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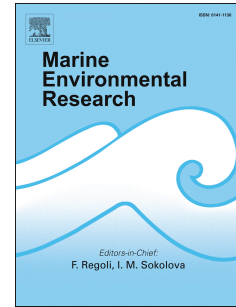
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Changes in the biochemical and nutrient composition of seafood due to ocean acidification and warming

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1 **Changes in the biochemical and nutrient composition of seafood due to ocean**
2 **acidification and warming**

3

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5

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12

13 **Abstract:**

14 Ocean acidification and warming may threaten future seafood production, safety and quality
15 by negatively impacting the fitness of marine species. Identifying changes in nutritional
16 quality, as well as species most at risk, is crucial if societies are to secure food production.
17 Here, changes in the biochemical composition and nutritional properties of the commercially
18 valuable oysters, *Magallana gigas* and *Ostrea edulis*, were evaluated following a 12-week
19 exposure to six ocean acidification and warming scenarios that were designed to reflect the
20 temperature (+3°C above ambient) and atmospheric $p\text{CO}_2$ conditions (increase of 350 –
21 600ppm) predicted for the mid- to end-of-century. Results suggest that *O. edulis*, and
22 especially *M. gigas*, are likely to become less nutritious (i.e. containing lower levels of
23 protein, lipid, and carbohydrate), and have reduced caloric content under ocean acidification
24 and warming. Important changes to essential mineral composition under ocean acidification
25 and warming were evident in both species; enhanced accumulation of copper in *M. gigas* may

26 be of concern regarding consumption safety. In light of these findings, the aquaculture
27 industry may wish to consider a shift in focus toward species that are most robust to climate
28 change and less prone to deterioration in quality, in order to secure future food provision and
29 socio-economic benefits of aquaculture.

30

31 **Keywords:** Oyster; living resources; biochemistry; food security; global change;

32 environmental stress; multi-stressors; *Magallana gigas*; *Crassostrea gigas*

33 1 Introduction

34 Seafood is the source of >15% of animal protein consumed globally, yet climate change is of
35 increasing threat to the security of this resource (FAO, 2014; Golam et al., 2017; Rice and
36 Garcia, 2011). This, as well as the continued burgeoning human population (Gerland *et al.*,
37 2014; United Nations, 2015), especially in coastal areas (Firth *et al.*, 2016), are placing
38 increasing and arguably unsustainable demands on sources of animal protein, which are
39 unlikely to be met by land farming (Campbell *et al.*, 2017; Cooley *et al.*, 2012; Delgado,
40 2003). Some argue the marine environment can make up the shortfall via a 'Blue Revolution'.
41 But as overfishing, habitat destruction, and climate change are already causing decline in fish
42 stocks in many areas (Macura *et al.*, 2016; McCauley *et al.*, 2015; Pauly *et al.*, 1998), there is
43 growing concern about the resilience of the marine environment to withstand increased
44 anthropogenic pressure and provide sustainable food provision in the future (Knights *et al.*,
45 2015; Porter *et al.*, 2014; UNEP, 2010; Weatherdon *et al.*, 2016).

46
47 Aquaculture is increasingly promoted as an alternative to land-based meat production and a
48 solution for securing food provision in the future (Gentry *et al.*, 2017; Naylor *et al.*, 2000;
49 Tacon & Metian, 2013). The aquaculture industry is the fastest growing food sector, with
50 production increasing nearly year-on-year since the 1950s (FAO, 2016), which has now
51 surpassed that of capture fisheries. Molluscan aquaculture is increasingly important, with
52 many molluscs strategically chosen due to their low production cost compared to that of other
53 fish and shellfish due to no requirement for feed (Tacon & Metian, 2013; Troell *et al.* 2014).
54 In 2015, ~15% of the total aquaculture production volume was attributed to molluscan
55 aquaculture (over 16 million tonnes; worth over US\$18billion) (FAO 2018). Additionally,
56 mollusc aquaculture has been found as having the lowest environmental production impacts

57 of all animal source food, and therefor may constitute a more sustainable source of protein
58 (Froehlich *et al.*, 2018; Hilborn *et al.*, 2018).

59

60 The increased prevalence of obesity in several regions of the world (Abarca-Gómez *et al.*,
61 2017) is leading to greater public awareness and desire to consume a healthy and balanced
62 diet. A healthy diet should include sufficient proteins, amino acids, essential fats such as
63 long-chain omega-3 fatty acids, vitamins and minerals (FAO, 2016; Simopoulos, 2002). The
64 proximate composition can be used as a measure of nutritional quality (see EFSA NDA Panel,
65 2014; Hart & Fisher, 1971; Nielsen, 2006; Tate *et al.*, 2017), dividing the food into fractions
66 including moisture, ash, protein, lipids and minerals. Seafood contains high levels of these
67 important components compared to other meats (reviewed in Tacon & Metian, 2013) and is
68 therefore viewed as highly nutritious, and key to human health and well-being (FAO/WHO,
69 2011; Lloret *et al.*, 2016; Simopoulos, 2002). Oysters, in particular, are a popular and well-
70 known natural source of these nutrients (Asha *et al.*, 2014; Cochet *et al.*, 2015; Orban *et al.*,
71 2004; Pogoda *et al.*, 2013; Sprague *et al.*, 2017).

72

73 In 2015, global oyster production exceeded 5.4 million tonnes, and was valued at >US\$4
74 billion. In the UK, oysters are one of the major aquaculture species (Pinnegar *et al.*, 2017)
75 with ~1600 tonnes produced in 2015, and worth more than US\$6.4 million. Yet there is
76 increasing concern over the long-term future of shellfish production due to the effects of
77 environmental stressors associated with rising atmospheric CO₂ levels such as warming and
78 marine heat waves, falling levels of seawater carbonate and oxygen plus rising sea levels and
79 increased storminess (Branch *et al.*, 2013; Cooley *et al.*, 2015; Dupont *et al.*, 2014; Ekstrom
80 *et al.*, 2015; Lemasson *et al.*, 2017b). Ocean acidification and sea-surface warming are
81 changing animal physiology and affecting the quality of seafood (Dupont *et al.*, 2014; Tate *et*

82 *al.*, 2017). In oysters, the effects of ocean acidification are already being detected (Lemasson
83 *et al.*, 2017a), with several hatcheries experiencing declines in production, jeopardising
84 economic revenues and necessitating adaptive actions (Barton *et al.*, 2015; Cooley *et al.*,
85 2017). However, physiological effects of ocean acidification and warming in oysters appear
86 species-specific (Lemasson *et al.*, 2018).

