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Warming Alters the Size Spectrum and Shifts the Distribution of Biomass in Aquatic Ecosystems

Gabriel Yvon-Durocher, Jose Maria Montoya, Mark Trimmer, Guy Woodward

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Warming Alters the Size Spectrum and Shifts the Distribution of Biomass in Aquatic Ecosystems



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Complete List of Authors:	Yvon-Durocher, Gabriel; Queen Mary University of London, School of Biological and Chemical Sciences Montoya, Jose; 2 Institute of Marine Sciences Trimmer, Mark; Queen Mary University of London, School of Biological and Chemical Sciences Woodward, Guy; Queen Mary University of London, School of Biological and Chemical Sciences
Keywords:	Global Warming, Body Size, Size Spectra, Mass-abundance relationships, Biomass
Abstract:	<p>Body size is one of the key determinants of community structure. The relationship between abundance and body size can explain how community biomass is partitioned among the biota of an ecosystem. We used an aquatic mesocosm experiment to determine how warming of $\sim 4^{\circ}\text{C}$ would affect the body size, biomass and taxonomic structure of planktonic communities. We found that warming increased the steepness of the slope of the community size spectrum, primarily by altering the phytoplankton size spectrum. Warming also reduced the mean and maximum body size of phytoplankton by approximately one order of magnitude. The observed shifts in phytoplankton size structure were reflected in large shifts in phytoplankton community composition, though zooplankton taxonomic composition was unaffected by warming. Furthermore, warming reduced community biomass and total phytoplankton biomass, although zooplankton biomass was unaffected. This resulted in an increase in the zooplankton to phytoplankton biomass ratio in the warmed mesocosms, which could be explained by faster turnover within the phytoplankton assemblages. Overall, warming shifted the distribution of phytoplankton body size towards smaller individuals with rapid turnover and low standing biomass, resulting in a reorganisation of the biomass structure of the food webs. These results indicate future environmental warming may have profound effects on the structure of aquatic communities.</p>

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3 29 **ABSTRACT**
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5 30 Body size is one of the key determinants of community structure. The relationship
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7 31 between abundance and body size can explain how community biomass is partitioned
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10 32 among the biota of an ecosystem. We used an aquatic mesocosm experiment to determine
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12 33 how warming of ~4°C would affect the body size, biomass and taxonomic structure of
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14 34 planktonic communities. We found that warming increased the steepness of the slope of
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17 35 the community size spectrum, primarily by altering the phytoplankton size spectrum.
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19 36 Warming also reduced the mean and maximum body size of phytoplankton by
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21 37 approximately one order of magnitude. The observed shifts in phytoplankton size
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24 38 structure were reflected in large shifts in phytoplankton community composition, though
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26 39 zooplankton taxonomic composition was unaffected by warming. Furthermore, warming
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29 40 reduced community biomass and total phytoplankton biomass, although zooplankton
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31 41 biomass was unaffected. This resulted in an increase in the zooplankton to phytoplankton
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33 42 biomass ratio in the warmed mesocosms, which could be explained by faster turnover
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36 43 within the phytoplankton assemblages. Overall, warming shifted the distribution of
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38 44 phytoplankton body size towards smaller individuals with rapid turnover and low
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40 45 standing biomass, resulting in a reorganisation of the biomass structure of the food webs.
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45 47 structure of aquatic communities.
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48 INTRODUCTION

49 Body size can play a key role in determining community structure (Elton 1927, Lindeman
50 1942, Damuth 1981, Peters 1983, Brown *et al.* 2004, Petchey *et al.* 2008) because it
51 influences ecological processes across multiple levels of organisation; from individuals
52 (Peters 1983, Brown *et al.* 2004), and their interactions (Emmerson & Raffaelli 2004,
53 Berlow *et al.* 2009), to populations (Damuth 1981, Jennings & Mackinson 2003, Reuman
54 *et al.* 2008), communities and ecosystems (Petchey *et al.* 2008). Understanding how this
55 “size-structure” might then be altered by human impacts is an important contemporary
56 challenge for ecology given recent concerns over accelerating rates of biodiversity loss
57 and climate change (Pimm 2009, Montoya & Raffaelli 2010).

58 The relationship between abundance and body size (equal to body mass; terms are
59 interchangeable hereafter) is potentially a very powerful descriptor of how energy and
60 nutrients are partitioned within the biomass of an ecosystem (White *et al.* 2007). It is also
61 an emergent property of size structure at lower levels of organisation: for example, body
62 size can be important for determining the presence and strength of trophic interactions
63 between individuals because it constrains their metabolic requirements (Berlow *et al.*
64 2009). The trophic architecture of the community determines the amount of energy
65 available to an organism of a given size, and therefore its population abundance (Damuth
66 1981). The relationship between abundance and body mass therefore integrates size-
67 structure over many levels of organisation.

68 Since the pioneering work of Sheldon *et al.* (1972) the relationship between
69 abundance and body size in pelagic food webs has typically been conceptualised as a
70 frequency distribution of individual body sizes (Sheldon *et al.* 1972). This relationship

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2
3 71 has been dubbed the “size spectrum” (Kerr & Dickie 2001). The negative slopes of size
4
5 72 spectra describe how quickly abundance decreases with size, and have often been used to
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7
8 73 assess the ecological status of ecosystems impacted by fisheries (Rice & Gislason 1995)
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10 74 and, more recently, agricultural practices in terrestrial ecosystems (Mulder & Elser 2009).
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12 75 For example, steep size spectra with negative slopes in marine ecosystems are indicative
13
14 76 of over-fishing because the relative abundance of large organisms is suppressed by size-
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17 77 selective harvesting (Pauly *et al.* 1998).

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20 78 Understanding how the distribution of biomass in aquatic ecosystems might
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22 79 respond to warming is crucial for predicting the robustness and functioning of these
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24 80 ecosystems in the future warmer climate. New evidence suggests that “*reduced body size*
25
26 81 *is the third universal response to global warming, besides range, and phenological*
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28 82 *shifts*” (Daufresne *et al.* 2009). Changes in the size-structure of communities in response
29
30 83 to warming are now being documented across a range of ecosystem types and spatial
31
32 84 scales. For instance, experiments on aquatic micro-organisms have found that warmed
33
34 85 communities tend to be dominated by smaller bacteria (Daufresne *et al.* 2009).
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36
37 86 Macroecological studies across latitudinal temperature gradients (Moran *et al.* 2010), and
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39 87 paleoecological studies (Finkel *et al.* 2005) in the open ocean have revealed an increased
40
41 88 prevalence of small phytoplankton in warmer oceanic regions. These studies suggest that
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43 89 the underlying size structure of aquatic ecosystems might not be robust to global warming
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46 90 (Finkel *et al.* 2005, Falkowski & Oliver 2007, Daufresne *et al.* 2009, Winder *et al.* 2009,
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48 91 Finkel *et al.* 2010, Moran *et al.* 2010).

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52 92 However, these studies have tended to focus on the effects of warming on
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54 93 restricted subsets of species (e.g. diatoms or phytoplankton) within an ecosystem (Finkel
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3 94 *et al.* 2005, Winder *et al.* 2009) and documented changes in body size across latitudinal
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5 95 gradients where other factors (i.e. nutrient limitation) are potentially confounded with
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8 96 temperature (Moran *et al.* 2010). At present, we still lack sufficient data documenting the
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10 97 effects of warming *per se* on the size-structure of entire local communities comprising
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12 98 multiple trophic levels to be able to isolate its effects at this level of biological
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15 99 organisation.
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18 100 Here we attempt to address this current knowledge gap by measuring for the first
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20 101 time the consequences of experimental warming on the community size structure and
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22 102 distribution of biomass of entire planktonic food webs from 20 replicated freshwater
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24 103 mesocosms. These experimental systems were maintained at either ambient temperature
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27 104 ($n = 10$), or $\sim 4^{\circ}\text{C}$ above ambient ($n = 10$), in line with warming scenarios predicted for
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29 105 temperate latitudes by the end of the 21st century (IPCC 2007). Mesocosm scale
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31 106 experiments such as these afford the opportunity to isolate the effects of temperature from
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34 107 other potentially confounding variables (e.g. spatial gradients in available nutrients) on
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36 108 the structure of entire replicated communities. They also permit direct comparisons to be
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38 109 made between the structure of communities under ambient conditions with that of their
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40 110 “future” warmed counterparts. We used this experiment to test the following hypotheses:
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44 111 (i) Warming will shift the distribution of body size by increasing the prevalence
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46 112 of small sized species, resulting in an overall steepening of the slope of the community
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48 113 size spectrum. We expect this effect to be most pronounced in the phytoplankton
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50 114 assemblages because phytoplankton size structure tends to be strongly related to the
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52 115 prevailing physical and chemical environment (Reynolds 1984) and recent observations
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55 116 in aquatic ecosystems suggest that warming tends to favour smaller phytoplankton
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3 117 (Finkel *et al.* 2005, Falkowski & Oliver 2007, Daufresne *et al.* 2009, Winder *et al.* 2009,
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5 118 Moran *et al.* 2010).

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8 119 (ii) Warming will reduce total standing community biomass. Again, we expect
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10 120 this effect to be most pronounced for phytoplankton for two reasons. First, a shift in the
11
12 121 community size spectrum towards smaller species should result in an overall reduction in
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14 122 the standing biomass. Second, theoretical expectations from the metabolic theory of
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16 123 ecology (MTE) suggest total standing biomass should decline with increasing
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18 124 temperature (Allen *et al.* 2002), such that the total standing biomass in a community (B_{tot})
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20 125 is predicted to vary as $B_{\text{tot}} = r_0 e^{-E/kT} M^{1/4}$ where r_0 is the resource supply rate, $e^{-E/kT}$ is
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22 126 the Boltzmann factor where E is the activation energy of metabolism, k is Boltzmann's
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24 127 constant and T is absolute temperature. Therefore, holding r_0 constant (i.e. if the supply
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26 128 rate of limiting resources does not vary with T), B_{tot} should decline with increases in
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28 129 environmental temperature according to $e^{-E/kT}$.

