Oceanogr* 53:477–486
- Weitere M, Vohmann A, Schulz N, Linn C, Dietrich D, Arndt H (2009) Linking environmental warming to the fitness of the invasive clam *Corbicula fluminea*. *Glob Change Biol* 15:2838–2851
- Wiedner C, Rucker J, Brüggemann R, Nixdorf B (2007) Climate change affects timing and size of populations of an invasive cyanobacterium in temperate regions. *Oecologia* 152:473–484
- Wiltshire KH, Manly BFJ (2004) The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Mar Res* 58:269–273
- Wiltshire KH, Malzahn AM, Wirtz K, Greve W, Janisch S, Mangelsdorf P, Manly BFJ, Boersma M (2008) Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnol Oceanogr* 53:1294–1302
- Wiltshire KH, Kraberg A, Bartsch I, Boersma M, Franke HD, Freund J, Gebühr C, Gerds G, Stockmann K, Wichels A (2010) Helgoland Roads: 45 years of change. *Estuaries Coasts* 33:295–310
- Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in a lake ecosystem. *Ecology* 85:2100–2106
- Winder M, Reuter JE, Schladow SG (2009) Lake warming favours small-sized planktonic diatom species. *Proc R Soc Lond B* 276:427–435
- Winder M, Berger SA, Lewandowska A, Aberle N, Lengfellner K, Sommer U, Diehl S (2012) Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. *Mar Biol* (in this issue). doi:10.1007/s00227-012-1964-z
- Winters G, Nelle P, Fricke B, Rauch G, Reusch TBH (2011) Effects of a simulated heat wave on photophysiology and gene expression of high- and low-latitude populations of *Zostera marina*. *Mar Ecol Progr Ser* 435:83–95
- Wohlers J, Engel A, Zöllner E, Breithaupt P, Jürgens K, Hoppe HG, Sommer U, Riebesell U (2009) Changes in biogenic carbon flow in response to sea surface warming. *Proc Nat Acad Sci* 106:7067–7072

- Wohlers-Zöllner J, Breithaupt P, Walther K, Jürgens K, Riebesell U (2011) Temperature and nutrient stoichiometry interactively modulate organic matter cycling in a pelagic algal–bacterial community. *Limnol Oceanogr* 56:599–610
- Wohlers-Zöllner J, Biermann A, Engel A, Dörge P, Lewandowska AM, Scheibner Mv, Riebesell U (2012) Effects of rising temperature on pelagic biogeochemistry in mesocosm systems: a comparative analysis of the AQUASHIFT Kiel experiments. *Mar Biol* (in this issue). doi:[10.1007/s00227-012-1958-x](https://doi.org/10.1007/s00227-012-1958-x)
- Yvon-Durocher G, Montoya JM, Trimmer M, Woodward G (2011) Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Glob Change Biol* 17:1681–1694
- Zeis B, Horn W, Gigengack U, Koch M, Paul RJ (2010) A major shift in *Daphnia* genetic structure after the first ice-free winter in a German reservoir. *Freshwat Biol* 55:2296–2304