87

88 To date, there has been limited consideration of potential changes in the quality of shellfish
89 under warming and acidification. The few published studies have shown changes, such as
90 reductions in protein and lipid content, and reductions in omega-3 fatty acids (Ab Lah *et al.*,
91 2018; Clements *et al.*, 2018; Tate *et al.*, 2017; Valles-Regino *et al.*, 2015). A better
92 understanding is needed if we are to shed light on the future of shellfish aquaculture. Here,
93 using two economically and commercially important species of oysters, *Magallana gigas* – a
94 non-native introduced species – and *Ostrea edulis* – a native species –, we tested if ocean
95 acidification and warming conditions predicted under future climate scenarios has the
96 potential to impact seafood nutritional quality. We also consider how condition indices – a
97 widely used metric in aquaculture for evaluating health and value of bivalves because they
98 are correlated with meat yield (Knights, 2012; Orban *et al.* 2002, 2006) – might change under
99 ocean acidification and warming scenarios.

100

101

102 **2 Methods**

103 2.1 Organism collection and treatments

104 Collection of organisms, acclimation, treatments, and mesocosm set-up followed the protocol
105 described in Lemasson *et al.* (2018). Following 14 days of acclimation to laboratory
106 conditions (16°C, salinity 33, ~400 ppm $p\text{CO}_2$, 12:12 dark:light cycle, fed *ad libitum* with a

107 mixed algal diet (Shellfish Diet, 1800; Reed Mariculture)), each oyster was placed in its own
108 3 L experimental tank and exposed for 12 weeks to three $p\text{CO}_2$ concentrations (ambient ~400
109 ppm, intermediate ~750 ppm, elevated ~1000 ppm), and two temperatures (control 16.8 °C,
110 elevated 20 °C) in an orthogonal experimental design (*M. gigas* n= 4; *O. edulis* n=8
111 individuals per treatment). This design aimed to simulate current and future ocean
112 acidification and warming scenarios, using scenarios in line with conditions predicted by the
113 IPCC (IPCC, 2013) and for the UK for mid- to end-century (see also Lemasson *et al.*, 2018).
114 Throughout the study, oysters were fed *ad libitum* with a mixed algal diet (Shellfish Diet,
115 1800; Reed Mariculture).

116

117 Temperature, salinity, and pH were measured daily in all replicate tanks. Salinity was
118 measured using a handheld refractometer (D&D The Aquarium Solution Ltd, Ilford, UK) and
119 temperature measured using a digital thermometer (TL; Fisher Scientific, Loughborough,
120 UK). pH was measured using a microelectrode (InLab® Expert Pro-ISM; Mettler- Toledo
121 Ltd, Beaumont Leys, UK) coupled to a pH meter (S400 SevenExcellence™; Mettler-Toledo
122 Ltd, Beaumont Leys, UK), following calibration with NIST traceable buffers. pH in the
123 header tanks was also monitored (data not shown). Total Alkalinity (AT) was measured once
124 a week in each of the replicate tanks. 125 mL water samples were transferred to borosilicate
125 bottle with Teflon caps and poisoned with 30 µL of saturated HgCl_2 solution (0.02% sample
126 volume) before being kept in the dark until measurement by automatic Gran titration
127 (Titralab AT1000 © Hach Company). Partial pressure of carbon dioxide ($p\text{CO}_2$) and
128 saturation states of calcite and aragonite (Ω_{calcite} and $\Omega_{\text{aragonite}}$), were calculated at the end
129 of the experiment using CO_2 SYS (Pierrot *et al.*, 2006), employing constants from Mehrbach
130 *et al.* (1973) refitted to the NBS pH scale by Dickson and Millero (1987) and the KSO_4
131 dissociation constant from Dickson (1990).

132

133 **Table 1:** Seawater chemistry for *Magallana gigas* and *Ostrea edulis* in each treatment. Data
 134 shown are means (\pm SD) values. T=Temperature in °C. ppm= parts per million. Ω_{Ca} =
 135 saturation state of calcite. Ω_{Ar} = saturation state of aragonite. A_T = Total alkalinity in mmol/kg
 136 seawater.

	Treatment (pCO_2 + Temperature)	Measured			Calculated			
		pH	T	A_T	S	pCO_2	Ω_{Ar}	Ω_{Ca}
<i>Magallana gigas</i>	Ambient + Control	7.79 \pm 0.10	16.9 \pm 0.2	2.13 \pm 0.32	33.9 \pm 1.1	597.2 \pm 146.1	1.70 \pm 0.32	2.64 \pm 0.50
	750 ppm + Control	7.67 \pm 0.12	16.9 \pm 0.2	2.13 \pm 0.33	33.9 \pm 1.2	816.9 \pm 296.4	1.4 \pm 0.36	2.10 \pm 0.55
	1000 ppm + Control	7.55 \pm 0.10	16.8 \pm 0.2	2.13 \pm 0.32	33.9 \pm 1.2	1174.6 \pm 420.9	0.99 \pm 0.22	1.53 \pm 0.34
	Ambient + Elevated	7.84 \pm 0.10	20.4 \pm 0.3	2.32 \pm 0.29	34.3 \pm 1.2	669.7 \pm 155.9	2.02 \pm 0.31	3.11 \pm 0.47
	750 ppm + Elevated	7.70 \pm 0.11	20.6 \pm 0.4	2.33 \pm 0.29	34.2 \pm 1.1	945.1 \pm 275.7	1.60 \pm 0.34	2.46 \pm 0.52
	1000 ppm + Elevated	7.56 \pm 0.10	20.2 \pm 0.3	2.34 \pm 0.31	34.3 \pm 1.2	1376.8 \pm 280.8	1.14 \pm 0.17	1.76 \pm 0.26
<i>Ostrea edulis</i>	Ambient + Control	8.00 \pm 0.08	16.5 \pm 0.3	3.04 \pm 0.18	34.2 \pm 0.8	481.4 \pm 90.9	3.70 \pm 0.65	5.75 \pm 1.01
	750 ppm + Control	7.84 \pm 0.08	16.6 \pm 0.2	3.04 \pm 0.19	34.2 \pm 0.8	760.1 \pm 178.2	2.68 \pm 0.51	4.17 \pm 0.80
	1000 ppm + Control	7.72 \pm 0.16	16.6 \pm 0.2	3.00 \pm 0.16	34.3 \pm 0.7	1053.6 \pm 223.3	2.15 \pm 1.20	3.34 \pm 1.87
	Ambient + Elevated	8.00 \pm 0.08	19.8 \pm 0.3	2.86 \pm 0.15	34.4 \pm 0.9	467.9 \pm 78.4	3.80 \pm 0.65	5.85 \pm 1.01
	750 ppm + Elevated	7.90 \pm 0.07	20.2 \pm 0.5	2.87 \pm 0.15	34.4 \pm 0.9	694.7 \pm 135.4	2.94 \pm 0.47	4.52 \pm 0.72
	1000 ppm + Elevated	7.70 \pm 0.09	19.8 \pm 0.3	2.6 \pm 0.22	34.4 \pm 0.9	1165.0 \pm 226.8	2.01 \pm 0.47	3.10 \pm 0.73

137

138 2.2 Condition index, proximate composition, and energy content

139 After 12 weeks exposure, oysters were manually shucked and their wet tissue mass (g) was
 140 recorded on an electronic balance (Mettler AE240), before being oven-dried at 105°C for 24
 141 hours until constant mass was achieved.