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31 130 (iii) Warming will alter the relative distribution of biomass between
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33 131 phytoplankton and zooplankton assemblages. We expect that a shift in phytoplankton size
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35 132 structure and a concomitant reduction in standing biomass will result in elevated
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37 133 zooplankton-to-phytoplankton biomass ratios in the warmed mesocosms. We also predict
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39 134 that relatively high zooplankton biomass will be retained in the warmed mesocosms,
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41 135 because phytoplankton turnover rates should increase in response to metabolic
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43 136 stimulation by warming and by a shift towards smaller species with faster generation
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45 137 times. Comparable shifts in the organisation of plankton communities have been
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47 138 observed in the open ocean (Gasol *et al.* 1997) and in lakes (del Giorgio & Gasol 1995)
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49 139 along large scale spatial gradients of nutrient limitation.
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5 141 **MATERIAL AND METHODS**6
7 142 *Experimental Design*

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10 143 The experiment was carried out between December 2005 and April 2008 at the
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12 144 Freshwater Biological Association, River Laboratory (2°10`W, 50°13`N), East Stoke,
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14 145 Dorset, UK. A detailed description of the experimental set-up has been described
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16 146 elsewhere (Yvon-Durocher *et al.* 2010). The experiment consisted of twenty freshwater
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18 147 mesocosms (~1 m³, 0.5 m water depth): ten replicates remained at ambient temperature,
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20 148 whilst the other ten were warmed and maintained at 3-5°C (mean 4°C) above ambient.
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22 149 The mesocosms were seeded in December 2005 with organic substrates and a suite of
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24 150 organisms to include the main components of organismal composition and physical
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26 151 structure of shallow lake ecosystems. The established communities contained
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28 152 representative species from primary producers (phytoplankton, including: *Botryococcus*,
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30 153 *Chlorella*, *Volvox*, *Scenedesmus*) to top predators (Roach, *Rutilus rutilus*. Linnaeus), and
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32 154 a suite of zooplankton consumers (including cyclopoid and calanoid copepods,
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34 155 caldocerans, and rotifers). The biota was left to establish for ten months prior to
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36 156 experimental warming, which commenced in September 2006, thereby allowing time for
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38 157 further, natural colonisation before the onset of the study in April 2007. Populations of
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40 158 the introduced top predator, *R. rutilus* were maintained at a constant densities [two
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42 159 individuals (age 1+) per mesocosm (~12 g C m⁻³)] in all mesocosms and monitored via
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44 160 regular electro-fishing surveys. Because the fish were maintained at predetermined
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46 161 biomass-densities they merely served to “complete” the food webs to mimic natural
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48 162 shallow lakes and were not considered further in the analyses.
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5 164 *Measuring the Size Spectrum*

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8 165 The plankton communities from each of the 20 mesocosms were sampled at the beginning
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10 166 and end of the growing season in April and October 2007 respectively (Yvon-Durocher *et*
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12 167 *al.* 2010). The entire water column (depth 0.5m) from the sediment surface to the water
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14 168 surface was sampled using a 0.8m – long tube sampler (Volume: 2L), which was
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16 169 positioned at random in each mesocosm on each date. Each sample was divided into two
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18 170 size categories for preservation and subsequent analyses, via filtration through a 80µm
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20 171 sieve: organisms that were retained were preserved in 4% Formalin, and of the remaining
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22 172 sample (i.e. organisms <80 µm), a 100ml sub-sample was preserved in 1% Lugol's iodine
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24 173 for microscopy analyses.

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29 174 Plankton >80 µm were counted, measured and identified by microscopy (using a
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31 175 Nikon SMZ1500 dissection microscope). Zooplankton > 80 µm were typically assigned
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33 176 to taxonomic orders, though in a number of cases rotifers were identified to species level.
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35 177 Planktonic organisms <80µm were counted, measured and identified by inverted
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37 178 microscopy. Phytoplankton <80µm were typically identified to genus level, which is
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39 179 generally considered to be of sufficient taxonomic resolution to detect the effects of a
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41 180 perturbation (Cottingham & Carpenter 1998). Organisms were settled for 24 h in a 10ml
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43 181 Utermöhl sedimentation chamber before viewing under an inverted light microscope
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45 182 (Leica DMIRE2). An initial scan of the sample, viewed under low magnification (150×),
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47 183 of a fixed area (50 mm²) was used to count and measure large, rare organisms. At higher
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49 184 magnification (630×), *n* fields of view were chosen at random and all organisms were
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51 185 counted, sized and identified until a minimum of 400 individuals were measured from
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3 186 each sample. This was sufficient to estimate 95% of the variance in the distribution of
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5 187 body size (Fig S1 in supplementary material) given that settlement of organisms followed
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8 188 a Poisson distribution within the sedimentation chamber (Fig S2 in supplementary
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10 189 material).

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13 190 Linear body dimensions were determined with an interactive image analysis
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15 191 system (Hamamatsu C4742-95 camera and Openlab software). Body size of all
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17 192 organisms was expressed in units of carbon ($\mu\text{g C}$). For organisms $>80\mu\text{m}$ (typically
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19 193 zooplankton), biovolumes were determined by assigning organisms to geometric shapes
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21 194 that closely represented the real shape of the organism (Ruttner-Kolisko 1977, Reiss &
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23 195 Schmid-Araya 2008). Body mass was determined by converting biovolume to
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25 196 freshweight using a factor of 1.1, and carbon content was then estimated from a dry/wet
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27 197 weight ratio of 0.25 and a dry carbon content of 40% (Reiss & Schmid-Araya 2008). For
28
29 198 organisms $<80\mu\text{m}$ (typically phytoplankton) biovolumes, were similarly estimated from
30
31 199 geometric shapes that were most similar to the shape of the organism (Hillebrand *et al.*
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33 200 1999). Biovolume was then converted into carbon units assuming a multiplication factor
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35 201 of 0.109 (Montagnes *et al.* 1994). In total 47,699 individual organisms of both
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37 202 phytoplankton and zooplankton were measured.
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204 ***Phytoplankton turnover***

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47 205 Turnover rates of the phytoplankton assemblages ($\mu\text{g C m}^{-3} \text{ d}^{-1}/\mu\text{g C m}^{-3}$) were estimated
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49 206 for each mesocosm on each sampling occasion ($n = 40$). Phytoplankton turnover was
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51 207 calculated as the quotient of primary production and standing phytoplankton biomass
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53 208 after Gasol *et al.* (1997). This gives an estimate of the biomass specific production, or the
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3 209 rate at which the carbon in the assemblage turns over. Measurements of primary
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5 210 production were made simultaneously using the dissolved oxygen change technique and
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8 211 are presented in detail in Yvon-Durocher *et al.* (2010). Benthic metabolism measured
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10 212 using *in-situ* benthic chambers contributed, on average, 35 % of whole system respiration
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12 213 (see S7 in supplementary material for further details). From this we infer that our
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14 214 measures of primary production predominantly reflect planktonic metabolism and
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16 215 provide reliable estimates of carbon turnover within the phytoplankton assemblages.
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21 217 ***Constructing the Size Spectrum***

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24 218 The community size spectrum ($n = 40$), which included phytoplankton and zooplankton,
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26 219 and the phytoplankton assemblage size spectrum ($n = 40$) were constructed for each
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28 220 mesocosm in April and October 2007. The size spectrum of the zooplankton assemblage
29
30 221 alone could not be constructed accurately due to the relatively small body mass range and
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32 222 the low number of individuals present in some samples. Size spectra were constructed by
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34 223 logarithmic binning of the body masses (M) of the individuals measured in each
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36 224 mesocosm (either the entire community or just the phytoplankton). The total range of
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38 225 $\log_{10}(M)$ values was divided into 10 bins of equal width and the \log_{10} of the total
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40 226 population abundance of all organisms with $\log_{10}(M)$ in each bin was regressed against
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42 227 the bin centres (Reuman *et al.* 2008, White *et al.* 2008). The slope of the linear model
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44 228 describes how quickly the abundance of individuals declines with increasing size in the
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46 229 size spectrum (see Tables S5 and S6 in supplementary material). We also measured two
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48 230 normalisation constants of the linear model. The intercept at $x = 0$: its variation between
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50 231 warmed and ambient treatments gives information on the relative abundance of large
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3 232 organisms, and the intercept at $x = -8$: its variation provides information on the
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5 233 differences among treatments in the relative abundance of the smallest organisms. For
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8 234 both the community and the phytoplankton size spectrum, non-significant coefficients of
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10 235 the linear models (i.e. at $P > 0.05$) were excluded from further analyses ($n = 5$ out of 40 for
11
12 236 the phytoplankton size spectrum).
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17 238 *Statistical Analyses*

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20 239 We analysed differences between treatments in the following community properties: size
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22 240 spectrum slopes and intercepts; total community biomass; total phytoplankton biomass;
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24 241 total zooplankton biomass; and mean individual body mass, using ANOVA, with
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27 242 treatment (either warmed or ambient) and sampling occasion (April or October) as fixed
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29 243 factors. The relationships between phytoplankton and zooplankton biomass and the
30
31 244 biomass ratio of zooplankton to phytoplankton were determined using ANCOVA, again
32
33 245 using treatment and sampling occasion as factors. In all statistical modelling procedures
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35 246 the most parsimonious model was identified using the Akaike Information Criterion
36
37 247 (AIC). Statistical analyses were performed using R statistical software (R. Development.
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39 248 Core. 2006).
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43 249 Multivariate analysis of phytoplankton taxonomic composition was conducted
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45 250 using the vegan package in R. Redundancy analysis (RDA) was used to test for a
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47 251 significant linear trend in community composition. RDA is a constrained form of
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49 252 principal components analysis and assesses the variation in taxonomic composition that
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51 253 can be explained by specific environmental variables defined as the constraints. Here, the
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53 254 first RDA axis quantified the linear component of the between treatment variation in
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3 255 phytoplankton taxonomic composition. Consequently, it was used to assess the strength
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5 256 of the trend and its significance was tested using permutation tests. The F -ratio of the first
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8 257 RDA axis was compared with those of 999 permutations, to assess the statistical
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10 258 significance of the linear trend. As well as treatment (warming), NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} ,
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12 259 and total inorganic N:P (see S3 for details on nutrient measurements) were tested as
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14 260 constraining environmental variables. Phytoplankton taxon biomass was transformed
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16 261 prior to the construction of the RDA by taking the proportional contribution of a given
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18 262 taxa as a fraction of the total biomass in a given mesocosm. Furthermore, rare genera
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20 263 defined as those occurring in less than two mesocosms per sampling date were excluded
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22 264 from the RDA analysis to reduce noise in the data.
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29 266 **RESULTS**

30 267 *Effects of Warming on the Size Spectrum*

31
32 268 Warming significantly increased the steepness of the slope of the community size
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34 269 spectrum from -0.86 (95% CI -0.83 to -0.89) in the systems at ambient temperature to -
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36 270 0.95 (95% CI -0.92 to -0.98) in the warmed mesocosms (Fig. 1 a, b & c; Table 1), i.e.,
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38 271 smaller organisms were relatively more abundant than large organisms in the warmed
39
40 272 communities. Furthermore, the intercept of the community size spectrum at $x = 0$ (i.e. at
41
42 273 large body masses) was significantly reduced, whilst the intercept at $x = -8$ (i.e. at small
43
44 274 body masses) was significantly elevated in the warmed mesocosms (Table 1). Thus, the
45
46 275 abundance of larger organisms declined on average, while the abundance of small
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48 276 organisms increased in response to warming.
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3 277 Comparable patterns were observed for the phytoplankton size spectrum (Fig. 1d,
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6 278 e & f). Warming significantly increased the steepness of the slope of the phytoplankton
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8 279 size spectrum from -0.36 (95% CI -0.32 to -0.40) in the systems at ambient temperature
9
10 280 to -0.49 (95% CI -0.43 to -0.55) in the warmed mesocosms (Table 1; Fig. 1d, e & f).
11
12 281 Warming also significantly reduced the intercept of the phytoplankton size spectrum
13
14 282 (Table 1). Therefore, small organisms were relatively more abundant than large
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16 283 organisms in the warmed mesocosms. Additionally, warming truncated the upper size
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18 284 classes of the phytoplankton size spectrum (Fig. 1 d). The maximum phytoplankton body
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20 285 mass in the ambient mesocosms was 1.36×10^{-2} $\mu\text{g C}$, while in the heated the maximum
21
22 286 body mass was only 3.88×10^{-3} $\mu\text{g C}$. Furthermore, the average body mass of an individual
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24 287 phytoplankter was almost an order of magnitude smaller in the warmed mesocosms
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26 288 relative to the ambient systems (Fig. 2; Table 1), while the average size of an individual
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28 289 zooplankter was unaffected by warming (Fig. 2; Table 1).
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36 291 *Effects of Warming on Community Composition*

