



## **Growth of marine ectotherms is regionally constrained and asymmetric with latitude**

Reed, Adam J.; Godbold, Jasmin; Grange, Laura; Solan, Martin

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**Growth of marine ectotherms is regionally constrained and  
asymmetric with latitude**

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1 **Title:** Growth of marine ectotherms is regionally constrained and asymmetric with latitude

3 **Running Title:** Global growth of marine ectotherms

For Peer Review

**Abstract****Aim**

Growth rates of organisms are routinely used to summarise physiological performance, but the consequences of local evolutionary history and ecology are largely missed by analyses on wide biogeographic scales. This broad approach has been commonly applied to other physiological parameters across terrestrial and aquatic environments. Here, we examine growth rates of marine bivalves across all biogeographic realms, latitude, and temperature, with analyses to determine regional effects on growth on global scales.

**Location**

Global: Marine Ecosystems

**Time Period**

1930–2018

**Major Taxa**

Bivalves

**Methods**

We use a comprehensive data-set of bivalve growth parameters ( $n=966$ , 243 species) representing all biogeographic realms to calculate overall growth performances. We use these data with environmental temperature to analyse global patterns in growth, accounting for regional primary productivity and phylogeny using general additive mixed and linear models. The Arrhenius relationship and corresponding activation energies are used to quantify the sensitivity to temperature in each biogeographic realm and province.

**Results**

Our analyses show that bivalve growth demonstrates latitudinal asymmetry and exhibits non-linear relationships with latitude. We find that overall growth performance is affected by temperature and particulate organic carbon, but the form of these relationships differ with phylogeny. Growth is slower in the Antarctic and more sensitive to increasing temperature than in the Arctic, and decrease with increasing temperature in some tropical realms, a previously unidentified and fundamental difference in growth and physiological sensitivity.

**Main Conclusions**

Our findings provide compelling evidence that the widely used curvilinear relationship between temperature and growth rates in marine ectotherms is an inappropriate descriptor of thermal sensitivity, because it normalises regional variations in physiological performance. Without a more detailed assessment of global physiological patterns, the responses of species to local variations associated with climate change will be under-appreciated in global assessments of climate risk, minimising the effectiveness of management and conservation.

Keywords: biogeography, climate change, growth, macroecology, physiology, regionally constrained, resource management

## 77 Introduction

78 Air and sea temperatures are rising globally, and modelled projections indicate that this trend will  
79 continue leading to significant risks of extinction in terrestrial and aquatic systems (Thomas et al.,  
80 2004; Urban, 2015), that are likely to disproportionately affect ectothermic (Deutsch et al., 2008;  
81 Ohlberger, 2013) and marine organisms (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019).  
82 However, global warming is not uniformly expressed (Brierley & Kingsford, 2009; Seneviratne et al.,  
83 2018), and observed ecological responses often reflect the thermal range and physiology of species  
84 (Burrows et al., 2011; Hoegh-Guldberg & Bruno, 2010; Root et al., 2003) rather than the expectation  
85 derived from the pooling of laboratory based studies that focus on acute thermal shock response  
86 (Peck, Webb, & Bailey, 2004; Pörtner, 2001). Further, some fundamental physiological assumptions,  
87 such as variation in lifespan (Moss et al., 2016), metabolic rates (Heilmayer, Brey, & Pörtner, 2004),  
88 growth (Pörtner, Storch, & Heilmayer, 2005), and acclimation capacity (Seebacher, White, & Franklin,  
89 2014) over wide geographical ranges are based on data with poor spatial resolution and/or are fitted  
90 with curvilinear models that do not adequately account for variation in regional environmental  
91 conditions. However, incorporation of local processes is vital, as environmental history and setting  
92 affects how individuals respond to altered environmental conditions (Calosi, De Wit, Thor, & Dupont,  
93 2016; Gladstone-Gallagher, Pilditch, Stephenson, & Thrush, 2019; Deutsch, Penn & Seibel, 2020)  
94 and affect ecosystem functioning (Godbold & Solan, 2013; Wohlgemuth, Solan, & Godbold, 2016).

95 The Arrhenius relationship defines how increasing temperature accelerates metabolic processes by  
96 speeding up reaction rates (Clarke, 2017), and derived activation energies quantify the sensitivity of  
97 the response measured (Peck, 2018). This relationship of log rate against inverse temperature  
98 produces a straight line, and is often used to fit the latitudinal temperature gradient to facilitate  
99 understanding of whole animal physiology (Heilmayer, Brey & Pörtner, 2004; Peck, 2018), yet  
100 departures from the projected relationship have been identified (Peck, 2016) and have typically been  
101 explained by constraints imposed by subtle ecological distinctions (Deutsch et al., 2008), evolutionary  
102 history (Moss, Ivany, Silver, Schue, & Artruc, 2017), or molecular constraints (Peck, 2016). However,  
103 these deviations are integral to the determination of relevant ecosystem responses to climate change  
104 (Godbold & Solan, 2013), and are especially important in regions where human well-being is highly  
105 dependent on ecosystem services (van der Schatte Olivier et al., 2018).

106 Measuring physiological variation across large spatial scales provides a definitive means to  
107 understand species-specific physiological responses to a dynamic environment, but is logistically  
108 challenging and not commonly achieved in aquatic systems (Osovitz & Hofmann, 2007). A pragmatic  
109 alternative is to use growth rates in natural populations (Reed, Linse, & Thatje, 2014) and, as growth  
110 is a trade-off with metabolic rates and reproduction, it represents a reasonable approximation of  
111 whole animal physiology (Clarke, 2003; Pörtner et al., 2001). Here, we use overall growth  
112 performance (OGP, the point of inflection in a von Bertalanffy growth curve; Brey, 1999) in marine  
113 bivalves to quantify growth constraints between biogeographical realms. Marine bivalves are globally  
114 distributed and their growth is integrated within their shells (Moss et al., 2016). OGP is preferential to  
115 the more frequently used growth constant ( $k$ ) as it takes into consideration the theoretical maximum

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3 116 shell length of individuals, allowing comparisons between taxa (Brey, 1999). By calculating activation  
4 117 energies in biogeographical realms we quantify the thermal sensitivity of regional growth and identify  
5 118 realms at greater risk to projected temperature change based on how local species growth differs  
6 119 across local temperature ranges. We anticipate that regional disparities will expose a fundamental  
7 120 misunderstanding of physiological responses in regions at the upper and lower thermal limits of these  
8 121 species, especially where previous efforts have pooled data or not taken into account evolutionary  
9 122 history or unique local ecologies. By exploring the spatiotemporal distribution of physiological  
10 123 characteristics across the globe (Osovitz & Hofmann, 2007), physiological projections within distinct  
11 124 regions can be determined (Chown, Sinclair, Leinaas, & Gaston, 2004; Pörtner & Knust, 2007;  
12 125 Somero, 2010), shifting paradigms that are likely to benefit conservation and management efforts  
13 126 (Stuart-Smith, Edgar, Barrett, Kininmonth, & Bates, 2015).

## 19 127 **Methods**

21 128 We searched the Thomson Reuters Web of Science collection (<http://www.webofknowledge.com>,  
22 129 accessed July, 2019) using the search terms (“*bivalve*”, “*growth*”, and “*von Bertalanffy*”) in the titles,  
23 130 keywords and abstracts of all document types from 1950-2018. Further relevant publications were  
24 131 obtained by manually checking references cited by the authors of the returns from our search. We  
25 132 excluded all publications that were based on data from cultured or artificially reared populations, but  
26 133 data from PhD theses or ‘grey literature’ were included after critical examination of the methodology to  
27 134 ensure consistency with published growth parameters. A list of the data sources is found in Appendix  
28 135 S1.

### 33 136 *Growth data*

35 137 Citation returns were manually searched for reported values of parameters of growth from von  
36 138 Bertalanffy growth functions ( $k$ ,  $L_{\infty}$ , and, if possible,  $L_T$ ). A total of 429 peer-reviewed publications  
37 139 revealed 966 growth parameters for 243 species of bivalve from 143 Genera, 44 families and three  
38 140 subclasses (Reed et al. 2020). As well as taxonomic information, geographical location, depth, and  
39 141 temperature were extracted when available (see *Environmental Data*). When the location of a study  
40 142 was not provided, latitude and longitude coordinates and/or water depth were retrieved from Google  
41 143 Earth (<http://earth.google.com/>) and manually cross referenced with site descriptions within the source  
42 144 publication. Taxonomy was verified and updated to latest classification using the World Online  
43 145 Register of Marine Species (WoRMS Editorial Board, 2020)

44 146 Where specific size-at-age values were not presented in the original publication and had to be  
45 147 derived, values were extracted from graphical summaries using Web Plot Digitiser  
46 148 (<https://automeris.io/WebPlotDigitizer/>). We determined the required growth data using these data by  
47 149 applying the von Bertalanffy model as described by Brey 1999:

$$56 \quad 150 \quad L_t = L_{\infty} (1 - e^{-k(t-t_0)})$$

57 151  
58 152 where  $k$  is the growth constant and  $L_{\infty}$  is the asymptotic length.

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3 153 In contrast to previous publications on global growth data, we were able to calculate Overall Growth  
4 154 Performance (OGP) as we only included publications with growth parameters from a von Bertalanffy  
5 155 growth curve. Previous global studies comparing growth have only used single parameters directly  
6 156 derived from the growth curve and typically use  $k$  (The Brody growth coefficient) as a measure of  
7 157 growth between species (Moss et al., 2016; Peck, 2016). However, growth is non-linear and it is not  
8 158 appropriate to compare growth using single parameters from the growth function in a statistical  
9 159 analysis (Brey, 1999). OGP derived from the Bertalanffy growth function makes growth comparable  
10 160 between populations and species by removing individual variation and is defined as the point of  
11 161 inflection on the Bertalanffy growth curve (Brey, 1999). Overall Growth Performance is calculated  
12 162 from the equation:

13 163

$$14 \text{ OGP} = \log(k L_{\infty})$$

#### 15 *Environmental data*

16 166 When temperature data was not reported, bottom water temperatures were extracted from Ocean  
17 167 Data View v. 5.1.0 and the World Ocean Atlas 2013 database (Locarnini et al., 2013) at a resolution  
18 168 of 0.25 degrees and using coordinates from the corresponding paper. We only used recorded bottom  
19 169 temperatures and not sea surface temperatures which are commonly used in global marine studies,  
20 170 as the bottom temperatures are more representative of the benthic environment.