142

143 The Condition Index (CI) of each oyster was calculated following the method recommended
 144 by Lucas and Beninger (1985) as follows:

$$CI = (\text{dry meat weight} / \text{dry shell weight}) \times 100$$

145

146 Moisture percentage of the meat was calculated for each individual oyster according to the
147 following formula:

$$\text{Moisture (\%)} = ((\text{Total weight} - \text{Dry weight}) / \text{Total weight}) \times 100$$

148
149 For each species, following estimation of Condition Index and moisture content for all
150 individuals, the dried meat samples were then pooled by treatment to provide sufficient tissue
151 material for proximate composition and energy content analyses. Pooled samples were
152 homogenised, then ground into a fine powder using a coffee grinder. Complete or partial
153 pooling of specimens from the same treatment or sampling site for biochemical analysis has
154 been reported in several studies (Fernandez *et al.*, 2015; Marin *et al.*, 2003; Soto-Jiménez *et*
155 *al.*, 2001). While not allowing individual comparisons, this approach provides nutritional
156 information at the population level. The following assays were performed in triplicate.

157
158 Ash content (a measure of the total amount of minerals present within a food) was
159 determined using 500mg of dried tissue samples and an adaptation of the Association of
160 Official Agricultural Chemists official method (AOAC, 1995). Lipid content was determined
161 by continuous extraction of fat from 2 g material using petroleum ether as a solvent following
162 the Soxhlet method (Luque de Castro & García-Ayuso, 1998; Manirakiza *et al.*, 2001) in a
163 Soxtherm Rapid Extraction Unit (C. Gerhardt GmbH & Co. KG). Total protein content was
164 determined using the Kjeldahl method (Kjeldahl, 1883) on ~150 mg samples with a Gerhardt
165 Kjeldatherm digestion block, a Gerhardt Turbosog scrubber unit and a Gerhardt Vapodest 50s
166 distillation unit (Gerhardt Laboratory Instruments, Bonn, Germany). Glycogen content was
167 determined indirectly by calculating carbohydrate content using the above results for
168 moisture, ash, lipid, and protein content following Maclean *et al.* (2003) as follows:

$$\text{Carbohydrates (\%)} = 100 - (\%M + \%A + \%L + \%P)$$

169 Where:

170 C=carbohydrate, M=moisture, A=ash, L=lipid, and P=protein. All values used were as
171 percentage of total weight.

172

173 Caloric (energy) content was measured as gross energy content ($\text{kJ}\cdot\text{g}^{-1}$) by bomb calorimetry
174 using an isoperibol oxygen bomb calorimeter (Parr Instrument Company, Moline, Illinois,
175 USA) on ~1 g of material per sample.

176

177 2.3 Macro and micro-minerals

178 Macro-mineral (calcium [Ca], potassium [K], magnesium [Mg], sodium [Na]) and micro-
179 mineral (copper [Cu], iron [Fe], zinc [Zn]) content was determined using an Inductively
180 Coupled Plasma Optical Emission Spectrometer (ICP-OES; iCAP 7000series Thermo
181 Scientific) following standard protocols as reported elsewhere (Rider *et al.*, 2010). The
182 content of the micro-mineral selenium [Se] was determined using an Inductively Coupled
183 Plasma Mass Spectrometer (ICP-MS; Xseries2, Thermo Scientific) following standard
184 protocols. Mineral composition was determined on ~100-150 mg of material per sample.
185 Before use, both ICP-OES and ICP-MS were calibrated using mixed, matrix-matched
186 standards ($0\text{--}100\ \mu\text{g}\cdot\text{L}^{-1}$) prepared from certified Aristar plasma emission grade solutions.
187 Quality control was assured by carrying out accuracy checks using a known standard or blank
188 every 10 samples during the analysis. Also, 2% internal iridium and indium standards
189 (P/N/4400-013 CPI, Quality control standard 26) were added to each sample. DORM-3
190 (dogfish certified reference material – CRM) from National Research Centre Canada (NRCC)
191 was used to verify the digestion procedure as reported elsewhere (Rossbach *et al.*, 2017).

192 2.4 Statistical analyses

193 The logistical constraints of the experimental infrastructure meant oyster species had to be
194 tested sequentially. There were natural variations in the chemistry of the seawater used
195 between experiments due to natural seasonal fluctuations in seawater properties combined
196 with differences in atmospheric partial pressure (barometric pressure). These fluctuations in
197 $p\text{CO}_2$ also led to fluctuations in CO_2 adsorbed by the seawater. The resulting $p\text{CO}_2$ and pH,
198 conditions were therefore different between experiments, but also within experiments were
199 different from the expected levels of ~400ppm, ~750ppm and ~1000ppm. Nevertheless, the
200 effect size (magnitude of difference in $p\text{CO}_2$ and pH between treatments within experiments)
201 were comparable. These constraints prevented a formal comparison of the two species in a
202 factorial design, so these were analysed separately. Analyses were performed using R
203 Version 3.2.5 (R Core Development Team, 2018) using the *base*, *MASS*, *stat* and *vegan*
204 packages. $p < 0.05$ was used as statistical threshold.

205

206

207 *Condition Index and Moisture content*

208 Condition index and moisture data (obtained before pooling of the samples) were tested for
209 homogeneity of variances using Levene's test (*car* package). Tests for differences in
210 condition index and moisture content between treatments were done using 2-factor ANOVA
211 with 'temperature' and ' $p\text{CO}_2$ ' as fixed factors.

212

213 *Proximate composition, energy content, and mineral composition*

214 As oyster tissues were pooled in order to provide sufficient material to perform these analyses,
215 there were no 'true replicates' (*sensu* Hurlbert, 1984). Triplicate measures of protein, lipid,
216 ash, calorimetry, and mineral analysis were performed to determine within sample
217 variability. Data were pooled, and averages used for statistical analysis to avoid Type I error.

218 The pooled samples used were therefore homogenised samples of multiple individuals (*M.*
219 *gigas* n=4; *O. edulis* n=8), and in effect the single values associated with each assay are
220 means without the variances. Analyses were thus performed on these single values.

221

222 Calorimetry data were analysed using a 2-way ANOVA with ‘temperature’ and ‘ $p\text{CO}_2$ ’ as
223 fixed factors (n=3 per Temperature level; n=2 per $p\text{CO}_2$ level). Due to this experimental
224 design, interactions between the two factors could not be assessed.