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38 292 Redundancy analysis of the phytoplankton taxa revealed that the composition of the
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40 293 phytoplankton assemblages were significantly different between warmed and ambient
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42 294 treatments in both April (Fig. 3a; F -ratio = 5.72; P = 0.011; permutation number = 999)
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44 295 and October (Fig. 3b; F -ratio = 5.87; P = 0.001; permutation number = 999). RDA1
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46 296 which was constrained by treatment, explained 24.1% and 24.6% of the variation in the
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48 297 taxonomic composition of the phytoplankton assemblages in April and October
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50 298 respectively, which in both cases was greater than the variation explained by PCA1,
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52 299 indicating that treatment effects were the dominant predictor of phytoplankton taxonomic
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3 300 composition. We also tested for significant relationships between phytoplankton
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5 301 taxonomic composition and other environmental variables (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} , total
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8 302 inorganic N:P) using permutation tests, though none of these variables significantly
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10 303 predicted taxonomic composition. Certain taxa were strongly associated with either
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12 304 warmed or ambient treatments. For example, in both April and October, the large
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14 305 chlorophyte, *Botryococcus* clustered towards the ambient treatment centroid, while the
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16 306 small cyanophyte *Synechocystis*, and the small chlorophyte *Monoraphidium*, typically
17
18 307 clustered towards the heated centroid. The phytoplankton assemblages consisted of many
19
20 308 rare, generalist taxa that were present in both treatments; however, in most of the
21
22 309 mesocosms the biomass was dominated by a few indicator taxa (named above) that were
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24 310 associated with either the heated or the ambient treatments. Furthermore, figures 3a and
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26 311 3b show that a large core contingent of the phytoplankton assemblages were present in
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28 312 both April and October and that only a few taxa were present in only one month,
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30 313 suggesting that temporal succession was less important than treatment effects in
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32 314 determining phytoplankton community composition.

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39 315 In contrast to the phytoplankton assemblages the taxonomic composition of the
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41 316 zooplankton assemblages differed very little between treatments in both April and
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43 317 October (Fig. 4a & b). In heated and ambient treatments calanoid and cyclopoid copepods
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45 318 dominated zooplankton biomass with cladocerans and rotifers forming a smaller
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47 319 secondary contingent of the assemblages. These patterns were consistent between April
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49 320 and October, though ostracods, oligochates and the rotifer *Asplanchna* were absent from
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51 321 the zooplankton assemblage in October.
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3 323 *Effects of Warming on the Distribution of Biomass*
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5 324 Total planktonic community biomass differed between April and October in the ambient
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8 325 but not in the warmed mesocosms (Fig. 5). Overall, warming significantly reduced total
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10 326 community biomass (Fig. 5; Table 1). This was principally driven by a considerable
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12 327 reduction in total phytoplankton biomass in the warmed mesocosms (Fig. 5; Table 1).
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15 328 Overall, warming shifted the distribution of biomass and body size of phytoplankton from
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17 329 assemblages comprised of large individuals with high standing biomass to assemblages
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19 330 with low standing biomass and many small individuals. In contrast, warming appeared to
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21 331 have no effect on the distribution of size and biomass within the zooplankton
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23 332 assemblages (Fig. 5; Table 1).
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27 333 Zooplankton and phytoplankton biomass were not correlated within the
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29 334 mesocosms (Fig. 6a; Table 2). The former varied by about two orders of magnitude and
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31 335 the latter by three orders of magnitude among mesocosms (Fig. 6a). The ratio of
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33 336 zooplankton to phytoplankton biomass (Z:P) was significantly and negatively correlated
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35 337 with phytoplankton biomass (Fig. 6b; Table 1). Therefore, zooplankton biomass exceeded
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37 338 phytoplankton biomass (i.e. Z:P >1) when phytoplankton biomass was low and vice versa
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39 339 (i.e. Z:P <1) when phytoplankton biomass was high. Warming significantly increased the
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41 340 ratio of Z:P biomass (Table 2). Furthermore, the ratio of Z:P biomass was strongly and
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43 341 positively correlated with the turnover rates of the phytoplankton assemblages, which
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45 342 exhibited distinct variation between warmed and ambient mesocosms (Fig. 6c; Table 2).
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47 343 In summary, the warmed mesocosms were characterised by phytoplankton assemblages
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49 344 comprised of small individuals with low standing stocks of biomass and rapid turnover
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3 345 rates which supported relatively high standing stocks of zooplankton, exemplified by
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5 346 high Z:P biomass ratios.
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10 348 **DISCUSSION**

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12 349 There is ample evidence that ecological responses to recent climate change are already
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14 350 occurring at the species (and therefore the population) level (Walther *et al.* 2002), but
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16 351 scaling from populations to communities and ecosystems is challenging because of the
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18 352 perceived indeterminacy of ecological interactions (Yodzis & Innes 1992). Therefore,
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20 353 there is an increasingly urgent need to explore the effects of the principal components of
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22 354 climate change (e.g., warming) on community structure and ecosystem functioning
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24 355 (Tylianakis *et al.* 2008, Montoya & Raffaelli 2010). Our results broadly supported our
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26 356 experimental hypotheses: i.e., that warming would increase the steepness of the size
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28 357 spectrum slope, reduce total community biomass, and increase the zooplankton to
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30 358 phytoplankton biomass ratio. These findings could provide some novel insights into how
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32 359 future warming might change the distribution of body size and biomass in aquatic
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34 360 ecosystems. The size structure of plankton communities in aquatic ecosystems is a key
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36 361 driver of rates of carbon sequestration and nutrient cycling (Laws *et al.* 2000), and
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38 362 therefore changes in the distribution of planktonic body size and biomass could alter the
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40 363 regulation of biotic feedbacks with warming on a potentially global scale (Falkowski *et*
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42 364 *al.* 1998).
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50 365 The general increase in the prevalence of small organisms with increases in
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52 366 environmental temperature that we observed experimentally agrees well with recent
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54 367 studies that have either focused on specific taxa, or subsets of taxa (Atkinson *et al.* 2003,
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3 368 Finkel *et al.* 2005, Daufresne *et al.* 2009, Winder *et al.* 2009), or analysed correlational
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5 369 trends in community structure across latitudinal gradients in temperature (Moran *et al.*
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8 370 2010). However, here we have developed this understanding further by documenting the
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10 371 effects of warming on the body size, biomass and taxonomic structure of entire
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12 372 planktonic food webs subjected to experimental warming. Experimental mesocosm
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15 373 studies, although inevitably an abstraction of natural ecosystems, afford us the
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17 374 opportunity to isolate the effects of temperature from other potentially confounding
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19 375 variables (e.g. latitudinal and biogeographical effects) whilst studying entire replicated
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21 376 plankton communities.
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24 377 The increase in the dominance of small phytoplankton and the truncation of the
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26 378 larger size classes in their size spectrum resulted in a general increase in the steepness of
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28 379 the slope of the community size spectrum in the warmed mesocosms. Changes in the
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30 380 distribution of organism size might arise from at least two broad mechanisms, which are
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32 381 not necessarily mutually exclusive. Firstly, organisms might exhibit a degree of
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34 382 phenotypic plasticity to changes in temperature. This hypothesis has been termed the
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36 383 temperature-size rule (Atkinson *et al.* 2003) and posits that reduced organism size at
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38 384 higher temperatures is an adaptive plastic response that results from selection for earlier
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40 385 reproduction as population growth rate increases. The accelerated completion of the life
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42 386 cycle occurs at the expense of maturation size (Atkinson *et al.* 2003). In the second
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44 387 mechanism, changes in the physicochemical environment created by warming select for
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46 388 smaller sized species. In this case, changes in community size structure occur as an
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48 389 indirect effect of warming, mediated for example, by concomitant nutrient limitation,
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51 390 resulting in the competitive exclusion of larger species (Finkel *et al.* 2005, Irwin *et al.*
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3 391 2006, Falkowski & Oliver 2007, Winder *et al.* 2009, Finkel *et al.* 2010). Here, small cell
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5 392 size increases the efficiency of the acquisition of limiting nutrients because of a higher
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8 393 surface area to volume ratio and is therefore competitively advantageous under conditions
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10 394 of nutrient limitation (Litchman *et al.* 2009).

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12 395 Our results support the second mechanism. Redundancy analysis revealed that
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14 396 warming dramatically shifted the taxonomic composition of the phytoplankton
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17 397 assemblages. Moreover, warming favoured smaller phytoplankton genera, resulting in a
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19 398 reduction in mean and maximum body size by almost an order of magnitude. For
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21 399 example, the large chlorophyte *Botryococcus* dominated the biomass of the ambient
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23 400 mesocosms in both April and October, but was almost entirely absent from the warmed
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25 401 mesocosms. Similarly the small cyanophyte *Synechocystis* and the small chlorophyte
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27 402 *Monoraphidium* were strongly associated with the warmed mesocosms but were only
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29 403 peripheral members of the assemblages in the ambient mesocosms. Warming therefore
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31 404 resulted in the establishment of phytoplankton assemblages dominated by small species,
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33 405 rather than reducing the body size of the same species composition present in the ambient
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35 406 mesocosms.