21 171 OGP data was grouped based on Spalding's classification of biogeographical latitude zones, realms,  
22 172 and provinces (Spalding et al., 2007). While all biogeographic realms are represented in our data-set,  
23 173 provinces with no samples are not included in our maps and are shown as data deficient gaps. Unlike  
24 174 previous studies examining physiological patterns across wide geographic areas, we differentiate  
25 175 OGP between the different biogeographical latitude zones, realms, and provinces which allows a  
26 176 higher resolution and critical examination of regional OGP.

27 177 POC flux to the seafloor was derived by applying a vertical flux attenuation equation to satellite-  
28 178 derived export fluxes. The export flux is calculated from satellite-derived primary production (Carr,  
29 179 2001) and sea surface temperature using the relationship defined in Henson et al. (2011). Flux  
30 180 attenuation is described by "Martin's b" parameter (Martin et al., 1987) and is estimated globally using  
31 181 a collation of deep moored sediment trap data as described in Henson et al. (2012). Seafloor depth is  
32 182 taken from the ETOP01 global relief model (Amante and Eakins, 2009). All data are spatially  
33 183 averaged onto a 1x1 degree grid prior to analysis. POC flux to the seafloor (in  $\text{gC m}^{-2} \text{yr}^{-1}$ ) is extracted  
34 184 from the global data at each sample location using a nearest neighbour approach. The POC flux to  
35 185 seafloor could not be estimated at several shallow shelf locations due to the limitations of satellite-  
36 186 derived data and the flux model in very shallow waters. In these instances, the nearest geographical  
37 187 point (linear Euclidean distance) with data was supplemented.

#### 38 *Arrhenius Relationship*

39 189 The Arrhenius relationship relates chemical reaction rates to temperature, and is expressed by;

$$k = Ae^{\left(\frac{-E_a}{RT}\right)}$$

Where  $k$  is the rate constant,  $R$  is the gas constant,  $T$  is absolute temperature, and  $E_a$  is the activation energy. Physiological processes have been proven to respond predictably by following the Arrhenius relationship within normal biological temperature ranges (Clarke & Johnston, 2003; Heilmayer et al., 2004). We calculate activation energies (ev) from the linear relationship between absolute temperature and overall growth performance to represent the sensitivity of OGP to temperature. These values can be used to directly compare biological reaction rates and processes such as growth. For biological processes activation energies can range between 0.2 and 1.2ev (Gillooly, Brown, West, Savage, & Charnov, 2001) but usually vary between 0.6 and 0.7ev (Dell, Pawar, & Savage, 2011).

### 200 *Statistical data analysis*

To determine the direction and significance of the relationship between OGP and latitudinal zone between Realms, we used a generalised additive model (GAM) with a Gaussian distribution using “REML” estimation. We further account for regional differences in temperature and primary productivity (POC  $\text{gC m}^{-2} \text{yr}^{-1}$ ;  $\ln$  transformed) and test for any differences in growth rates of related species occurring at similar temperatures but in different regions (Subclass, 2 levels: Heterodonta and Pterimorphia; the subclass Protobranchia (9 observations) were excluded from the analysis). To investigate the relationship between OGP, temperature and  $\ln(\text{POC})$  we used a Generalized Additive Mixed Model (GAMM) incorporating the factor “Realm” as a random effect. To estimate the optimal amount of smoothing in both analyses ( $s(\text{latitude})$  and  $s(\text{temperature})$ ,  $s(\ln(\text{POC}))$ ) we used cross-validation (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; Zuur, Saveliev, Ieno, 2015) followed by optimisation of  $k$  following Wood et al. (2017). Smoothers for Latitude and  $\ln(\text{POC})$  were fitted with cubic spline regression ( $cs$ ), whilst the smoother for temperature was fitted with thin plate regression ( $tp$ ). For both analyses final best models were based on Akaike information criterion (AIC) and residual fits were examined (Zuur, Saveliev, Ieno, 2015; Wood et al. 2017). Predicted values and 95% Confidence Intervals of final models were determined and fitted following Zuur, Saveliev & Ieno (2015).

To determine the importance of latitudinal zone and the Arrhenius model on  $\ln(\text{OGP})$  we developed an ANCOVA model containing latitudinal zone as a nominal explanatory variable with 4 levels (Antarctic, Arctic, Temperate and Tropical) and the Arrhenius model represented by inverse temperature (Kelvins) as a continuous explanatory variable. We visually assessed model assumptions (homogeneity of variances and normality) which revealed patterns in the residual spread. To model the heteroscedasticity in the variance structure we incorporated the variable “latitude” as a variance covariate using  $\text{varIdent}$  (Pinheiro & Bates, 2000).

Latitude and longitude coordinates of the individual data points were used to visually assess the effects of spatial autocorrelation using bubble plots (Pebesma & Graeler 2019) and variograms (Zuur et al., 2009). Analyses were conducted in R (R Development Core Team 2018) using the “nlme”



227 library for the extended linear model (Pinheiro, Bates, DebRoy, & Sarkar, 2018), the “mgcv” library for  
228 the additive (mixed) models (Wood, 2019) and “gstat” for investigating spatial autocorrelation  
229 (Pebesma et al., 2019).

## 230 **Results**

231 We established 966 measurements of bivalve growth parameters spanning 243 species and  
232 representing all 12 biogeographic realms. Measurements of overall growth performance (OGP)  
233 ranged from 0.01 to 2.68 and extended from 80 °N to 77 °S and from 176 °W to 175 °E. Depth was  
234 rarely reported in the literature, however most growth measurements were from species known from  
235 the coast or shelf (<200 m) regions with 8 species specifically reported from deeper waters (250 –  
236 4600 m) and no observations from hadal depths. The distribution of data corresponds mostly to the  
237 Temperate North Atlantic Realm, (n = 367), followed by the Temperate North Pacific (n = 173) and  
238 Temperate South America (n = 148) Realms, and indicates that most observations emanate from the  
239 northern hemisphere (73.3%). Temperate Latitude Zones are highly represented (n = 737), followed  
240 by Tropical (n = 124) and Polar (n = 105) Latitude Zones.

241 Using these data, our analyses reveal that OGP in marine bivalves increases with decreasing latitude  
242 and, for the first time, we show that the form of this relationship is non-linear (GAM, edf= 8.651, F =  
243 13.927 p<0.0001, Figure 1a) and that OGP differs between Realms (GAM, F = 10.13, p <0.0001,  
244 Figure 1b). Specifically, we find that there is an increase in mean OGP in the North Atlantic above  
245 50°N driven by species in the Northern European Seas, whilst the Mediterranean Sea is characterised  
246 by lower mean OGP ( $1.14 \pm 0.31$ , Figure 1c, Figure S2.1). In the Southern Hemisphere, the highest  
247 mean OGP ( $\pm$  95% CI) is observed in the tropical regions of the Central and East Indo-Pacific ( $1.93$   
248  $\pm 0.16$  and  $1.67 \pm 0.20$ , respectively), decreasing towards the temperate realms and into the Southern  
249 Ocean ( $0.57 \pm 0.17$ ). In the Northern Hemisphere, the results indicate a second peak in OGP (Figure  
250 1a) at around 50°N in the Temperate North Pacific and North Atlantic realms. Between latitudinal  
251 zones, mean OGP ( $\pm$  95% CI) was lowest in the Antarctic and Arctic ( $0.575 \pm 0.173$  and  $0.930 \pm$   
252  $0.073$ , respectively) and highest in Tropical areas ( $1.569 \pm 0.078$ ) (Figure 1a), albeit influenced by a  
253 high mean OGP in the Central and East Indo-Pacific realms (Figure 1b).

254 Our analyses confirm a positive relationship between temperature and decreasing latitude (Figure  
255 S2.2). Whilst OGP increases with temperature (GAMM, edf=7.821, F = 14.21, p<0.0001), we find a  
256 non-linear, stepwise relationship (Figure 2a) that broadly corresponds to Polar (-2 to 6°C), Temperate  
257 (7 to 17°C), and Tropical (18 to 27°C) latitudinal zones. Furthermore, the requirement to incorporate  
258 Realm as a random effect confirms the important role of biogeographical divisions in determining  
259 temperature dependent OGP. We found that particulate organic carbon levels are highest in  
260 temperate latitude zones and overlap with the Arctic, whilst are low throughout the Antarctic and  
261 tropical areas (Figure S2.3), but that the shape of the relationship between OGP and ln(POC) differs  
262 between the two Subclasses of bivalves and is only significant for the Pteriomorphia (ln(POC) :  
263 Pteriomorphia: edf = 5.9, F = 10.142, p<0.0001; Heterodonta: edf = 1, F = 1.506, p = 0.22). For the  
264 Pteriomorphia (8 families, n = 408) there is a peak in OGP at intermediate levels of ln(POC), whilst for

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3 265 the Heterodonta (29 families,  $n = 549$ ) there is no difference in OGP with changing  $\ln(\text{POC})$  (Figure  
4 266 2b). Overall, OGP is significantly higher in the Pteriomorphia (mean =  $1.409 \pm 0.047$ ,  $n = 407$ ) than  
5 267 the Heterodonta (mean =  $1.228 \pm 0.032$ ,  $n = 550$ ; GAMM,  $t = 11.55$ ,  $p < 0.0001$ ; Figure 2c., Figure  
6 268 S2.4; S2.5).