225

226 To compare proximate and mineral compositions across species, temperature and $p\text{CO}_2$,
227 nonmetric multidimensional scaling (nMDS) coupled with Permutational Multivariate
228 Analysis of Variance (PERMANOVA, Anderson, 2001) was used to evaluate the
229 significance of observed patterns (based on Euclidian distance and 1000 permutations of the
230 data) and test hypotheses related to changes in composition due to experimental treatment.

231

232 For tests using ANOVA, when significant differences were present, *post-hoc* Tukey tests
233 were performed to assess differences between treatment levels.

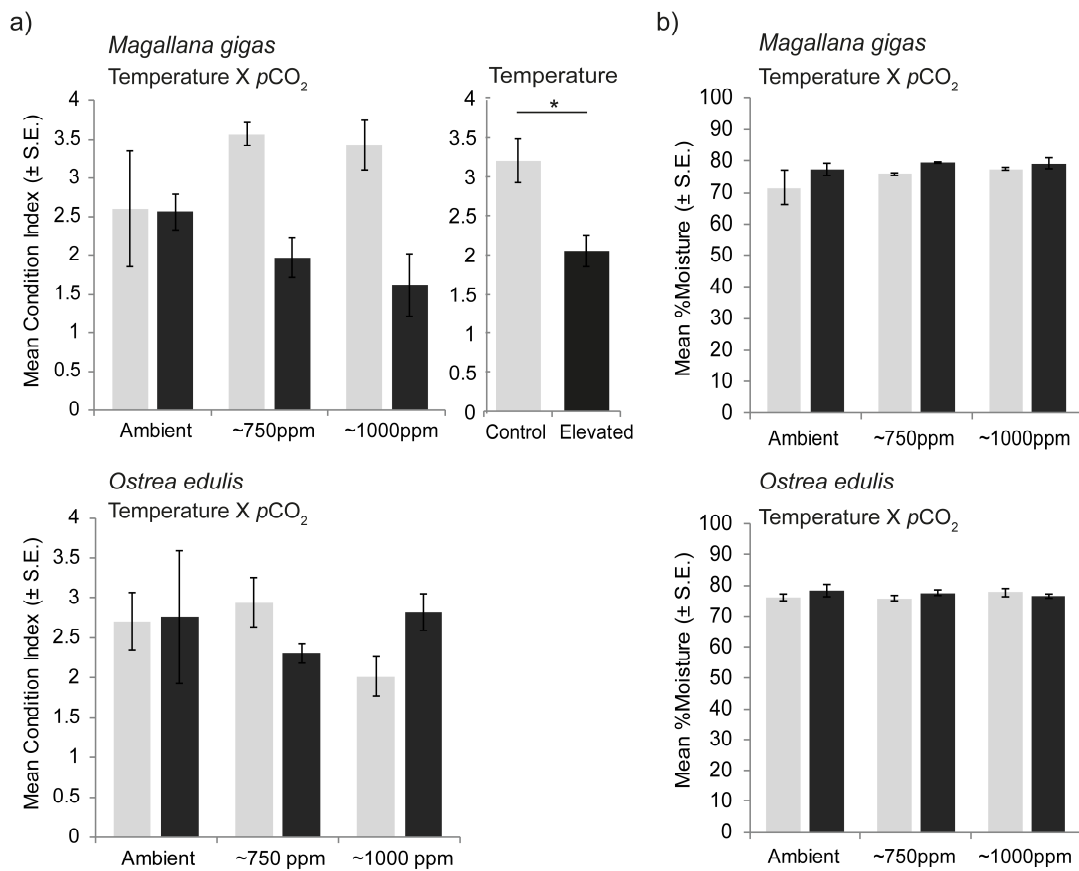
234

235 **3 Results**

236 **3.1 Condition Index and Moisture**

237 Temperature, but not $p\text{CO}_2$, had a significant effect on the condition index of *M. gigas* ($F_{1,12}$
238 = 12.298; $p < 0.01$), with condition index negatively impacted by elevated temperature (Figure
239 1a). Mean condition index decreased 35% with increased temperature, from ~3.2 (± 0.3) at
240 ambient temperature to ~2.1 (± 0.20) at elevated temperature. While marginally not
241 significant ($F_{2,18} = 2.97$; $p = 0.07$), there were clear differences in condition index between *M.*
242 *gigas* cultured under different temperature and $p\text{CO}_2$ regimes, with a trend toward increasing

243 condition index with increasing $p\text{CO}_2$ at the control temperature, and decreasing condition
 244 index with increasing $p\text{CO}_2$ at elevated temperature (Figure 1a). The condition index of
 245 *O. edulis* was unaffected by any of the treatments. Moisture – the principal contributor to
 246 oyster flesh – was also unaffected by temperature or $p\text{CO}_2$ treatment and ranged between 70-
 247 80% for both species (Table 2; Figure 1b).
 248



249

250 **Figure 1** Difference in a) Condition Index and b) moisture content (as % of total weight), of
 251 *Magallana gigas* and *Ostrea edulis* across temperature and $p\text{CO}_2$ treatments. ppm= part per
 252 million; s.e. = standard error. Grey = control temperature. Black= elevated temperature. *
 253 indicates significant difference.

254

255 3.2 Proximate composition analysis

256 There were significant differences in proximate composition with temperature and $p\text{CO}_2$ for
257 both species (*Magallana gigas*: perm $F_{2,24}=75.41$; $p < 0.001$; *Ostrea edulis*: perm $F_{2,24}=14.37$;
258 $p < 0.001$) (Table 2, Figures 2 & 3a-d). For all treatments, after moisture, protein was the
259 second largest component in both *M. gigas* and *O. edulis* under ambient $p\text{CO}_2$ and control
260 temperature, representing 16.6% and 9.9% of the total composition, respectively (Table 2;
261 Figure 2). *Ostrea edulis* was characterised by higher carbohydrates (10.5g per 100g) than *M.*
262 *gigas* (4.5g per 100g), but *M. gigas* had higher percentages of proteins and lipids (Table 2).
263 Temperature (Figure 3a-b) and $p\text{CO}_2$ (Figure 3c-d) both led to clear dissimilarity in
264 proximate composition between species, with greater changes apparent in *M. gigas*, largely
265 driven by reductions in proteins and lipids (Table 2, Figure 2) from 16.6g to 11.8g and from
266 4.8g to 1.4g, respectively. The treatments also appeared to a lesser degree to negatively
267 impact the carbohydrate proportion in *M. gigas*, which dropped from 4.9g to 3.3g (Table 2;
268 Figure 2). There were significant differences in proximate composition between all $p\text{CO}_2$
269 treatments in *M. gigas*, but in *O. edulis*, there was no difference between oysters cultured in
270 400 and 1000 ppm, whereas those cultured in intermediate $p\text{CO}_2$ (750ppm) were significantly
271 different (Figure 3c). This was particularly evident in *O. edulis* for the lipid proportions,
272 which were reduced from 1.3g to 0.9g at elevated temperature and intermediate $p\text{CO}_2$ (~750
273 ppm) (Table 2; Figure 2).