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39 407 Our experimental design adopted a space-for-time substitution approach to
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41 408 attempt to understand the consequences of warming on the structure of plankton
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43 409 communities. The relatively infrequent but highly replicated sampling regime adopted in
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45 410 our study was a necessary compromise. For example, we documented the size, biomass
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47 411 and taxonomic structure of 20 replicated experimental ecosystems on two separate
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49 412 sampling occasion at the beginning and end of the growing season (identified from
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51 413 measures of primary production; see Yvon-Durocher *et al.*, (2010) for details) rather than
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3 414 focusing on the complex temporal dynamics of the plankton assemblages of one or two
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5 415 systems, as would typically be logistically feasible within such a study. As a result, our
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7 416 results come with an associated caveat: we are unable to discern the effects of warming
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9 417 on the temporal succession of the plankton communities. However, analysis of the
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11 418 phytoplankton taxonomic composition suggests that a large, core contingent of these
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13 419 assemblages are present in both April and October but which differ markedly between
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15 420 treatments in both months. These results suggest that temporal succession in the plankton
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17 421 communities was less important than the effect of treatment (i.e. warming) in determining
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19 422 the taxonomic and therefore the body size and biomass structure of these assemblages.
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24 423 Inorganic nitrogen was limiting in our experiment (N:P ratios were $\approx 11:1$, and
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26 424 were below the 16N:1P expected at Redfield; see S3 & S4 in supplementary material for
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28 425 further details) but to the same extent in both warmed and ambient treatments: i.e.,
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30 426 warming did not exacerbate nutrient limitation. Therefore, it is unlikely that a direct
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32 427 effect of nutrient limitation induced by warming caused the observed shifts in
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34 428 phytoplankton size structure that have been frequently documented in the open ocean and
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36 429 in lake ecosystems (Finkel *et al.* 2005, Falkowski & Oliver 2007, Winder *et al.* 2009,
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38 430 Finkel *et al.* 2010). Furthermore, redundancy analysis revealed that inorganic nutrient
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40 431 concentrations (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} , and total inorganic N:P) were not significantly
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42 432 correlated with phytoplankton taxonomic composition. Therefore, the shift in
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44 433 phytoplankton size and taxonomic structure in the warmed treatments might simply
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46 434 reflect the fact that smaller phytoplankton have lower specific nitrogen requirements than
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48 435 large phytoplankton (Litchman *et al.* 2007). Litchman *et al.* (2007) found that the
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50 436 minimum nitrogen quota required to support growth, Q_{\min} , across a wide range of
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3 437 phytoplankton taxa increases allometrically, resulting in a disproportionate increase in
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5 438 cellular nitrogen quota with size. Because metabolic rates and nutrient uptake rates
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8 439 increase with temperature and size (Gillooly *et al.* 2001, Allen & Gillooly 2009), under
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10 440 conditions of nutrient limitation, small cell size should provide a competitive advantage
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12 441 as environmental temperatures rise. This is because species with lower Q_{\min} will be better
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14 442 able to balance the increased demand for limiting nutrients imposed by temperature
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16 443 driven elevated metabolic rates.
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20 444 An alternative mechanism for the shifts in phytoplankton size and taxonomic
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22 445 structure in the warmed mesocosms is that warming served to increase “top down”
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24 446 control of the phytoplankton community by increasing zooplankton grazing rates. We
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26 447 have previously demonstrated that heterotrophic metabolism increased more rapidly than
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28 448 autotrophic metabolism with increasing temperature in the same experimental system
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30 449 (measurements made simultaneously; see Yvon-Durocher *et al.*, (2010) for details).
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32 450 Therefore, because ingestion rates increase in proportion with metabolic rates (Berlow *et*
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34 451 *al.* 2009), warming might have increased the strength of top down control of
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36 452 phytoplankton populations by zooplankton grazing. Moreover, zooplankton are often size
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38 453 selective when feeding on phytoplankton, typically consuming the largest size classes
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40 454 possible (Porter 1973, Hall *et al.* 1976, Katechakis *et al.* 2002). Warming might therefore
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42 455 have increased the prevalence of small sized phytoplankton indirectly, by elevating
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44 456 grazing pressure on the larger size classes of the phytoplankton community due to the
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46 457 elevated metabolic demands of zooplankton at higher temperature. Importantly, both the
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48 458 “top down” and “bottom up” hypotheses stated here are not mutually exclusive: both
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50 459 bottom up regulation of phytoplankton competitive ability for limiting nutrients, and top
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3 460 down control of large phytoplankters by zooplankton grazing could occur simultaneously,
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5 461 and combine with the direct effects of warming on metabolism to produce the observed
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8 462 shifts in size, biomass taxonomic structure.
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10 463 Warming reduced total standing community biomass, largely via a reduction in
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12 464 phytoplankton biomass. These results confirmed our qualitative theoretical predictions.
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14 465 For example, because the potential resource supply rate (i.e. the concentrations of
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17 466 limiting inorganic nutrients) remained constant, we predicted that elevated metabolic
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19 467 demands at higher temperatures should have resulted in a decline in standing community
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21 468 biomass in the warmed mesocosms. Assuming $B_{\text{tot}} = r_0 e^{-E/kT} M^{1/4}$ and that r_0 (i.e. the
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23 469 resource supply rate) and $M^{1/4}$ (i.e. the allometric scaling of biomass with body mass) are
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26 470 constant with temperature we can predict that for $\approx 4^\circ\text{C}$ warming (i.e. the average annual
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28 471 temperature increase in our experiment) standing community biomass should decline
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30 472 approximately 1.54 fold according to: $e^{-E/kT_h} / e^{-E/kT_a}$ where T_h and T_a are the mean annual
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32 473 temperatures of the heated and ambient mesocosms (290.9 and 286.1 K, respectively) and
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34 474 E is the activation energy of metabolism $\approx 0.65\text{eV}$ (Gillooly *et al.* 2001). In our
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36 475 experiment average total community biomass declined 2.53 fold (i.e. the ratio of mean
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38 476 biomass in the heated and ambient mesocosms), almost double that predicted by
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40 477 metabolic costs alone, suggesting that additional factors may be operating.
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46 478 The large shift in the distribution of body size from large to small phytoplankton
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48 479 might further reduce standing biomass. For example, the above prediction assumes that
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50 480 the allometric scaling of biomass with body mass (i.e. $B_{\text{tot}} = M^{1/4}$) remains constant with
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52 481 warming. However, we have demonstrated that the slope of the community size spectrum
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55 482 (i.e. the log-log relationship) which is equivalent to the exponent (i.e. $-\alpha$) of $N = M^\alpha$,
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3 483 where N is abundance (White *et al.* 2007, Reuman *et al.* 2008, White *et al.* 2008),
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5 484 changes from -0.86 to -0.95 in response to warming. Therefore, because $B_{\text{tot}} = N \times M$ the
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8 485 allometric scaling of B_{tot} declined from $B_{\text{tot}} = M^{0.14}$ in the ambient mesocosms to
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10 486 $B_{\text{tot}} = M^{0.05}$ in the warmed mesocosm: i.e., more standing biomass was retained in larger
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12 487 body size classes in the ambient relative to the warmed mesocosms. We suggest that the
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15 488 effects of increased metabolic costs, associated with warmer temperatures and the shift in
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17 489 the distribution of body size and taxonomic composition of the phytoplankton
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20 490 assemblage, could have acted synergistically to reduce total community biomass in the
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22 491 warmed mesocosms.

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25 492 The ratio of zooplankton to phytoplankton biomass, Z:P, declined as a function of
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27 493 phytoplankton biomass, in line with our third experimental hypothesis. Our results are
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29 494 qualitatively similar to the findings of Gasol *et al.* (1997) who also demonstrated that the
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31 495 ratio of heterotroph to autotroph biomass (H:A) was a declining function of autotroph
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33 496 biomass in the open ocean and coastal seas, although they attributed the relationship to a
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36 497 nutrient gradient rather than temperature. In our case, the large shifts in community size
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38 498 structure and the distribution of biomass between zooplankton and phytoplankton were
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40 499 independent of the inorganic nutrient status of the mesocosms and appear to have been
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43 500 driven largely by the effects of temperature on metabolism and the relative competitive
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45 501 abilities of large and small phytoplankton.

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48 502 We found a strong, positive correlation between the Z:P biomass ratio and the
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50 503 turnover rate of the phytoplankton assemblages, which differed profoundly between
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52 504 warmed and ambient treatments. These results offer insight into how these communities
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55 505 might function: the inverted pyramid or squared biomass distributions (i.e. $Z > P$ or $Z = P$)
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3 506 in the warmed mesocosms contrasted markedly with the pyramidal biomass structure (i.e.
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5 507 $Z < P$) of the mesocosms at ambient temperature. This suggests that warming of $\sim 4^\circ\text{C}$
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8 508 fundamentally altered the structure and functioning (i.e. energy transfer) of our
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10 509 experimental ecosystems. For instance, in the heated mesocosms the high relative
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12 510 biomass of zooplankton may have been supported by a fast turnover rate of the
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14 511 phytoplankton assemblage. For example, for the low standing stocks of phytoplankton
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16 512 biomass in the warmed mesocosms ($2.93 \times 10^5 \mu\text{g C m}^{-3}$ in heated; $1.12 \times 10^6 \mu\text{g C m}^{-3}$ in
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18 513 ambient) to sustain the equivalent biomass of zooplankton as the mesocosms at ambient
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20 514 temperature ($1.71 \times 10^5 \mu\text{g C m}^{-3}$ in ambient; $1.36 \times 10^5 \mu\text{g C m}^{-3}$ heated), the turnover rate
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22 515 of the phytoplankton community would need to be elevated by a factor of ~ 4 . The
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24 516 average turnover rates of the phytoplankton community in the warmed treatments was
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26 517 actually elevated by a factor of ~ 5 (i.e. $40.9 \mu\text{g C m}^{-3} \text{ d}^{-1} / \mu\text{g C m}^{-3}$ in heated; $8.25 \mu\text{g C}$
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28 518 $\text{m}^{-3} \text{ d}^{-1} / \mu\text{g C m}^{-3}$ in the ambient) and was therefore sufficient to support the biomass of
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30 519 zooplankton in these systems. Taken together, these results suggest that warming
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32 520 increases the rate of carbon flux between autotrophs and heterotrophs. This effect appears
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34 521 to be driven by the relative increase in small phytoplankton, which have faster turnover
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36 522 times due to the $-1/4$ allometry of mass specific metabolic rate and generation time
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38 523 (Gillooly *et al.* 2002, Brown *et al.* 2004), and also the direct stimulation of metabolism
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40 524 and generation time by temperature (Gillooly *et al.* 2002).
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51 **Conclusion**

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53 527 In general, the results of our experiment reflect patterns in empirical surveys that
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55 528 have analysed phytoplankton communities over macroevolutionary time (Finkel *et al.*
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3 529 2005, Finkel *et al.* 2007), across latitudinal gradients in temperature (Moran *et al.* 2010),
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5 530 and across gradients of nutrient regime and productivity (del Giorgio & Gasol 1995,
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8 531 Gasol *et al.* 1997). Our results, however, represent the first experimental evidence for a
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10 532 shift in the distribution of body size and biomass of whole plankton communities that can
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12 533 be attributed directly to the effects of warming via a controlled and replicated whole
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14 534 ecosystem manipulation. Although we now have some tantalising hints, the precise
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16 535 mechanism behind the size shifts we observed requires further research. Also, the
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18 536 consequences of such shifts in community size structure for the functioning (e.g. carbon
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20 537 sequestration capacity) of aquatic ecosystems remains an unexplored avenue in
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22 538 ecological research, though with no doubt one that will prove fundamental in addressing
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24 539 the future challenges posed by environmental change.
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682 **Figure Legends**

683 **Figure. 1.** The size spectrum. (a) The community size spectrum of a heated (red circles)
684 and ambient (black circles) mesocosm, highlighting the increase in the steepness of the
685 slope in the warmed mesocosm. (b) Frequency distribution of the slope of the community