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10 269 We fitted an Arrhenius model using inverse temperature ( $1000/T$  in Kelvins) and  $\ln(\text{OGP})$ , and their  
11 270 interaction, to test OGP against the expected physiological relationship with temperature (Figure 3a)  
12 271 We find that  $\ln(\text{OGP})$  is positively affected by the independent effects of latitude (GLS, L. ratio =  
13 272  $33.561$ , d.f. = 1,  $p < 0.0001$ ) and inverse temperature (GLS, L. ratio =  $31.967$ , d.f. = 3,  $p < 0.0001$ ), but  
14 273 deviate from the expected relationship in the Antarctic at temperatures  $< 0^\circ\text{C}$  (Figure 3b). The  
15 274 activation energies which quantify the Arrhenius relationship within each biogeographical Latitudinal  
16 275 Zone and Realm (Figure 4) reveal high sensitivity to temperature in the Antarctic Latitude Zone ( $0.987$   
17 276 eV) and low sensitivity across the Tropical Latitude Zone ( $0.035$  eV) (Figure 4a; Figure S2.6).  
18 277 However, between the biogeographical realms the heterogeneity within tropical and polar zones  
19 278 becomes more apparent, with values between  $-0.770$  eV and  $0.987$  eV (Figure 4b; Figure S2.7).  
20 279 These data show a negative relationship of OGP with increasing temperature in East Indo-Pacific,  
21 280 West Indo-Pacific, Tropical Pacific and Temperate Australia, indicating reduced growth in species in  
22 281 these regions with increasing temperatures, while all temperature and polar biogeographic realms  
23 282 show a positive relationship with temperature.

## 30 283 **Discussion**

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32 284 This global database of overall growth performance (OGP) in marine bivalves confirms that growth  
33 285 increases with decreasing latitude (Moss et al., 2016; Pörtner, Storch, & Heilmayer, 2005), but we  
34 286 reveal that the form of this relationship is non-linear and depends on biogeographical context.  
35 287 Latitudinal variation of physiological parameters has previously been associated with seasonality and  
36 288 genetic adaptations to a specific temperature range (Yamahira & Conover, 2002), although  
37 289 temperature dependent hypoxia may also have a major role in determining biogeographical patterns  
38 290 (Deutch, Penn, & Seibel, 2020). Regional disparities observed here can, however, be linked to  
39 291 specific circumstances; for example, the lower mean OGP found in the Mediterranean is likely related  
40 292 to growth limitation through lower food availability in this largely oligotrophic region (Siokou-Frangou  
41 293 et al., 2010), a view supported by laboratory experiments on bryozoans (Svensson & Marshall, 2015)  
42 294 and Antarctic bivalves (Román-González et al., 2017). Such observations emphasise that, whilst  
43 295 deviation from the global mean can form an important means of determining local effects that are  
44 296 driven by subtle ecological variation, spatial analysis of a larger biogeographical range can highlight  
45 297 variation in physiological characteristics otherwise invisible in studies conducted over smaller scales  
46 298 (Chown, Gaston, & Robinson, 2004; Parmesan & Yohe, 2003). This is important as unique local  
47 299 environmental characteristics and history may have a greater affect than previously recognised when  
48 300 data has been pooled from perceived identical environments.

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58 301 Whilst our analysis confirms that overall growth performance at lower temperature deviates from the  
59 302 expected thermodynamic relationship (e.g. Peck, 2016), we identify a critical difference between  
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3 303 Arctic and Antarctic environments that has not been previously recognised or distinguished  
4 304 (Heilmayer et al., 2004; Peck, 2016). Specifically, when average bottom temperatures are  $< 0^{\circ}\text{C}$ , the  
5 305 growth of Arctic bivalve species are consistent with physiological expectations, whereas the growth of  
6 306 Antarctic bivalve species deviates below the expected relationship. The only exception to this pattern  
7 307 is the Antarctic scallop *Adamussium colbecki* which remains within expectation. This revelation is  
8 308 striking, because *A. colbecki* is routinely used as a model species for physiological studies in the  
9 309 Antarctic (Moro et al., 2019), meaning that *a priori* assessments of the physiological responses of  
10 310 polar ecosystems to climate warming may underestimate species vulnerability in the Antarctic whilst  
11 311 overestimating species vulnerability in the Arctic. Further, differences in growth performance between  
12 312 subclasses are likely to be reflected in their overall physiology (Pörtner et al., 2001); the subclass  
13 313 Pteriomorpha contains fewer, but larger, families, which include commercially valuable species (van  
14 314 der Schatte Olivier et al., 2018), such as Mussels (Mytillidae), Oysters (Ostreidae), and Scallops  
15 315 (Pectinidae), which may dominate regional assessments of physiological fitness. Should a high  
16 316 proportion of studies focus on a limited subset of regionally adapted species, or physiological  
17 317 typology, there is potential for model projections to perpetuate skewed conclusions about the most  
18 318 likely effects of climate change at larger scales (Wernberg, Smale, & Thomsen, 2012). These  
19 319 observations are consistent with other research in global marine environments that has shown  
20 320 regional and temporal differentiation in the severity and direction of effects associated with climatic  
21 321 forcing (Dijkstra, Westerman, & Harris, 2011; Godbold & Solan, 2013).

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31 322 Although our analyses confirm a positive relationship between sea temperatures and decreasing  
32 323 latitude, it is important to emphasise that sea temperature is also influenced by local environmental  
33 324 cycles and other phenomena (e.g. depth, upwelling, El Niño) which can affect regional physiological  
34 325 responses. In this respect, it is noteworthy that the large degree of overlap of the Arctic and  
35 326 Temperate latitudinal zone reflects the boreal origins of many benthic species (Piepenburg, 2005),  
36 327 and that the large degree of overlap in high POC in the Arctic and Temperate regions reflects food  
37 328 availability to the benthos and species distribution (Solan et al. 2020). A key characteristic of the  
38 329 Arctic is the Atlantic influence and overlap of species distributions and physiological responses over  
39 330 the polar front (Piepenburg, 2005; Richard, Morley, Deloffre, & Peck, 2012), which contrasts to the  
40 331 Antarctic which is effectively isolated by the Antarctic Circumpolar Current from the southern  
41 332 Temperate Zone (Clarke & Crame, 2010) resulting in a relatively long evolutionary isolation of the  
42 333 Southern Ocean (Chown et al., 2015; Crame et al., 2014; Clarke, Barnes, & Hodgson, 2005).  
43 334 Isolation over evolutionary relevant timescales in the Antarctic has led to unique fauna and  
44 335 adaptations in response to low temperature (Barnes, Fuentes, Clarke, Schloss, & Wallace, 2006)  
45 336 which slow their biological processes beyond expectations (Peck, 2016; Peck, Heiser, & Clark, 2016).  
46 337 Hence, we observe greater thermal sensitivity and reduced OGP in the Antarctic relative to the Arctic  
47 338 (Richard et al., 2012). An important implication of this finding is that the common practice of pooling  
48 339 data from realms that are perceived as being similar to one another in order to overcome paucity of  
49 340 data is undesirable, as species responses are unlikely to be uniform across ecoregions.  
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3 341 The activation energies, representing all the reactions involved in the synthesis of proteins for growth,  
4 342 and calcification of the shell, strongly indicate that tropical realms and the Southern Ocean will be  
5 343 disproportionately affected by projected climate change in the 21<sup>st</sup> Century (IPCC, 2018), albeit with  
6 344 different population responses. A decrease in growth rate with increasing temperatures suggests that  
7 345 species may be beyond their thermal optimum, and is supported by theories of tropical species living  
8 346 close to their thermal limits (Dell, Pauer, & Savage, 2011; Amarasekare and Savage, 2012). Despite  
9 347 the importance of temperature however, the maximum rates of growth in an individual is unlikely to be  
10 348 achieved because of, for example, resource limitation (Siokou-Frangou et al., 2010) or highly  
11 349 seasonal food input (Zuo, Moses, West, Hou, & Brown, 2012). The regions of negative or very high  
12 350 activation energy in our study reflect these two environmental conditions. In the Antarctic, where  
13 351 temperature variations are very small, seasonality in metabolism can positively relate to food input in  
14 352 species of sponge (Dayton, Robilliard, Paine, & Dayton, 1974), echinoderm (Brockington & Clarke,  
15 353 2001), and bryozoan (Barnes, 1995), which show faster growth and metabolic rates than expected  
16 354 during periods of high food availability. However, immature Southern Ocean *A. colbecki* show no  
17 355 uncoupling of metabolic rate from temperature, suggesting an ontogenetic component to relationships  
18 356 between somatic growth, food availability, and temperature (Heilmayer et al., 2005). The Arctic is also  
19 357 food limited with an observed mismatch between shell growth and body mass in the bivalves *Serripes*  
20 358 *groenlandicus* and *Chlamys islandica* before the onset of phytoplankton bloom (Blicher, Rysgaard, &  
21 359 Sejr, 2010; Carroll et al., 2011). Here, food quality rather than quantity is shown to be fundamental  
22 360 factor, and can be observed through the transition of lower quality phytoplankton to nutrient rich sea  
23 361 ice algae during the seasonal sea ice retreat, and a projected negative response to warming related  
24 362 changes in sea ice primary production in Arctic fjords (Carroll et al., 2011).