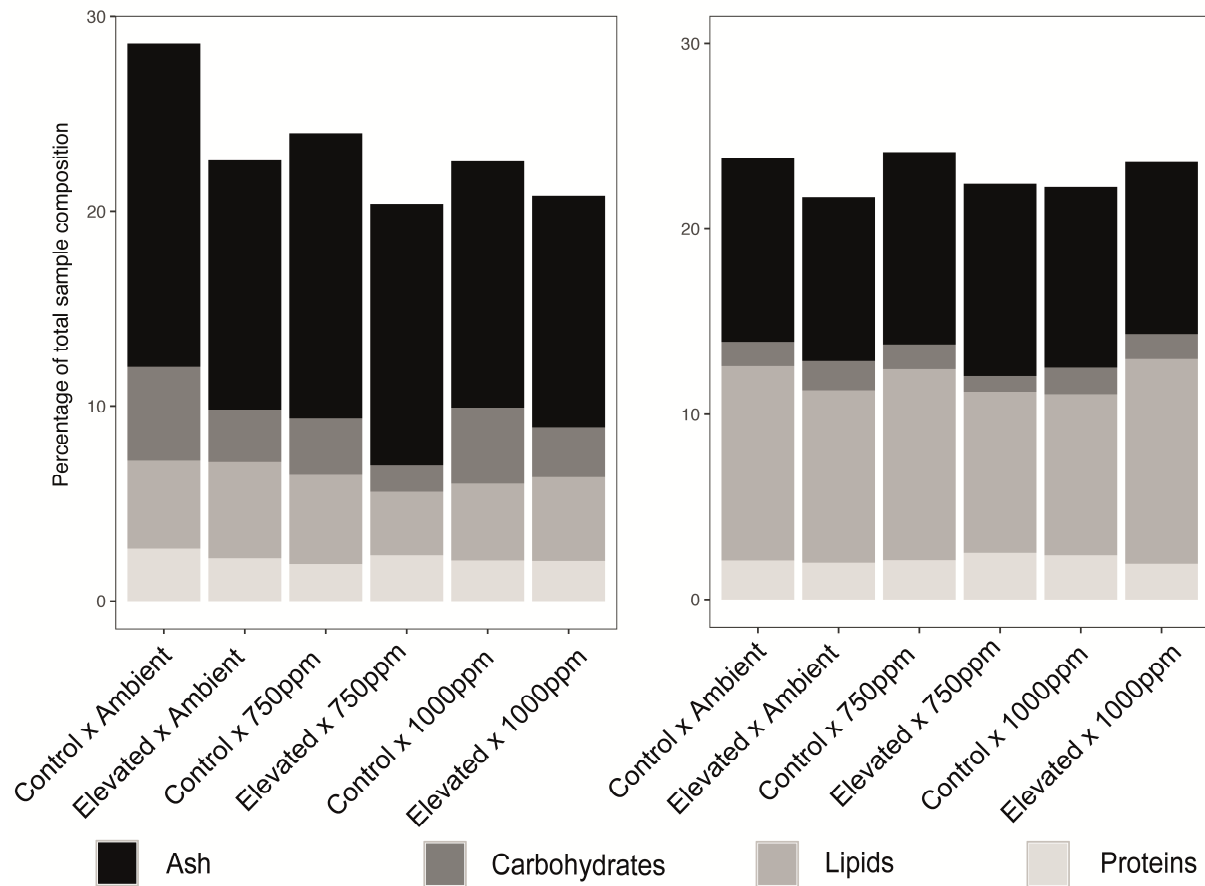
274

275 **Table 2:** Proximate composition of *Magallana gigas* and *Ostrea edulis* under six ocean
 276 acidification and warming scenarios. Moisture represents the remaining component, adding
 277 up to 100g. In g per 100g sample (wet weight).

278

	Treatment ($p\text{CO}_2$ x T)	Protein	Carbo- hydrate	Lipid	Ash	Moisture
<i>Magallana gigas</i>	Ambient x Control	16.6	4.5	4.8	2.7	71.4
	~750ppm x Control	14.6	4.6	2.9	1.9	76.0
	~1000ppm x Control	12.6	3.9	3.9	2.1	77.5
	Ambient x Elevated	12.8	4.9	2.7	2.2	77.4
	~750ppm x Elevated	13.7	3.3	1.4	2.4	79.6
	~1000ppm x Elevated	11.8	4.3	2.6	2.1	79.2
<i>Ostrea edulis</i>	Ambient x Control	9.9	10.5	1.3	2.1	76.2
	~750ppm x Control	10.3	10.3	1.3	2.1	75.9
	~1000ppm x Control	9.7	8.7	1.5	2.4	77.7
	Ambient x Elevated	8.8	9.3	1.6	2.0	78.3
	~750ppm x Elevated	10.4	8.7	0.9	2.5	77.6
	~1000ppm x Elevated	9.2	11.1	1.3	1.9	76.4