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3 686 size spectrum in the ambient mesocosms ($n=20$), (c) frequency distribution of the slope
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5 687 of the community size spectrum in the warmed mesocosms ($n=20$). On average the
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8 688 slope of the community size spectrum in the warmed mesocosms was significantly
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10 689 steeper than the ambient mesocosms (Table 1). (d) The phytoplankton size spectrum of a
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12 690 heated (red circles) and ambient (black circles) mesocosm, highlighting the increase in
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14 691 the steepness of the slope and the truncation of large sized individuals in the warmed
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16 692 mesocosm. (e) Frequency distribution of the slope of the phytoplankton size spectrum in
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18 693 the ambient mesocosms ($n=17$), (f) frequency distribution of the slope of the community
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20 694 size spectrum in the warmed mesocosms ($n=18$).
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27 696 **Figure. 2.** Effects of warming on mean body mass (± 1 s.e.m) of phytoplankton (a) and
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29 697 zooplankton (b) individuals. Data are presented as the overall average of the mean body
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31 698 mass of phytoplankton and zooplankton individuals over 20 mesocosms for each
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33 699 treatment. The mean cell mass of phytoplankton is significantly reduced in response to
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35 700 warming while there is no significant difference in the mean body mass of zooplankton
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37 701 between heated and unheated treatments (table 1).
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43 703 **Figure. 3.** Redundancy analysis (RDA) biplot for sites (i.e. mesocosms) and species
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45 704 scores for phytoplankton taxa recorded in the mesocosm experiment in April (a) and
46
47 705 October (b). In both cases RDA 1 was constrained by treatment and accounted for 24.1%
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49 706 and 24.6% of the variation in the taxonomic composition of the mesocosms in April and
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51 707 October respectively. In the plot the dotted lines denote the 95% confidence ellipses
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53 708 around the centroids for both treatments. In both April and October these ellipses do not
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3 709 overlap indicating that the community composition was significantly different between
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5 710 warmed and ambient treatments. The solid lines enclose all mesocosms that belong to a
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8 711 particular treatment; in both cases heated treatments (1, 4, 6, 8, 9, 12, 14, 15, 17, 19)
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10 712 cluster to the left, while ambient treatments (2, 3, 5, 7, 10, 11, 13, 16, 18, 20) cluster to
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12 713 the right. Genus abbreviations are as follows: *Aphanothece* (Aph), *Asterococcus* (Ast),
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14 714 *Botryococcus* (Bty), *Bumilleriopsis* (Bum), *C.dinobryonis* (C.d), *Chlorella* (Chl),
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16 715 *Chlorococcum* (Coc), *Chroococcus* (Chr), *Chroomonas* (Cho), *Coencococcus* (Coe),
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18 716 *Cosmarium* (Cos), *Cryptomonas* (Cry), *Goniochloris* (Gon), *Kirchneriella* (Kri),
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20 717 *Monoraphidium* (Mon), *Navicula* (Nav), *Nephrocytium* (Nep), *Rhodomonas* (Rho),
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22 718 *Scenedesmus* (Sce), *Synechococcus* (Syn), *Synechocystis* (Syc), *Spermatozopsis* (Spe).
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29 720 **Figure. 4.** Mean biomass of the major zooplankton taxonomic groups documented in the
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31 721 mesocosms in (a) April and (b) October. Note that there is very little difference in the
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33 722 biomass contribution of the different zooplankton taxa between treatments suggesting
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35 723 that the zooplankton community composition was unaffected by warming.
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41 725 **Figure.5.** Effects of warming on mean total planktonic biomass (± 1 s.e.m). Data are
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43 726 presented as the averages of the total biomass of either phytoplankton and/or zooplankton
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45 727 across the mesocosms for each treatment (n=20 per treatment for the overall mean; n=10
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47 728 per treatment for each sampling occasion). Total biomass is significantly reduced by
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49 729 warming. This is mainly driven by a reduction in phytoplankton biomass, while there is
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51 730 no significant difference in the biomass of zooplankton in response to warming (table 1).
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3 732 **Figure. 6.** (a) Relationship between zooplankton and phytoplankton biomass. (b)
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5 733 Relationship between the ratio of zooplankton to phytoplankton biomass (Z:P) and total
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8 734 phytoplankton biomass. (c) The relationship between Z:P and the turnover rate of the
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10 735 phytoplankton communities. Each data point corresponds to either the total zooplankton
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12 736 or phytoplankton biomass or the Z:P in either a heated (red circles) or ambient mesocosm
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739 **Table 1.** The effect of treatment (heated or ambient) on community-level properties. CSS
 740 is the community size spectrum and PSS is the phytoplankton size spectrum. ANOVAs
 741 were used to isolate treatment effects on individual community-level properties. In each
 742 ANOVA month (either April or October) was added as a factor. For each community-
 743 level property there was no significant effect of month, which was removed from the
 744 model using the AIC score.

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Community Property	DF	<i>F</i>	<i>P</i>
CSS slope	1, 38	11.1	0.002
CSS intercept ($x = 0$)	1, 38	8.2	0.007
CSS intercept ($x = -8$)	1, 38	4.2	0.047
PSS slope	1, 33	11.8	0.002
PSS intercept	1, 33	8.27	0.007
Total community biomass	1, 38	10.8	0.002
Total phytoplankton biomass	1, 38	13.1	<0.001
Total zooplankton biomass	1, 38	0.47	0.5 (NS)
Mean phytoplankton body mass	1, 38	18.9	<0.001
Mean zooplankton body mass	1, 38	1.4	0.2 (NS)
Z:P Biomass ratio	1, 38	4.82	0.034

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748 **Table 2.** Analysis of covariance for the relationships between zooplankton and
 749 phytoplankton biomass, the Z:P biomass ratio and phytoplankton biomass, and the Z:P
 750 biomass ratio and phytoplankton turnover time.

Relationship	DF	F	P	r ²
Log₁₀(Zoo biomass) vs Log₁₀ (Phyto biomass)	1, 38	0.062	0.805 (NS)	0.002
<i>Difference in slope</i>	1, 38	3.021	0.073(NS)	N/A
<i>Difference in intercept</i>	1, 38	0.195	0.661 (NS)	N/A
Log₁₀(Z:P) vs Log₁₀ (Phytoplankton biomass)	1, 38	32.65	<0.0001	0.58
<i>Difference in slope</i>	1, 38	1.806	0.187 (NS)	N/A
<i>Difference in intercept</i>	1, 38	0.002	0.956 (NS)	N/A
Log₁₀(Z:P) vs Log₁₀ (Phytoplankton turnover)	1, 38	52.51	<0.0001	0.58
<i>Difference in slope</i>	1, 38	2.171	0.147 (NS)	N/A
<i>Difference in intercept</i>	1, 38	0.538	0.468 (NS)	N/A

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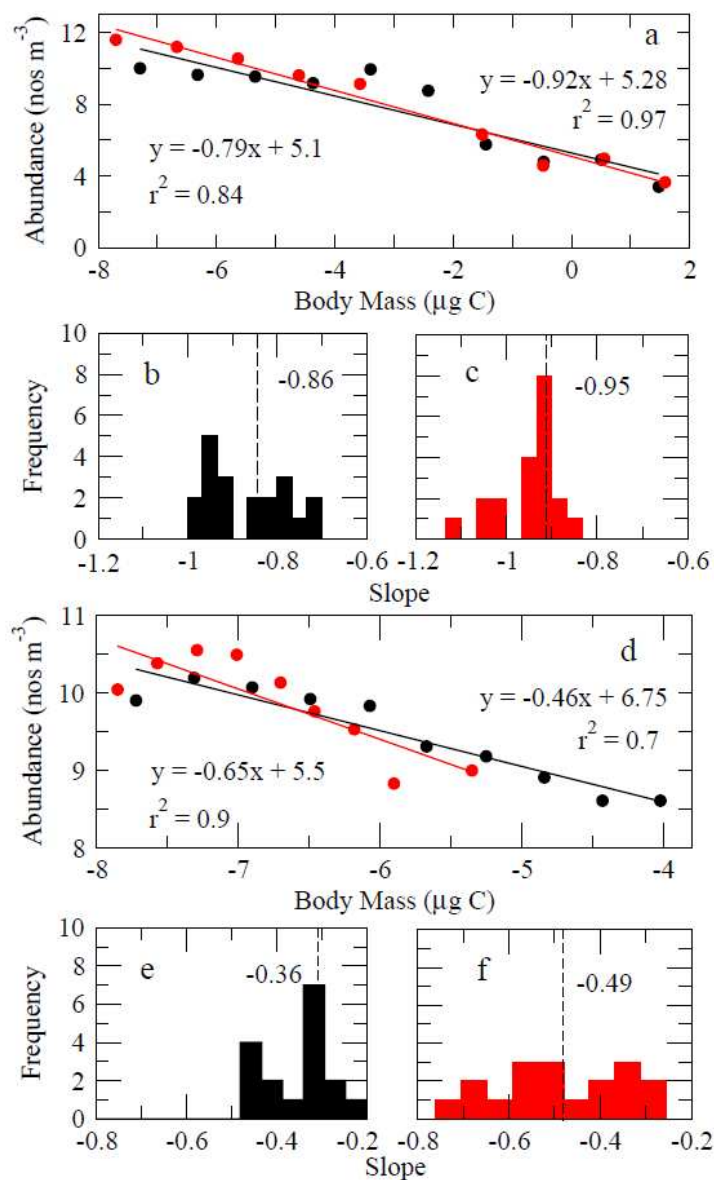


Figure. 1. The size spectrum. (a) The community size spectrum of a heated (red circles) and ambient (black circles) mesocosm, highlighting the increase in the steepness of the slope in the warmed mesocosm. (b) Frequency distribution of the slope of the community size spectrum in the ambient mesocosms (n=20), (c) frequency distribution of the slope of the community size spectrum in the warmed mesocosms (n=20). On average the slope of the community size spectrum in the warmed mesocosms was significantly steeper than the ambient mesocosms (Table 1). (d) The phytoplankton size spectrum of a heated (red circles) and ambient (black circles) mesocosm, highlighting the increase in the steepness of the slope and the truncation of large sized individuals in the warmed mesocosm. (e) Frequency distribution of the slope of the phytoplankton size spectrum in the ambient mesocosms (n=17), (f) frequency distribution of the slope of the community size spectrum in the warmed mesocosms (n=18).