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26 363 An alternative explanation to the constrained growth in Antarctic bivalves is protein synthesis, a vital  
27 364 process in somatic growth widely hypothesised to be limited at low or high temperatures (Dell, Pauer,  
28 365 & Savage, 2011; Peck, 2016). How this might be negated at low temperatures by projected warming  
29 366 is, however, currently unclear (Clark et al., 2019). The pathways involved in the synthesis and folding  
30 367 of functional proteins, generally occurs faster as temperatures increase and is widely postulated to be  
31 368 expensive and sensitive at low temperature (Clarke, 2017; Fraser & Rogers, 2007). However,  
32 369 adaptive changes within the genome can overcome protein efficiency to some extent (Chen et al.,  
33 370 2008). The sensitivities of growth performance to warming in the tropical and polar biogeographical  
34 371 realms may reflect these molecular constraints, however, research into protein function and synthesis  
35 372 in marine organisms is still in its infancy (Tomanek, 2011). This emerging area of research may well  
36 373 elucidate the molecular mechanisms behind limitations to growth in the lowest and highest  
37 374 temperature environments, and identify the constraints that maintain their sensitivity to temperature  
38 375 changes (Clark et al., 2019), especially when comparing the contrasting physiological responses from  
39 376 the Arctic and Antarctic realms from an evolutionary perspective (Feder, Bennett, & Huey, 2000).

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56 377 Macroecological approaches to examine growth rates of important marine ectotherms, as used here,  
57 378 form an essential link between laboratory experiments and appropriate regionally adjusted  
58 379 assessment of risk (Chown, Gaston, et al., 2004; Chown, Sinclair, et al., 2004). The non-linear  
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380 relationship of OGP with temperature and latitude suggests that other ecological and phylogenetic  
 381 constraints will exist across a latitudinal gradient and between ecological realms (Parmesan & Yohe,  
 382 2003), but these may be underestimated or ignored when traditional assumptions on thermal  
 383 relationships are applied in isolation. This carries implications to the way we assess physiological  
 384 responses to climate change scenarios (Clarke, 2003; Feder et al., 2000) as the consequences of  
 385 climate change will differ at local scales (Stuart-Smith et al., 2015), or across species distributions  
 386 (Deutch, Penn, & Siebel, 2020). Climate change is not consistently expressed across latitude ranges  
 387 and while experimental approaches have persistently shown the greatest severity of warming on  
 388 physiology to be within tropical (Deutsch et al., 2008; Tewksbury, Huey, & Deutsch, 2008) and across  
 389 both polar realms (Peck et al., 2004; Pörtner, Peck, & Somero, 2007), contradictory linear  
 390 relationships with greatest thermal capacity at the tropics have also been identified (Seebacher et al.,  
 391 2014). With this in mind, identification of where management and conservation efforts should be  
 392 focussed can be achieved by using better fitting statistical models, which do not assume linearity in  
 393 thermal relationships with physiological parameters. Linking regional and global physiological patterns  
 394 with acclimation capacity, plasticity, and ultimately adaptation to projected environmental change will  
 395 be essential to ameliorating the consequences of climate change on ecosystem function to protect  
 396 against the loss of ecosystem services.

#### 397 **Data Accessibility**

398 The growth and corresponding environmental data (Particulate Organic Carbon and Temperature)  
 399 used in this study is available through figshare with appropriate descriptors  
 400 (<https://doi.org/10.6084/m9.figshare.9943058.v1>)

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## 656 Figure Legends

657 **Figure 1. Variation in overall growth performance with latitude, realm, and biogeographic**  
658 **province** a) Trend in overall growth performance with latitude, b) Mean overall growth performance ( $\pm$ )  
659 95% confidence intervals) in each biogeographical Realm, and c) Global map of mean overall growth

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3 660 performance within each biogeographic Province and data points overlaid with colour representing  
4 661 mean annual average bottom temperature. In a) Model prediction (solid line) and 95% confidence  
5 662 intervals (dotted line) for changes in overall growth performance with latitude are shown, with data  
6 663 point colours representing the four latitudinal zones.

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8 664 **Figure 2. Trends in overall growth performance of bivalves with a) average annual bottom**  
9 665 **temperature (°C) and b) particulate organic carbon (In g C m<sup>-2</sup> yr<sup>-1</sup>) and in c) overall growth**  
10 666 **performance for each Subclass.** In a) and b) model predictions (solid lines) and 95% confidence  
11 667 intervals (dashed lines) are shown for changes in overall growth performance for the Subclasses  
12 668 Heterodonta (light blue) and Pteriomorphia (light blue); c) median is indicated at the midpoint, the  
13 669 upper and lower quartiles are indicated by the hinges, and open circles indicate outliers. Data points  
14 670 are superimposed.

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16 671 **Figure 3. Geographically differentiated relationships of overall growth performance and**  
17 672 **absolute temperature** a) Arrhenius model of global overall growth performance values against  
18 673 inverse temperature (in Kelvins) (n.b. temperature scale from high to low); b) Arrhenius model using  
19 674 Arctic (dark blue) and Antarctic (red) data points with regression line of the global relation of overall  
20 675 growth performance to inverse temperature (in Kelvins).

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22 676 **Figure 4. Activation energies derived from Arrhenius models for geographic regions** a)  
23 677 Activation energy (ev) as calculated from the slope of the line in each latitude zone; b) Activation  
24 678 energy (ev) as calculated from the slope of the line within each geographical Realm. Realm codes  
25 679 given in parenthesis; 1 – Arctic; 2 – Temperate North Atlantic; 3 – Temperate North Pacific; 4 –  
26 680 Tropical Atlantic; 5 – West Indo-Pacific; 6 – Central Indo-Pacific; 7 – East Indo-Pacific; 8 – Tropical  
27 681 East Pacific; 9 – Temperate South America; 10 – Temperate South Africa; 11 – Temperate Australia;  
28 682 12 – Southern Ocean.

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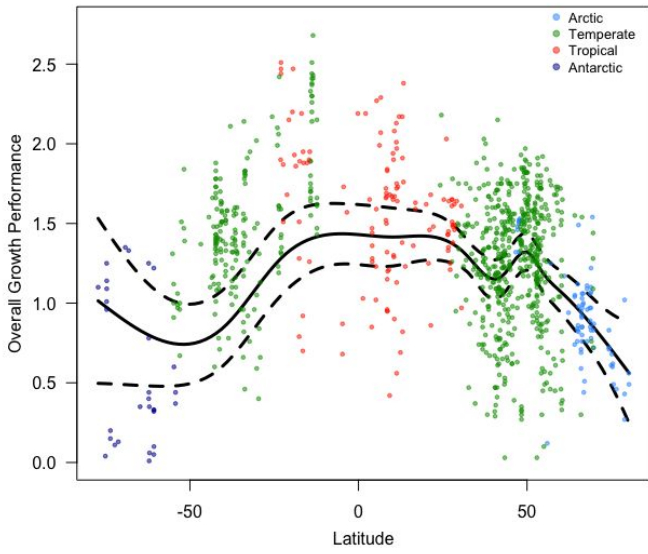
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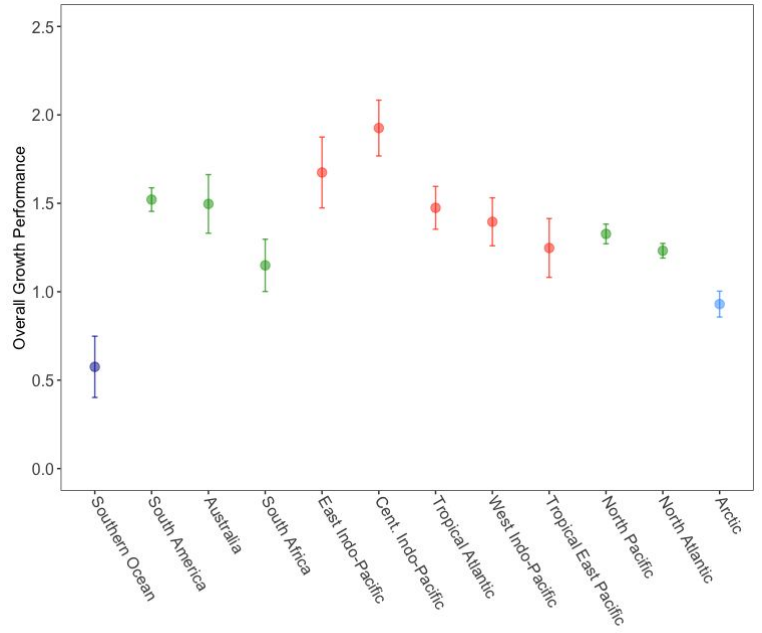
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Figure 1

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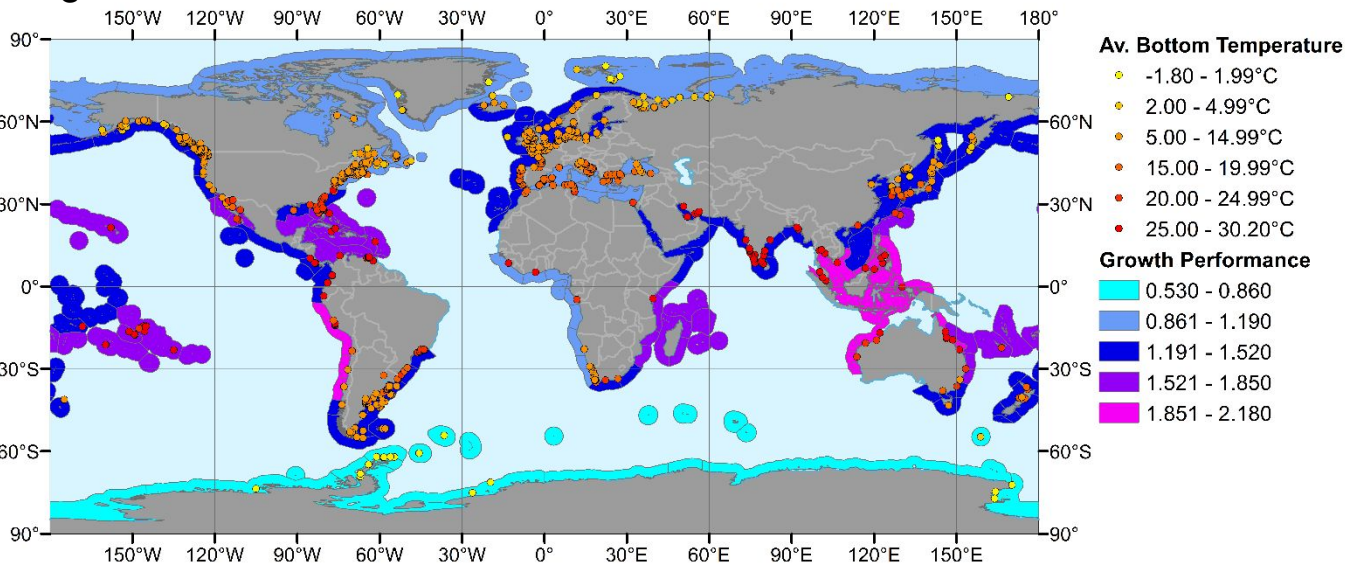