279

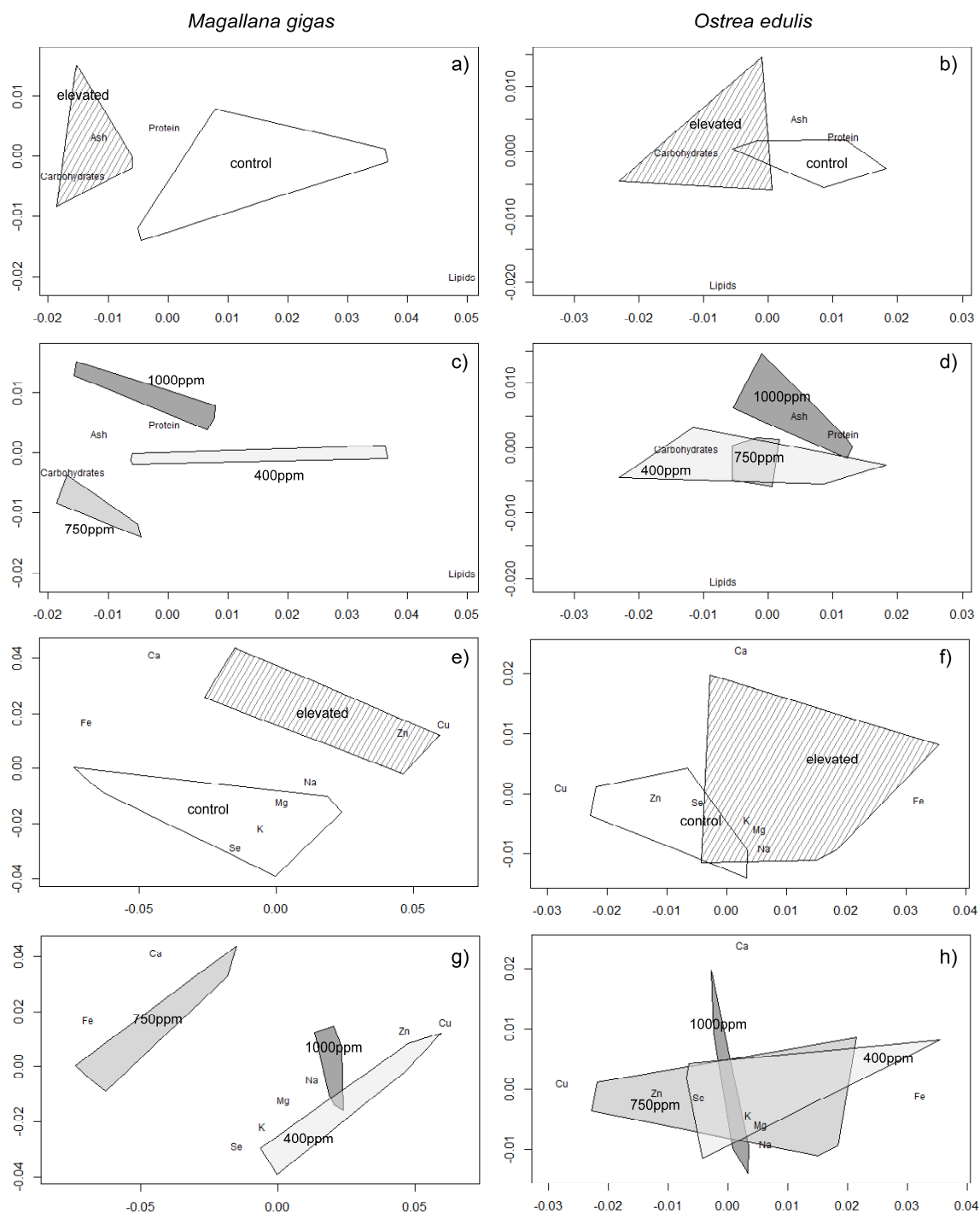
a) *Magallana gigas*b) *Ostrea edulis*

280

281

282 **Figure 2:** Relative composition of proximate components present in a) *Magallana gigas* and
 283 b) *Ostrea edulis* across temperature and $p\text{CO}_2$ treatments. The values for each treatment
 284 represent the means of the three procedural replicates of the pooled samples. ppm= part per
 285 million.

286



287

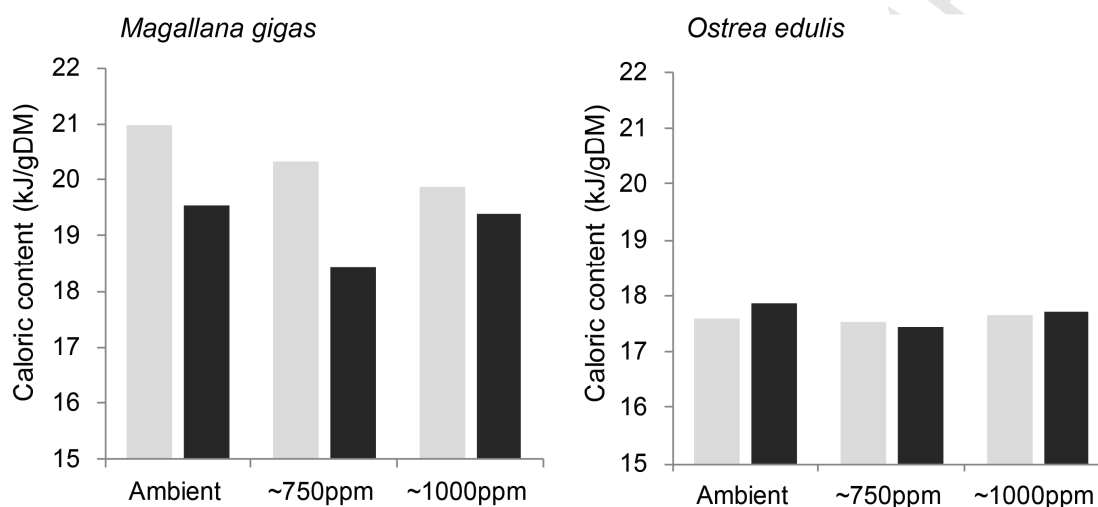
288 **Figure 3:** nMDS plots of proximate (a-d) and mineral compositions (e-h) of *Magallana*
 289 *gigas* (left column) and *Ostrea edulis* (right column). Dispersion of points within temperature
 290 (plots a, b, e, f) and $p\text{CO}_2$ (plots c, d, g, h) treatments are illustrated using cluster hulls plotted
 291 using the R package 'ggplot2'. Centroids of each proximate composition and mineral
 292 components are shown. 2D stress for all plots < 0.08.

293

294 3.3 Energy content

295 There was a 13% reduction in the caloric content of *M. gigas* with temperature and $p\text{CO}_2$
 296 from 20.97 kJ/gDW at control temperature and ambient $p\text{CO}_2$ to 18.41 kJ/gDW at elevated
 297 temperature and intermediate $p\text{CO}_2$ (~750 ppm) (Figure 4). The energetic value of *O. edulis*
 298 did not change (17.63 kJ/gDW) with treatment (Figure 4).

299



300

301 **Figure 4:** Variations in the caloric content of oysters across temperature and $p\text{CO}_2$ treatments
 302 for *Magallana gigas* (left) and *Ostrea edulis* (right). ppm= part per million; Light grey =
 303 control temperature. Dark grey= elevated temperature. The value for each treatment
 304 represents the mean of the three procedural replicates of the pooled samples, therefore no
 305 error bars were obtained. Values are per kg of oyster dry matter (DM).

306

307 3.4 Trace elements

308 There were significant differences in trace elements composition with, temperature and $p\text{CO}_2$
 309 levels for both species (*Magallana gigas*: perm $F_{2,24}=166.75$; $p < 0.001$; *Ostrea edulis*: perm
 310 $F_{2,24}=16.27$; $p < 0.001$) (Table 3, Figure 3e-h). *Magallana gigas* was characterised by higher
 311 Se, Fe, K, Mg, and Na content than *O. edulis* (Table 3, Figure 3e-h), but *O. edulis* displayed
 312 higher Zn levels. Temperature led to clear dissimilarity in the mineral composition of each

313 oyster species, with greater change apparent in *M. gigas* (Figure 3e-fa). $p\text{CO}_2$ also had
 314 notable effects, but only on *M. gigas* (Table 3, Figure 3g-h). Overall, the mineral composition
 315 of *M. gigas* was clearly affected by the treatments (Table 3), with notable increases in Cu and
 316 Zn content, and decreases in Fe and Se contents.