198x328mm (72 x 72 DPI)

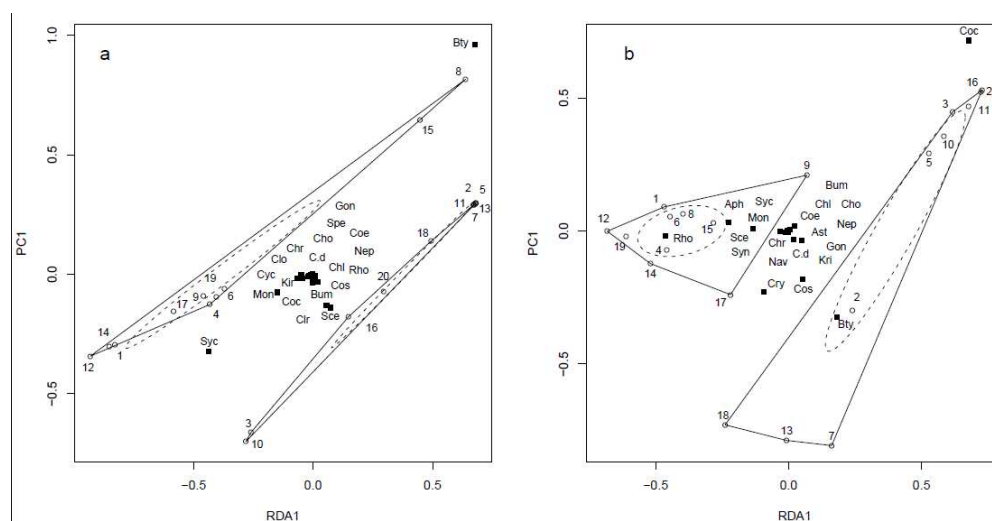


Figure 3. Redundancy analysis (RDA) biplot for sites (i.e. mesocosms) and species scores for phytoplankton taxa recorded in the mesocosm experiment in April (a) and October (b). In both cases RDA 1 was constrained by treatment and accounted for 24.1% and 24.6% of the variation in the taxonomic composition of the mesocosms in April and October respectively. In the plot the dotted lines denote the 95% confidence ellipses around the centroids for both treatments. In both April and October these ellipses do not overlap indicating that the community composition was significantly different between warmed and ambient treatments. The solid lines enclose all mesocosms that belong to a particular treatment; in both cases heated treatments (1, 4, 6, 8, 9, 12, 14, 15, 17, 19) cluster to the left, while ambient treatments (2, 3, 5, 7, 10, 11, 13, 16, 18, 20) cluster to the right. Genus abbreviations are as follows: Aphanothece (Aph), Asterococcus (Ast), Botryococcus (Bty), Bumilleriopsis (Bum), C.dinobryonis (C.d), Chlorella (Chl), Chlorococcum (Coc), Chroococcus (Chr), Chroomonas (Cho), Coencococcus (Coe), Cosmarium (Cos), Cryptomonas (Cry), Goniochloris (Gon), Kirchneriella (Kri), Monoraphidium (Mon), Navicula (Nav), Nephrocystium (Nep), Rhodomonas (Rho), Scenedesmus (Sce), Synechococcus (Syn), Synechocystis (Syc), Spermatozopsis (Spe).

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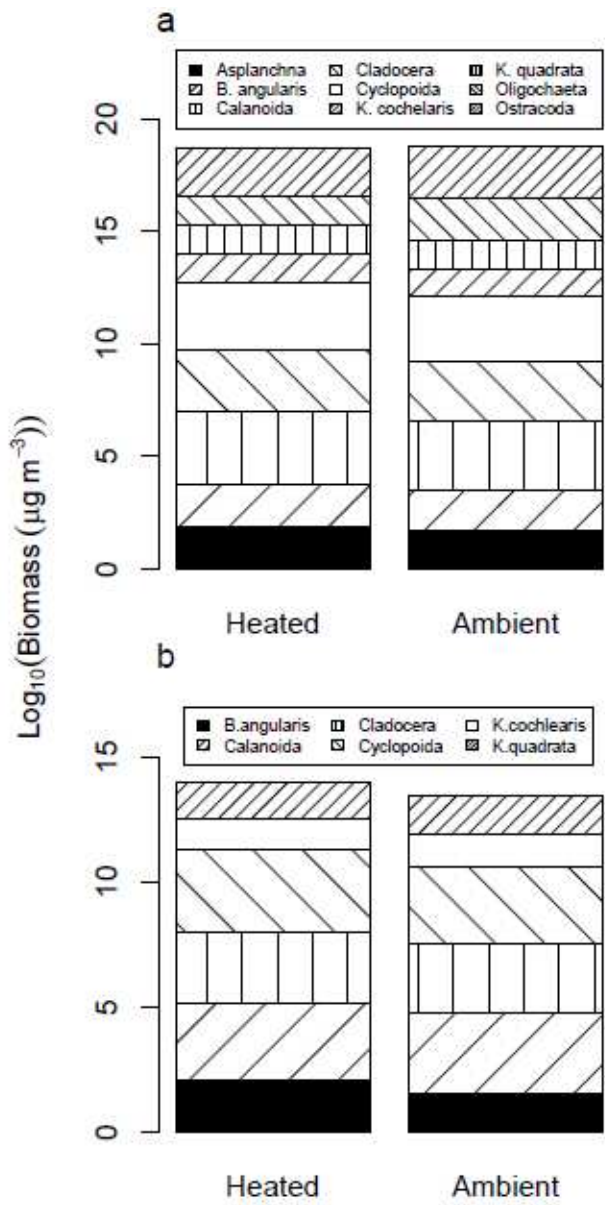


Figure 4. Mean biomass of the major zooplankton taxonomic groups documented in the mesocosms in (a) April and (b) October. Note that there is very little difference in the biomass contribution of the different zooplankton taxa between treatments suggesting that the zooplankton community composition was unaffected by warming.
 119x220mm (72 x 72 DPI)

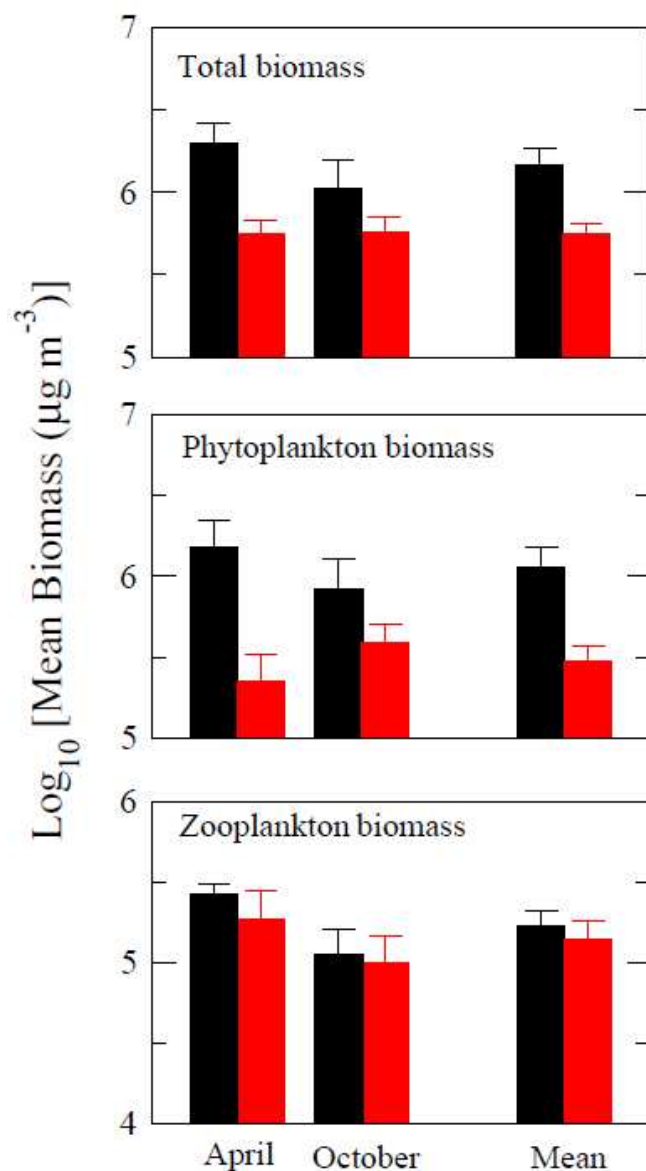


Figure.5. Effects of warming on mean total planktonic biomass (± 1 s.e.m). Data are presented as the averages of the total biomass of either phytoplankton and/or zooplankton across the mesocosms for each treatment ($n=20$ per treatment for the overall mean; $n=10$ per treatment for each sampling occasion). Total biomass is significantly reduced by warming. This is mainly driven by a reduction in phytoplankton biomass, while there is no significant difference in the biomass of zooplankton in response to warming (table 1).

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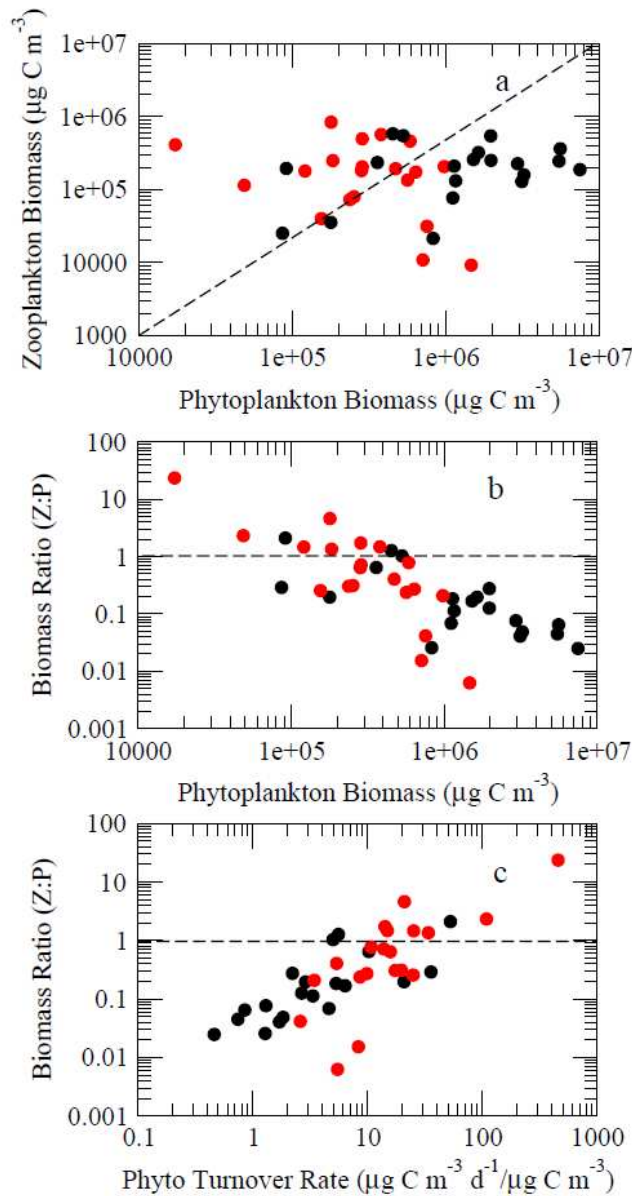