Figure 2

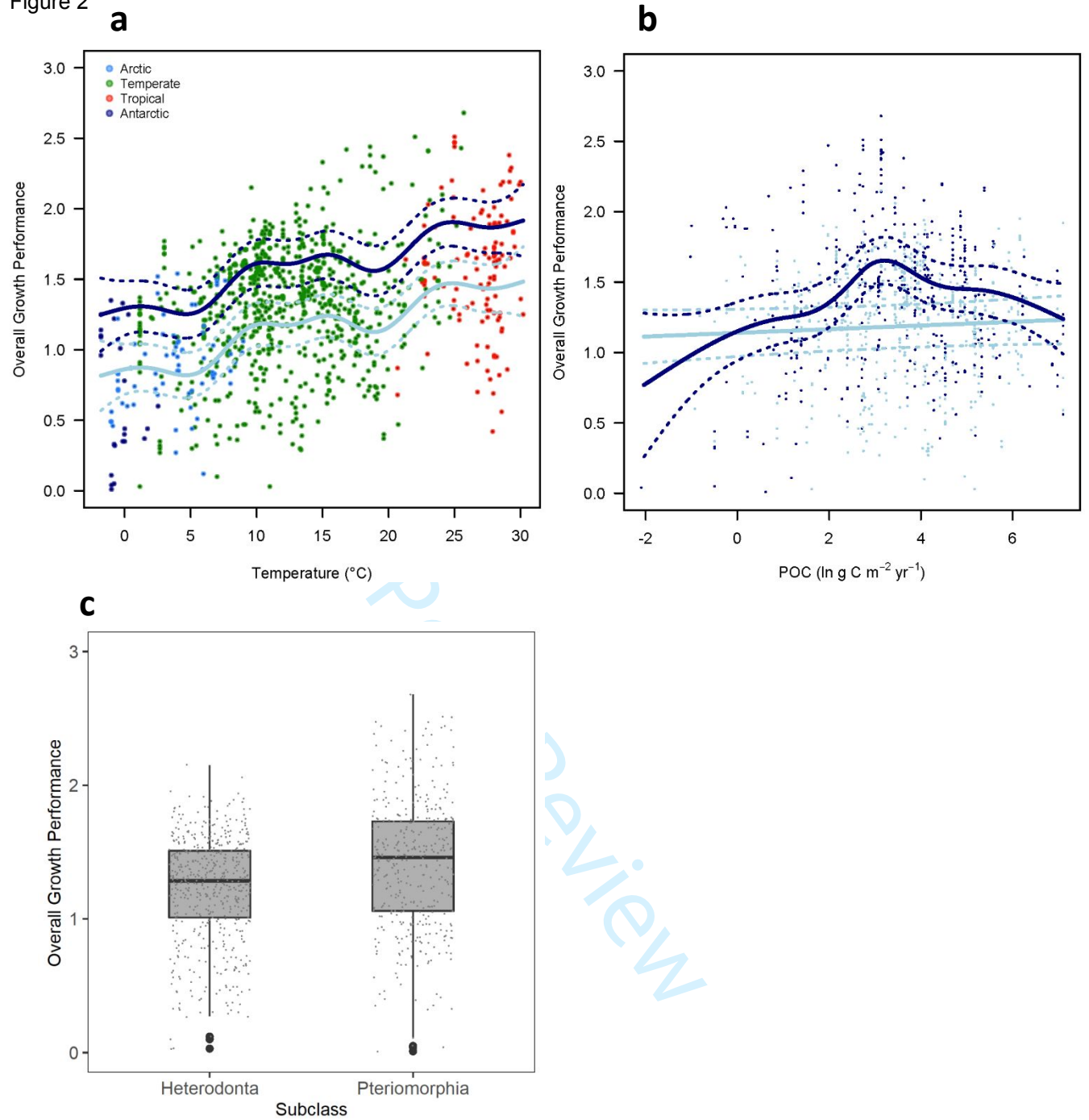
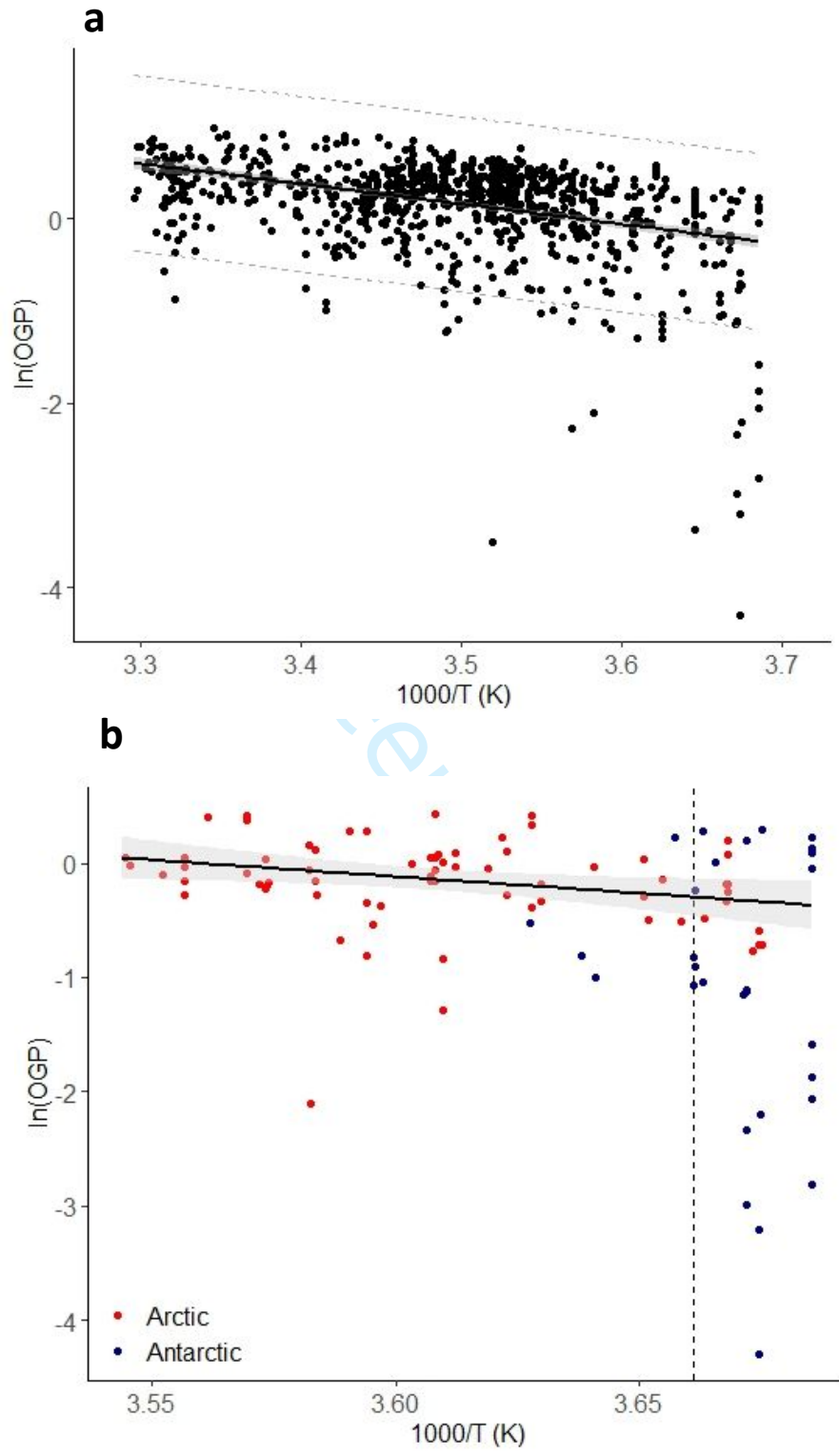
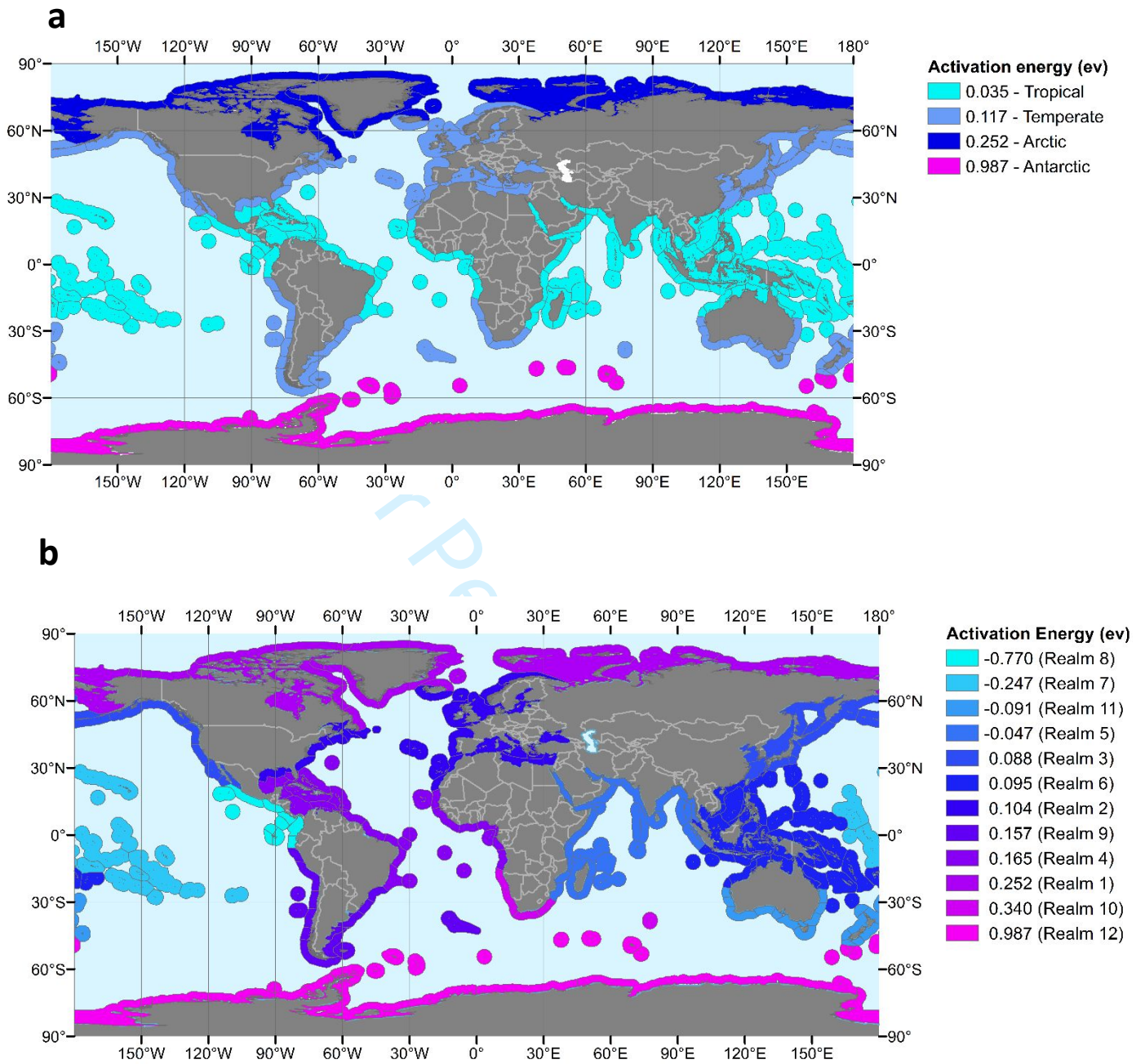