317

318 **Table 3:** Mineral composition of *Magallana gigas* and *Ostrea edulis* under six ocean
 319 acidification and warming scenarios. T= temperature. ppm= part per million. Ca=calcium;
 320 Cu=copper; Fe=Iron; K=potassium; Mg=magnesium; Na=sodium; Zn=zinc; Se=selenium.
 321 All values are in mg.kg^{-1} , except Se which is in $\mu\text{g.kg}^{-1}$.

322

	Treatment ($p\text{CO}_2$ x T)	Ca	Cu	Fe	K	Mg	Na	Zn	Se
<i>Magallana gigas</i>	Ambient x Control	1250.0	64.7	205.5	322.1	847.1	4626.3	450.3	537.1
	~750ppm x Control	492.8	60.0	35.7	268.1	553.5	3101.7	404.9	313.1
	~1000ppm x Control	618.1	149.0	54.0	270.2	676.7	3811.5	749.2	459.7
	Ambient x Elevated	1409.6	92.5	74.7	219.2	509.6	3111.3	566.8	248.8
	~750ppm x Elevated	544.5	202.0	57.7	260.4	793.6	5476.6	1063.2	309.4
	~1000ppm x Elevated	719.1	143.5	69.4	214.2	609.5	3969.1	798.3	314.0
<i>Ostrea edulis</i>	Ambient x Control	1567.2	196.2	48.4	277.4	546.0	3747.0	1077.3	263.6
	~750ppm x Control	1535.5	127.1	39.3	253.3	496.8	3390.0	862.9	232.8
	~1000ppm x Control	1353.5	103.0	42.0	270.7	636.7	4571.7	940.0	252.1
	Ambient x Elevated	1267.3	87.6	55.9	257.4	501.3	3503.5	623.8	192.0
	~750ppm x Elevated	1560.6	111.1	64.8	258.8	539.5	3842.1	879.7	256.1
	~1000ppm x Elevated	2142.2	113.4	37.8	258.0	545.5	3672.5	898.1	248.8

323

324

325

326 4 Discussion

327 The ability of human society to feed the ever-growing population is a major ongoing concern,
328 particularly as climate change is already negatively impacting food production from both
329 terrestrial and marine environments (Brander *et al.*, 2017; Campbell *et al.*, 2017; UNEP,
330 2010). Mollusc aquaculture is increasingly recognised as a solution to this issue. Here,
331 following exposure to temperature and $p\text{CO}_2$ levels predicted for 2050 to 2100, we show
332 species-specific variations in the nutritional quality of two commercially important oyster
333 species. Both *O. edulis* and *M. gigas* displayed changes in biochemical (proximate and
334 mineral) composition; in particular *M. gigas* had lower lipid, carbohydrate, and protein levels,
335 but higher copper concentration, which could pose concerns for both future food safety and
336 security.

337

338 4.1 Condition Index and Moisture content

339 Condition indices are widely used in aquaculture to evaluate the overall health and value of
340 bivalves, and select specimens of the highest quality (Knights, 2012; Orban *et al.*, 2006;
341 Orban *et al.*, 2002). These indices are correlated with the meat yield, which declines in
342 bivalves under stressful environmental conditions the require significant energetic
343 expenditure (Orban *et al.*, 2002). The condition index of *M. gigas* was negatively impacted by
344 elevated temperature but not elevated $p\text{CO}_2$, whereas the condition index of *O. edulis* was
345 unaffected by any of the treatment conditions, suggesting that the two species did not
346 experience or respond to environmental change in the same way. Changes in condition index
347 reflect the respective changes in feeding and respiration rates to ocean acidification and
348 warming of the two species, as observed by Lemasson *et al.* (2018). In the Lemasson *et al.*
349 (2018) study, *M. gigas* increased its metabolic rate at elevated temperatures and reduced its

350 feeding rate at elevated levels of $p\text{CO}_2$ (~750 ppm), leading to reduced condition index,
351 whereas the metabolic rate and feeding rate of *O. edulis* was unaffected by ocean
352 acidification and warming. These results are in contrast to those of Lannig *et al.*, (2010) on *M.*
353 *gigas* who recorded a decrease of ~20% in condition index between individuals exposed to
354 ambient and elevated $p\text{CO}_2$ (see further discussion on the effects of ocean acidification and
355 warming on bivalves in Lemasson *et al.*, 2018). In bivalves, declines in condition index
356 usually suggest depletion of reserves following energetic reallocation, which can lead to
357 changes in individuals biochemical composition (proximate and mineral) and consequently in
358 their nutritional value (see EFSA NDA Panel, 2014; Tate *et al.*, 2017).

359 Water constitutes the major part of oysters (Asha *et al.*, 2014). This component is linked to
360 juiciness, which is an important sensory trait of oysters and influences their marketability
361 (Cruz-Romero *et al.*, 2004). Sensory traits, such as juiciness, texture, appearance, odour or
362 taste, are linked to biochemical composition, and have recently been shown to be unchanged
363 in oysters under ocean acidification and warming (Lemasson *et al.*, 2017b). As was also
364 observed in *Turbo militaris* (Ab Lah, 2018), here the moisture content of either *M. gigas* or
365 *O. edulis* did not change when exposed to ocean acidification and warming conditions.

366

367 4.2 Energetic reserves

368 Protein, lipids, and carbohydrates constitute the main energy storage compounds in bivalves,
369 which all have important functions in physiological processes, for instance gametogenesis
370 and reproduction (Dridi *et al.*, 2007). By influencing oysters physiology and metabolic
371 responses, environmental conditions, such as ocean acidification and warming, can dictate the
372 accumulation and depletion of energetic reserves in bivalves (Clements *et al.*, 2018)..