Figure 6. (a) Relationship between zooplankton and phytoplankton biomass. (b) Relationship between the ratio of zooplankton to phytoplankton biomass (Z:P) and total phytoplankton biomass. (c) The relationship between Z:P and the turnover rate of the phytoplankton communities. Each data point corresponds to either the total zooplankton or phytoplankton biomass or the Z:P in either a heated (red circles) or ambient mesocosm (black circles).
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4 1 **Warming Alters the Size Spectrum and Shifts the Distribution of Biomass in**
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16 6 **Gabriel Yvon-Durocher¹, José M. Montoya^{1,2}, Mark Trimmer¹, and Guy Woodward¹**
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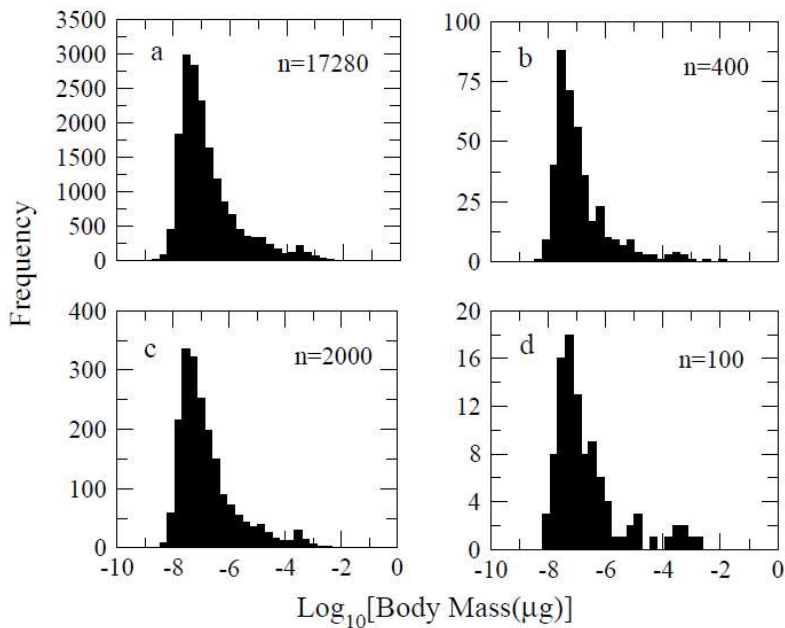
19 8 ¹ *School of Biological & Chemical Sciences, Queen Mary University of London, London E1 4NS.*
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29 13 **Authors for correspondence:** Gabriel Yvon-Durocher (g.yvon-durocher@qmul.ac.uk) and Guy
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31 14 Woodward (g.woodward@qmul.ac.uk)
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33 15 School of Biological & Chemical Sciences,
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Figure S1. Frequency distributions of individual body mass for (a) all individuals measured, (b) a random sample of 400 (i.e. the number of individuals actually measured in a sample) from a, (c) a random sample of 2000 from a, (d) a random sample of 100 from a. Data highlight that a sample of 400 individuals is sufficient to estimate the variance in the distribution of body size comparable to the whole community. When measuring the phytoplankton a minimum of 400 individuals from any given pond were measured over the number of fields of view required to count 400 from the sample in the sedimentation chamber. It is also clear that a sample of 100 is not sufficient to accurately reproduce the variance in the body mass distribution of the whole community. Assuming that organisms of a given body mass are Poisson distributed (figure S2, table S3) on the surface of the sedimentation chamber, the measurement of 400 individuals should be sufficient to attain an error of 5% [if error = $1/\sqrt{n}$].

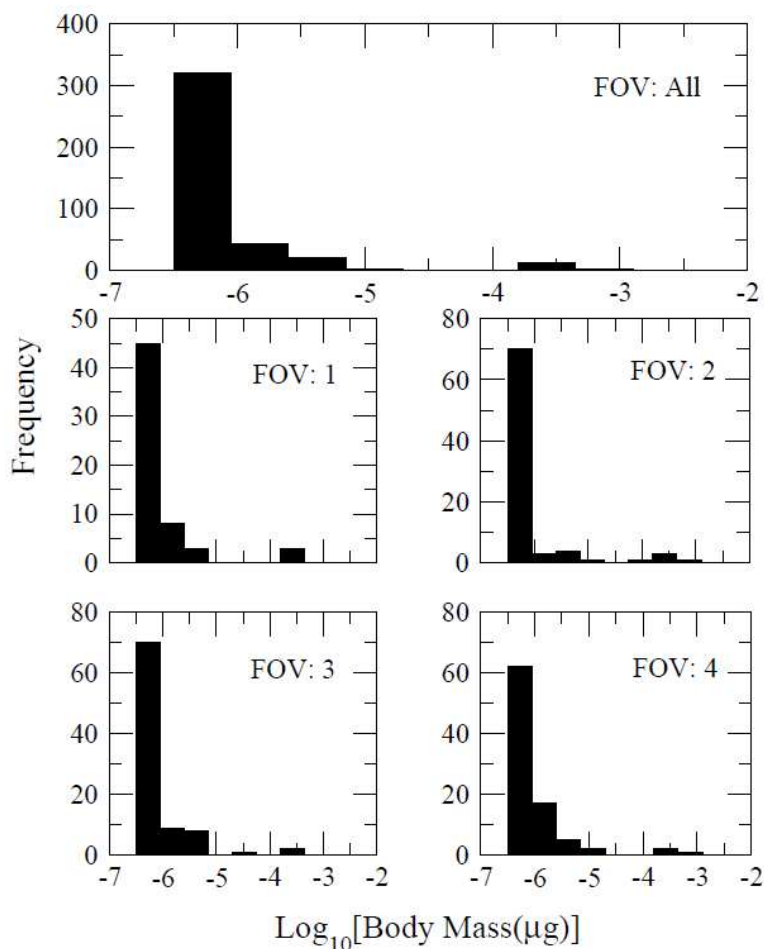
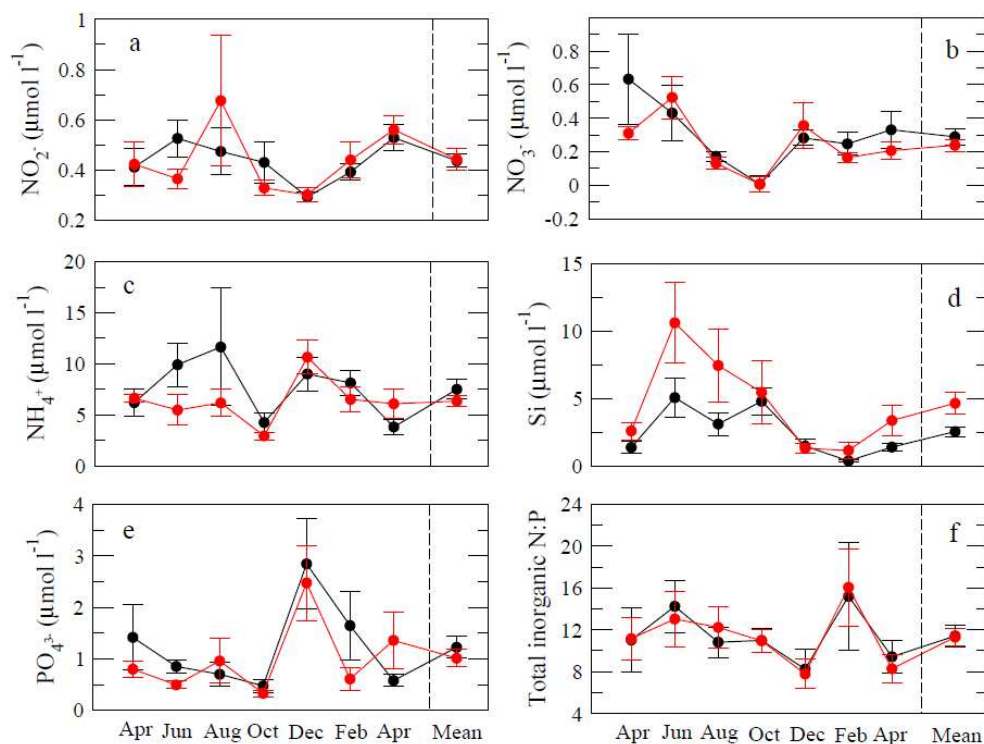


Figure S2. Size-frequency distribution for phytoplankton in pond 14 from April 2007. Panels show the size-frequency distribution after analysing all fields of view (FOV) taken to measure ~400 individuals in the sedimentation chamber, 1 FOV, 2 FOVs, 3 FOVs and 4 FOVs. Data highlight the equitable distribution of body size among fields of view which reflects the random settlement of phytoplankton cells in the sedimentation chamber. Tests for dispersion were carried for all samples and settlement conformed to Poisson statistics in every case (data not shown).



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44 **Figure S3.** Seasonality of inorganic nutrients in the warmed (red lines) and ambient (black lines)
45 mesocosms. (a) Nitrite, (b) Nitrate, (c) Ammonium, (d) Silicate, (e) Phosphate, (f) the
46 stoichiometry of the inorganic nutrient pool, N:P. Water samples for measuring dissolved
47 inorganic nutrient concentrations were collected from mid depth in the mesocosm at 9am on each
48 sampling occasion. Samples were filtered (Whatmann GF/F) and stored frozen (-20°C) for
49 subsequent determination of NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} and dissolved silica (Si) using a segmented
50 flow auto-analyser (Skalar, San++, Breda, Netherlands), according to (Kirkwood 1996).
51 Inorganic nutrients (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} & Si) exhibited strong seasonal trends. For
52 example, NO_3^- concentrations peaked in spring and declined progressively throughout the
53 summer, when rates of primary production were maximal (Yvon-Durocher *et al.* 2010), and were
54 depleted to $\approx 0.005 \mu\text{mol l}^{-1}$ by October, before regeneration in the winter. Concentrations of
55 NO_3^- , NO_2^- , NH_4^+ and PO_4^{3-} showed identical seasonal patterns in the warmed and ambient

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3 56 treatments, with no significant differences in the overall mean annual concentrations of these
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5 57 nutrients (table S4). Furthermore, the stoichiometry of the inorganic nutrient pool exhibited
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8 58 remarkable similarity between treatments, with a mean annual ratio of total inorganic N to P of
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10 59 $\approx 11:1$ in both heated and ambient mesocosms.
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15 61 **Table S4.** Results of the linear mixed effects model testing for differences in the concentration of
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17 62 inorganic nutrients between heated and ambient mesocosms. A linear mixed effects model was
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19 63 conducted with restricted maximum likelihood methods using the *lme* (linear mixed-effects
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21 64 model) function in R, treatment (heated or unheated) was the fixed effect, and temporal pseudo-
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23 65 replication from repeated sampling of the mesocosms over the year was accounted for by
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25 66 including mesocosm identity nested with sampling occasion as random effects.
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Inorganic Nutrient	DF	F	P
NO ₂ ⁻	1, 120	0.06	0.812 (NS)
NO ₃ ⁻	1, 120	0.65	0.420 (NS)
NH ₄ ⁺	1, 120	0.23	0.632 (NS)
Si	1, 120	6.08	0.015
PO ₄ ³⁻	1, 120	0.68	0.412 (NS)
Total inorganic N to P	1, 120	0.009	0.922 (NS)

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69 **Table S5.** Regression statistics for the community size spectrum of each mesocosm for the
 70 relationship: $\log(N_i) = b * \log(M_i) + a$. Where N_i is the abundance of the size class i and is the
 71 mass at the centre of the i^{th} size bin, b and a are the slope and the intercept respectively. These
 72 data highlight that the size spectrum was linear for each of the mesocosms and that the individual
 73 size distribution was a power law.