Figure 3



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Figure 4



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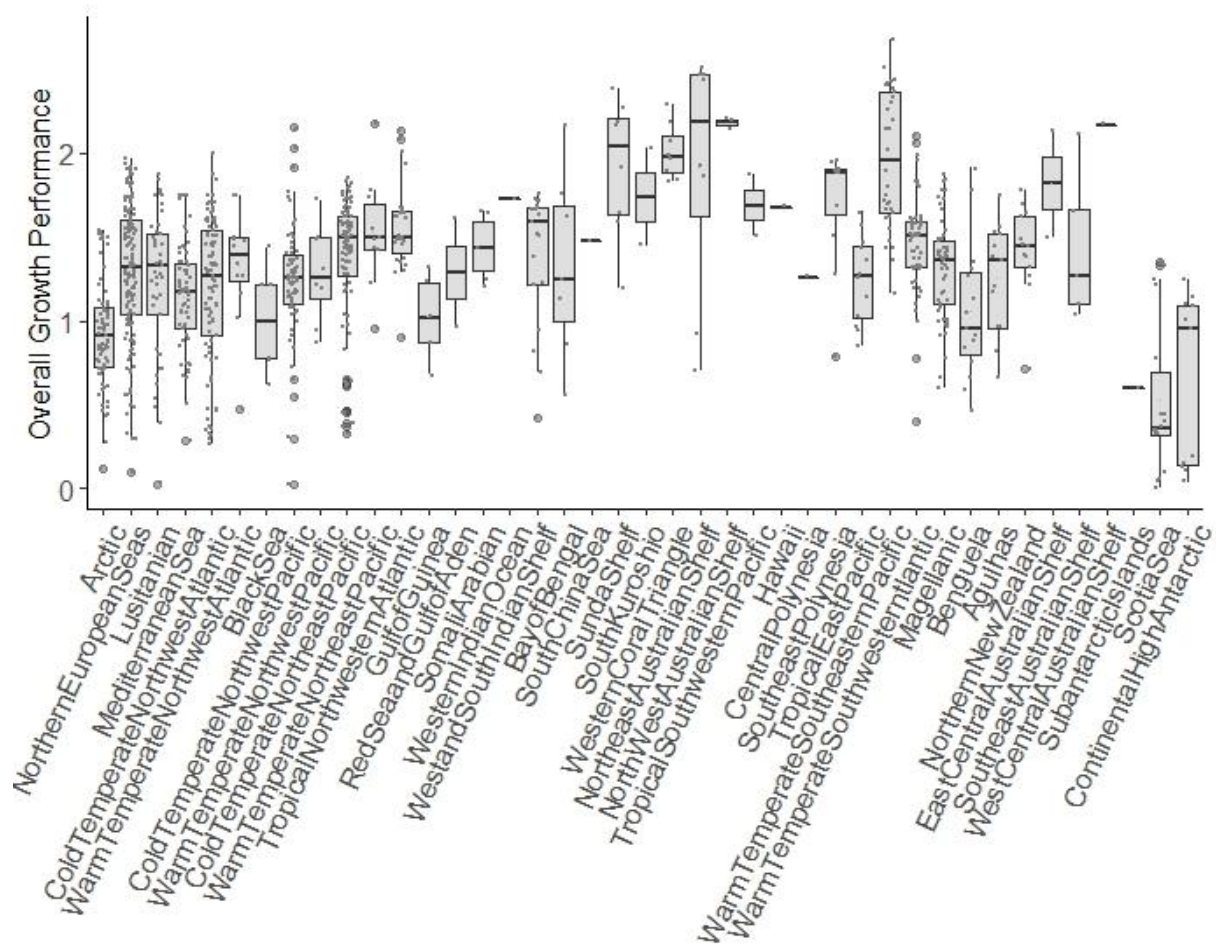
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## Supplementary Appendix 2

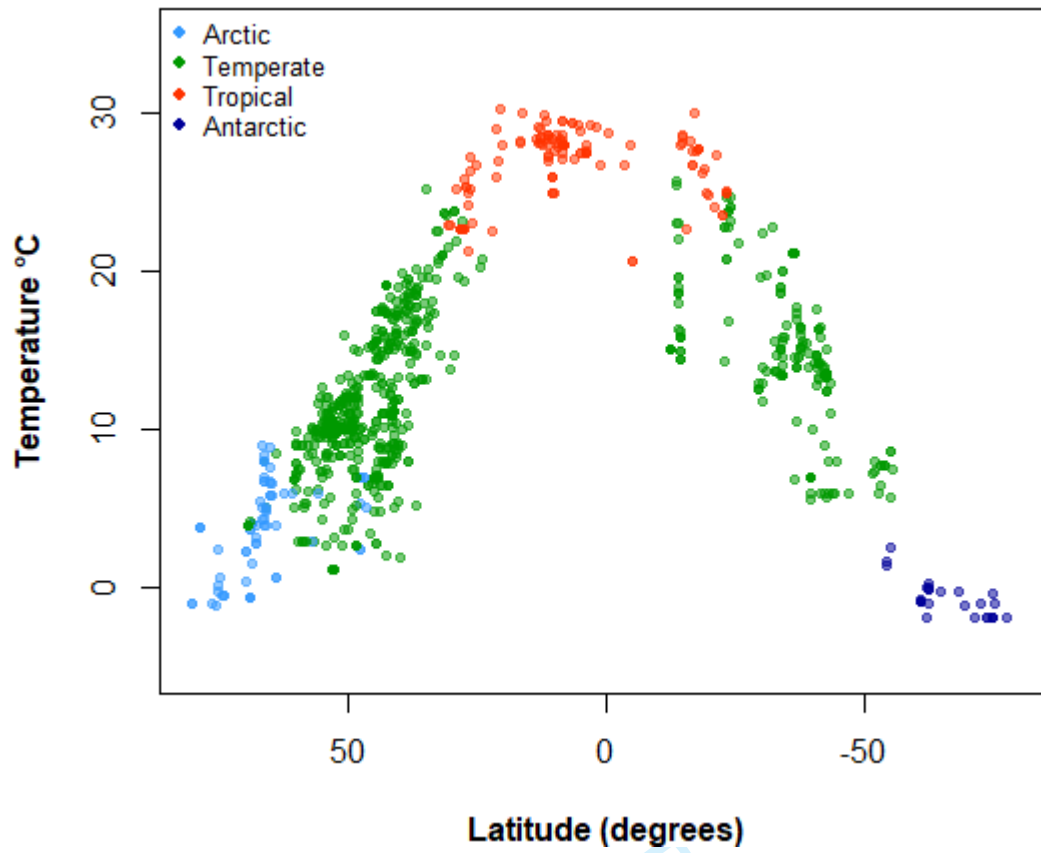
Figure S2.1



**Figure S2.1.** Overall growth performance in each biogeographical Province. In each case, the median is indicated at the midpoint, the upper and lower quartiles are indicated by the hinges, lines represent the spread and open circles indicate outliers. Data points are superimposed.

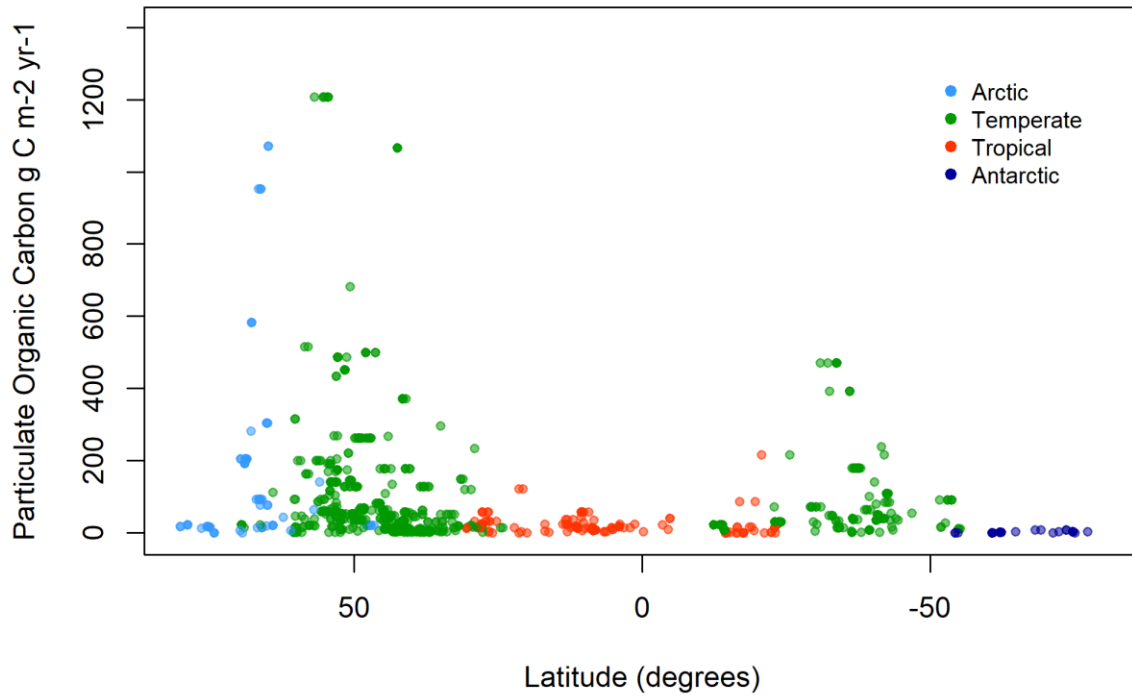


Figure S2.2

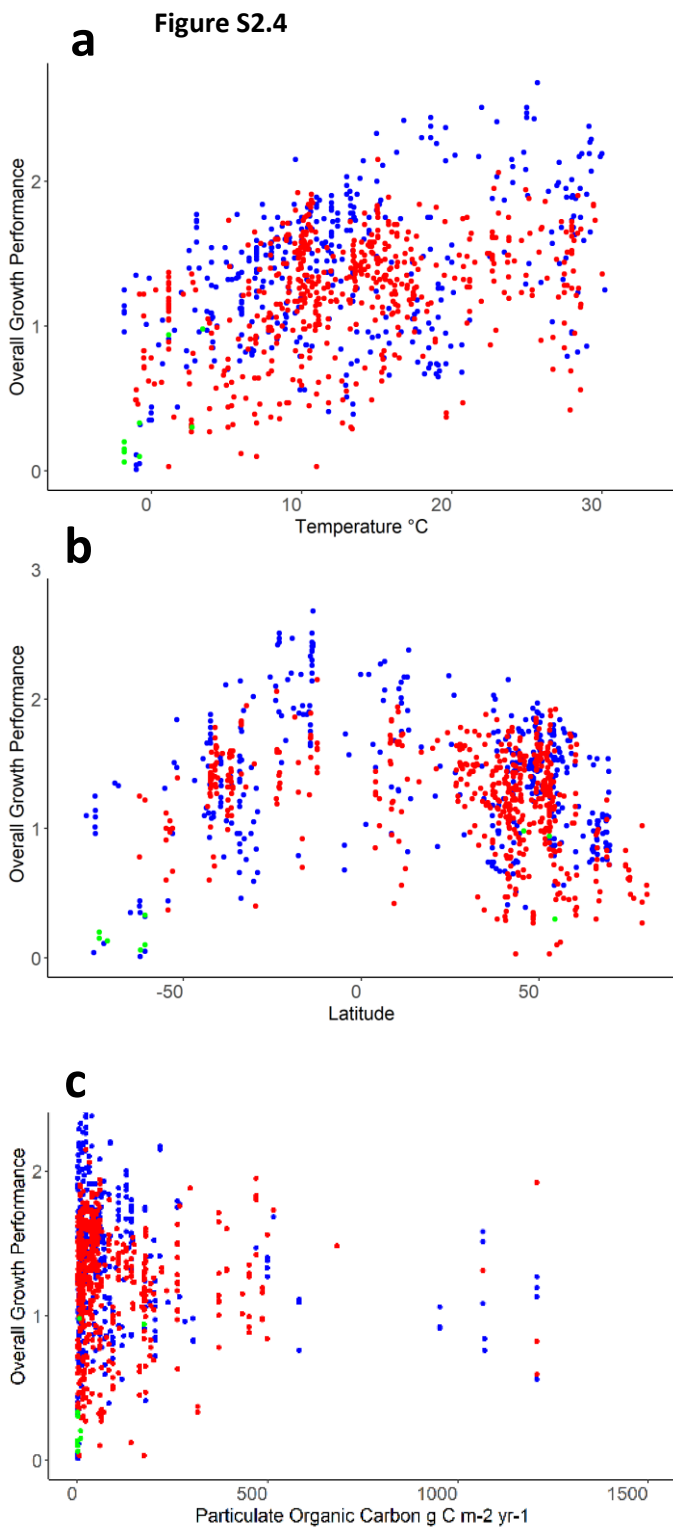


**Figure S2.2** Relationship of temperature (derived from World Ocean Atlas 2013) and latitude based on each data point used in this study. Geographic realms are indicated by colour (see inset legend).

Figure S2.3

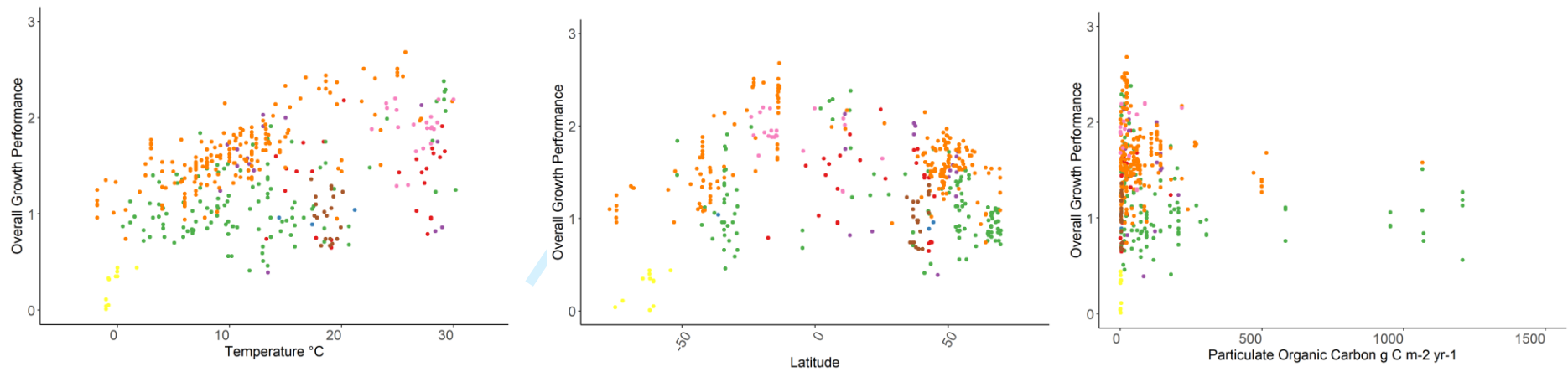


**Figure S2.3** Relationship of particulate organic carbon and latitude for each data point used in this study. Geographic realms are indicated by colour (see inset legend).

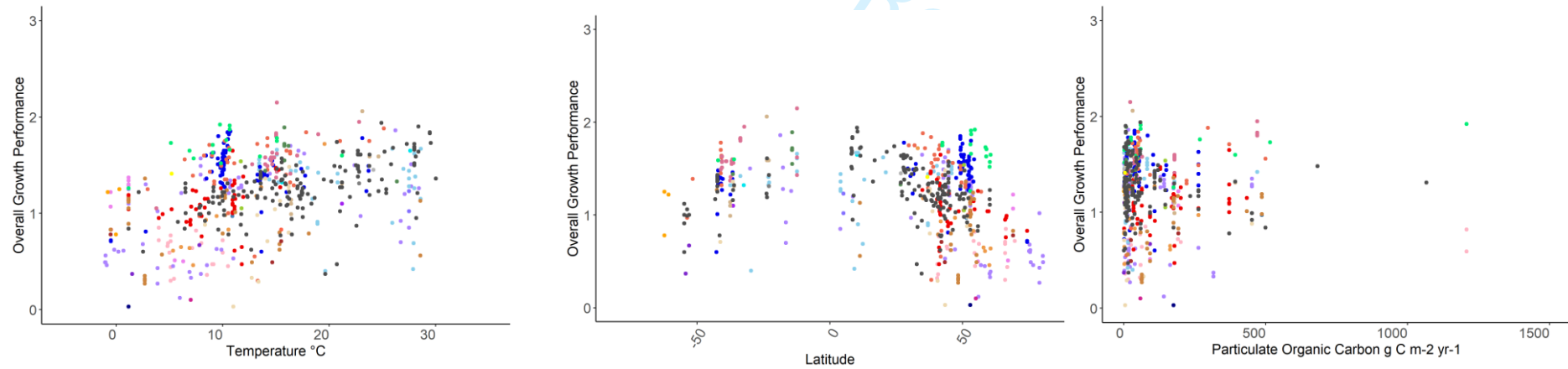


**Figure S2.4** Relationship of overall growth performance in the subclasses Pteriomorpha (blue), Heterodonta (red) and Protobranchia (green) with a) temperature; b) latitude; c) Particulate Organic Carbon.