Pond	Treatment	Month	Slope	Intercept	r^2	P -value
1	Heated	April	-0.92	4.64	0.91	0.00020
2	Ambient	April	-0.94	4.58	0.81	0.00040
3	Ambient	April	-0.93	4.80	0.86	0.00030
4	Heated	April	-0.93	4.50	0.90	0.00003
5	Ambient	April	-0.79	5.28	0.84	0.00020
6	Heated	April	-1.12	3.30	0.78	0.00060
7	Ambient	April	-0.83	5.09	0.84	0.00020
8	Heated	April	-0.90	4.39	0.80	0.00040
9	Heated	April	-1.03	3.94	0.85	0.00040
10	Ambient	April	-0.92	3.89	0.80	0.00100
11	Ambient	April	-0.86	4.71	0.78	0.00200
12	Heated	April	-0.90	4.52	0.97	0.00004
13	Ambient	April	-0.98	4.21	0.74	0.00100
14	Heated	April	-0.88	4.25	0.91	0.00080
15	Heated	April	-0.94	4.64	0.80	0.00100
16	Ambient	April	-0.91	4.90	0.93	0.00001
17	Heated	April	-1.05	4.05	0.88	0.00050
18	Ambient	April	-0.71	5.58	0.81	0.00030
19	Heated	April	-0.92	5.09	0.97	0.00000
20	Ambient	April	-0.75	5.49	0.90	0.00010
1	Heated	October	-0.87	4.58	0.94	0.00001
2	Ambient	October	-0.94	4.15	0.95	0.00001
3	Ambient	October	-0.72	5.46	0.70	0.00200
4	Heated	October	-0.94	4.02	0.90	0.00001
5	Ambient	October	-0.94	4.10	0.81	0.00040
6	Heated	October	-1.06	3.68	0.85	0.00100
7	Ambient	October	-0.97	4.12	0.83	0.00020
8	Heated	October	-0.92	4.50	0.89	0.00040
9	Heated	October	-0.90	4.50	0.84	0.00040
10	Ambient	October	-0.84	5.09	0.87	0.00070
11	Ambient	October	-0.80	5.27	0.83	0.00020
12	Heated	October	-0.93	4.42	0.88	0.00006

13	Ambient	October	-0.78	5.30	0.88	0.00010
14	Heated	October	-0.94	3.75	0.82	0.00080
15	Heated	October	-0.95	4.17	0.93	0.00010
16	Ambient	October	-0.79	5.00	0.87	0.00020
17	Heated	October	-1.01	4.25	0.93	0.00010
18	Ambient	October	-0.95	3.77	0.93	0.00009
19	Heated	October	-0.85	4.70	0.89	0.00010
20	Ambient	October	-0.94	4.24	0.92	0.00004

Table S6. Regression statistics for the phytoplankton size spectrum of each mesocosm for the relationship: $\log(N_i) = b * \log(M_i) + a$. Where N_i is the abundance of the size class i and is the mass at the centre of the i^{th} size bin, b and a are the slope and the intercept respectively.

Pond	Treatment	Month	Slope	Intercept	r^2	P -Value
1	Heated	April	-0.41	7.50	0.42	0.040000
2	Ambient	April	-0.31	8.20	0.70	0.005000
4	Heated	April	-0.50	6.89	0.90	0.000092
6	Heated	April	-0.35	7.70	0.71	0.002200
7	Ambient	April	-0.22	8.39	0.57	0.012000
8	Heated	April	-0.27	8.03	0.55	0.014000
9	Heated	April	-0.55	6.78	0.88	0.000160
10	Ambient	April	-0.47	6.72	0.91	0.000020
11	Ambient	April	-0.30	7.82	0.53	0.018000
12	Heated	April	-0.76	5.08	0.62	0.011000
13	Ambient	April	-0.34	7.77	0.56	0.013000
14	Heated	April	-0.65	5.52	0.70	0.004600
15	Heated	April	-0.57	6.86	0.87	0.000200
16	Ambient	April	-0.45	7.28	0.75	0.001200
17	Heated	April	-0.52	7.20	0.67	0.004000
18	Ambient	April	-0.27	7.90	0.48	0.030000
19	Heated	April	-0.65	6.36	0.93	0.000006
20	Ambient	April	-0.34	7.60	0.77	0.000900
2	Ambient	October	-0.48	6.65	0.82	0.000300
4	Heated	October	-0.50	6.41	0.78	0.000680
5	Ambient	October	-0.34	7.70	0.85	0.000300
7	Ambient	October	-0.34	7.70	0.62	0.007000
8	Heated	October	-0.30	8.14	0.68	0.004000
9	Heated	October	-0.42	7.16	0.94	0.000005
10	Ambient	October	-0.43	7.50	0.79	0.001400

11	Ambient	October	-0.32	7.90	0.77	0.000880
12	Heated	October	-0.45	7.09	0.87	0.000240
13	Ambient	October	-0.40	7.43	0.90	0.000099
14	Heated	October	-0.35	7.41	0.58	0.010000
15	Heated	October	-0.57	6.25	0.80	0.000400
16	Ambient	October	-0.25	8.20	0.60	0.023000
17	Heated	October	-0.60	6.70	0.91	0.000200
18	Ambient	October	-0.46	6.70	0.82	0.000300
19	Heated	October	-0.36	7.49	0.69	0.003000
20	Ambient	October	-0.38	7.38	0.86	0.000300

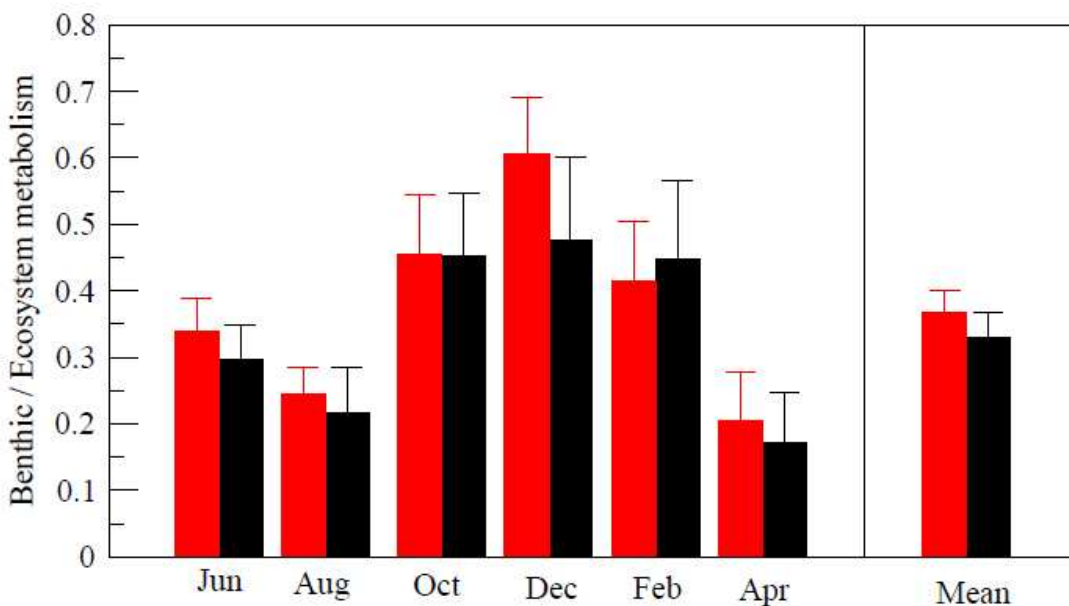


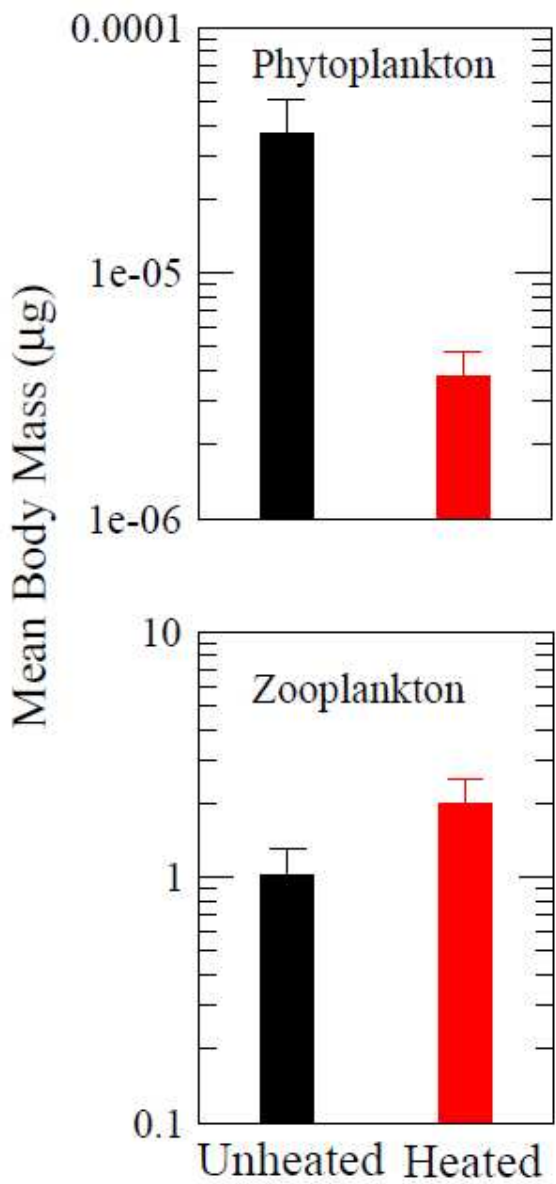
Figure S7. Quotient of benthic to ecosystem metabolism. On average over the course of the year benthic metabolism represented ~35% of whole ecosystem metabolism measured using the dissolved oxygen change technique (see Yvon-Durocher *et al.*, (2010) for details). Benthic metabolism was measured using dark in-situ benthic chambers which enclosed a sample of 500 mL at the sediment-water interface. A magnetic stirrer in the chamber ensured that the sample was evenly mixed. Benthic respiration was measured by the removal of 25mL samples at the beginning and the end of the 6 hour incubations. The samples were gently discharged into gas-

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3 91 tight vials (12ml, Exetainers, Labco Ltd, High Wycombe, UK) and allowed to overflow twice (to
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5 92 minimize atmospheric gas exchange), and fixed for Winkler analysis. The samples were
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8 93 immediately fixed and stored in a fridge at 5 °C to minimize light and temperature fluctuations
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10 94 until they could be titrated in the laboratory (< 5 d). To ensure linearity of oxygen uptake a timed
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12 95 series of samples were taken, subsequently only T = 0 and T = final samples were taken to limit
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14 96 sample extraction from the chambers.
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