Figure S2.5



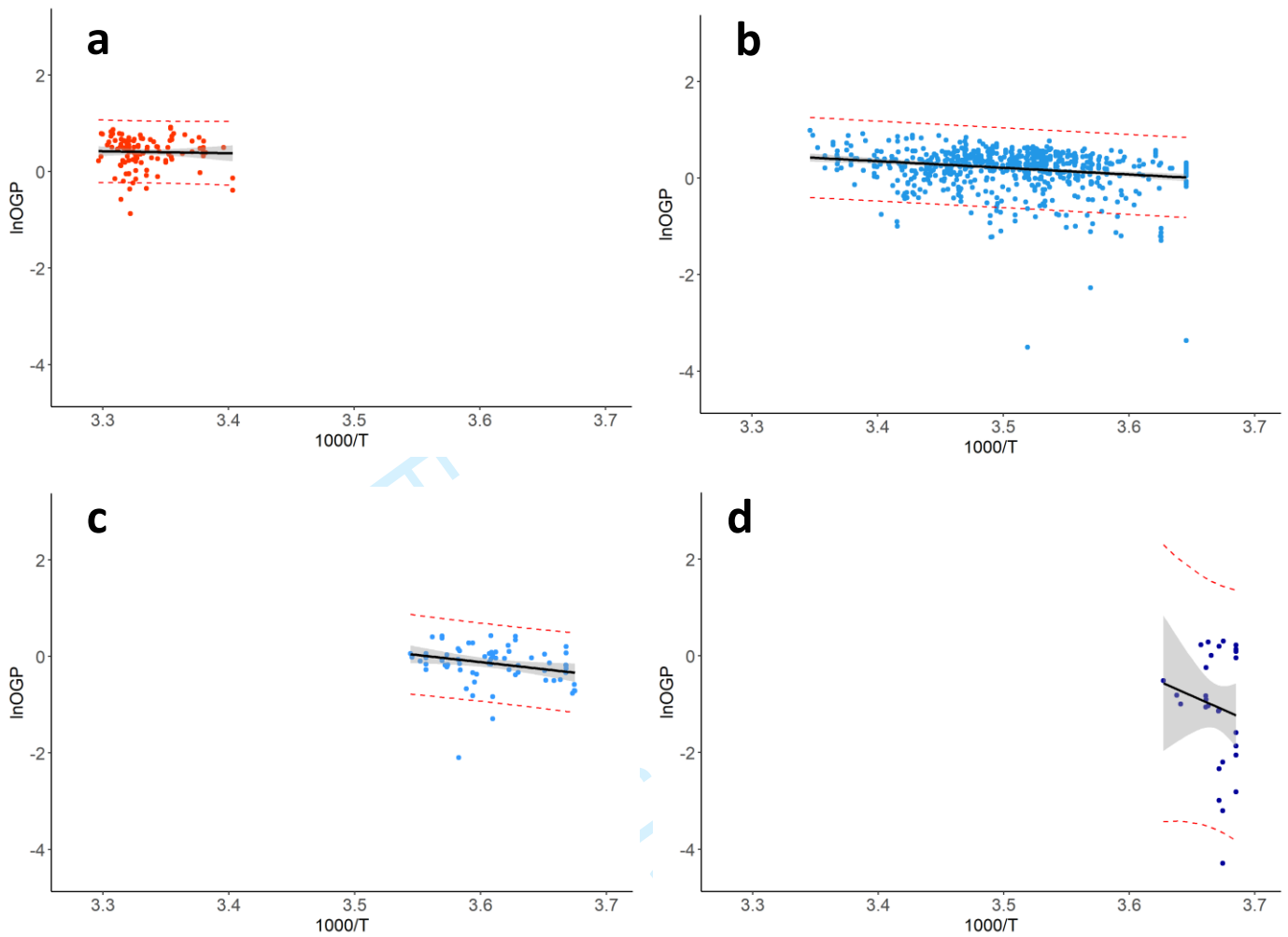
- Family
- Arcidae
  - Mytilidae
  - Pectinidae
  - Pinnidae
  - Glycymerididae
  - Ostreidae
  - Philobryidae
  - Pteriidae



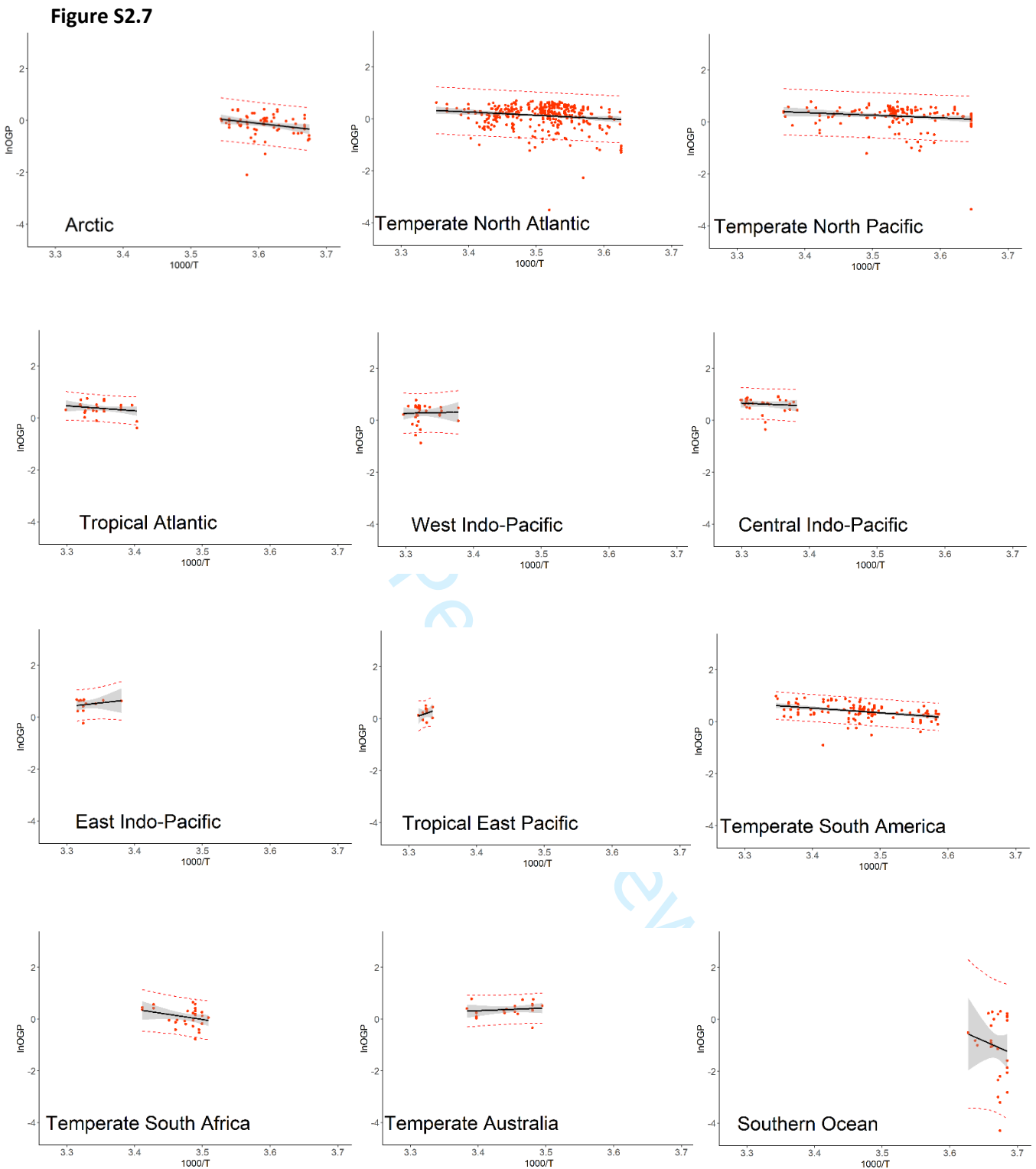
- Family
- Arctiidae
  - Cyrenidae
  - Lucinidae
  - Pholadidae
  - Thyasiridae
  - Astartidae
  - Donacidae
  - Mactridae
  - Psammobiidae
  - Trapezidae
  - Cardiidae
  - Dreissenidae
  - Mesodesmatidae
  - Semelidae
  - Ungulinidae
  - Corbulidae
  - Hiatellidae
  - Montacutidae
  - Solecurtidae
  - Veneridae
  - Crassatellidae
  - Lasaeidae
  - Myidae
  - Solenidae
  - Vesicomiyidae
  - Cyamiidae
  - Laternulidae
  - Pharidae
  - Tellinidae

**Figure S2.5** Relationship of overall growth performance at the taxonomic resolution of family (indicated below panels) within the subclasses Pteriomorphia (top panel), and Heterodonta (bottom panel) with Temperature, Latitude, and Particulate Organic Carbon.

Figure S2.6



**Figure S2.6.** Linear regressions of inverse temperature (Kelvins) and natural log of Overall Growth Performance, representing the Arrhenius Relationship in four biogeographic latitude zones a) Tropical; b) Temperate; c) Arctic; d) Antarctic.



**Figure S2.7.** Linear regressions of inverse temperature (Kelvins) and natural log of Overall Growth Performance, representing the Arrhenius Relationship, in twelve biogeographic realms.