373

374 *Carbohydrates*

375 Carbohydrate, in the form of glycogen, is thought to be the energy reserve present in the
376 highest quantity in bivalves and is used to sustain routine metabolic processes (Anacleto *et al.*,
377 2014, and references therein). A decline in glycogen content under environmental stress (e.g.
378 hypercapnia, hyposalinity, increased temperature) is common in oysters and can indicate
379 physiological stress (Dickinson *et al.*, 2012). Here, the carbohydrate content of *M. gigas* was
380 reduced under ocean acidification and warming, particularly at ~750 ppm $p\text{CO}_2$ and elevated
381 temperature, but was unaffected in *O. edulis*. Carbohydrate content remained high in
382 *O. edulis* (>8.5% wet weight) compared to *M. gigas* (<5% wet weight). Native bivalve
383 species have previously been shown to have higher glycogen content than non-native and
384 invasive species, this may be a metabolic adaptive strategy to cope with environmental
385 change (Anacleto *et al.*, 2014), and may account for the lack of response of *O. edulis* to ocean
386 acidification and warming here. Given the importance of carbohydrates for oyster
387 maintenance, condition, and their ability to sustain physiological processes, depletion of
388 carbohydrate reserves in *M. gigas* might jeopardize organisms survival in the long term,
389 which aligns with results showing reduced condition (Lemasson *et al.*, 2018).

390

391 *Proteins*

392 Proteins supply structural elements and have a crucial role in metabolic reactions. Under
393 sustained stress, bivalves can catabolise proteins to mobilise energy once carbohydrates and
394 lipids have been depleted (Barber & Blake, 1985). *Magallana gigas* and *O. edulis* were both
395 high in protein, but under ocean acidification and warming *M. gigas* displayed important
396 reductions. A similar response was shown in the whelk *Dicathais orbita*, large declines
397 (>50%) in protein content under ocean acidification and warming (Tate *et al.*, 2017), but in
398 *Mytilus edulis* (Clements *et al.*, 2018) and *T. militaris* (Ab Lah *et al.*, 2018), no reductions in
399 protein were observed suggesting taxon-specific responses.

400

401 *Lipids*

402 The array of lipids in molluscs, with a low proportion of saturated fatty acids and high
403 proportion of polyunsaturated fatty acids (including Ω -3), offer numerous health benefits to
404 people (Sprague *et al.*, 2017). Here, *M. gigas* contained higher levels of lipids (~1.4-4.8%
405 wet weight) compared to *O. edulis*, in the range reported elsewhere (Cochet *et al.*, 2015;
406 Pogoda *et al.*, 2013; Shpigel *et al.*, 1992). In contrast, *O. edulis* used in this study were
407 relatively poor in crude lipids (~0.8-1.6% wet weight), with values below those reported
408 elsewhere (Pogoda *et al.*, 2013). Ocean acidification and warming scenarios led to a decrease
409 in lipid content in both species, particularly notable at ~750 ppm $p\text{CO}_2$. Larger absolute
410 reductions occurred in *M. gigas* (30%; wet weight percentage) which possessed a higher
411 baseline lipid content under control conditions, but larger percentage reductions were
412 apparent in *O. edulis* (~50%; wet weight percentage). Reductions in total lipid content and
413 differences in fatty acid composition (including decreases in polyunsaturated fatty acids)
414 under ocean acidification and warming have been shown in other molluscs (Ab Lah *et al.*,
415 2018; Tate *et al.*, 2017; Valles-Regino *et al.*, 2015 but see Clements *et al.* 2018), with
416 variation attributed to differential deposition and energy use rates between species (Child &
417 Laing, 1998; Pogoda *et al.*, 2013).

418

419 Although carbohydrates (and especially glycogen) are often the preferred source of energy
420 for oysters, species-specific differences may exist (see discussion in Pogoda *et al.*, 2013). It
421 has previously been suggested that *O. edulis* preferentially use lipids whereas *M. gigas* use
422 proteins as their principal energy source for metabolic activity when subjected to food
423 limitation (Child & Laing, 1998). Here, both oyster species when exposed to ocean
424 acidification and warming appeared to use lipids and carbohydrates as their primary source of

425 energetic reserves, but to a lesser extent by *O. edulis*, possibly because they did not have
426 important lipid reserves in the first place. Depletions of energetic reserves were indeed
427 particularly apparent for *M. gigas*, with additional reductions in proteins reflected in the
428 reduced condition index and caloric content, especially at intermediate $p\text{CO}_2$ level. The
429 differential use of energetic reserves by oysters is therefore likely a consequence of the
430 differential physiological stress endured when exposed to ocean acidification and warming
431 conditions (Lemasson et al., under review).

432

433 4.3 Mineral content

434 Seafood quality also varies based on the proportion (total ash) and composition of inorganic
435 minerals. In particular, minerals are an essential component of a healthy diet in humans
436 (EFSA NDA Panel, 2014). Here, the two oyster species displayed similar ash content (~1.9-
437 2.6%), which was unimpacted by ocean acidification and warming. In fact, a modest increase
438 in ash content in *O. edulis* under elevated $p\text{CO}_2$ might indicate mineral accumulation within
439 the tissue. Ab Lah *et al.*, (2018) have also found no changes in ash content of *T. militaris*
440 under ocean warming and acidification.

441

442 Although nutritionists often focus on macronutrients, such as calcium (Ca) and magnesium
443 (Mg), which are beneficial for teeth and bones (Lambert *et al.*, 2017), there is an increasing
444 understanding of the dietary benefits of trace minerals (FAO, 2016). For instance, potassium
445 (K)-rich foods are considered particularly healthy; selenium (Se) strengthens the immune
446 system and reduces oxidative stress in tissue (Rayman, 2000); and zinc (Zn) and iron (Fe) are
447 critical for stamina and disease resistance (Knez *et al.*, 2017; Solomons & Schümann, 2017).
448 Moreover, micronutrient deficiencies afflict an enormous proportion of the population. For

449 instance, over 2 billion people are diagnosed as iron-deficient, and an estimated 800,000
450 children die every year from zinc deficiency (FAO, 2016).

451

452 In this study, large differences in the levels of macro and micro-nutrients between *M. gigas*
453 and *O. edulis* were evident, which is unsurprising as species-specific differences in mineral
454 composition is common in bivalves (Bray *et al.*, 2015). Notably, *M. gigas* exposed to the
455 current climate conditions were relatively high in K, sodium (Na), Mg, Fe, and Se when
456 compared to *O. edulis*, which was high in Zn. While the values presented here for macro- and
457 micro-minerals are within the ranges described in other studies on oysters and may not be
458 locally dependent (Se: Cantillo, 1998; Fe: Diaz Rizo *et al.*, 2010; Na, K, Mg, Fe, Se: Orban
459 *et al.*, 2004), concentrations of copper (Cu) and Zn in this study were significantly higher
460 than those commonly found in literature (Cantillo, 1998). High Cu and Zn contents have been
461 described for oysters growing in contaminated locations associated with mining and harbour
462 activities (Diaz Rizo *et al.*, 2010; Frias-Espericueta *et al.*, 2009). Plymouth Sound – the
463 location of oyster collection for this study – has a long history of mining that has led to
464 significant contamination of its waters and substrates (see Knights *et al.*, 2016 and references
465 therein), which could explain the elevated Cu and Zn levels obtained here.

466

467 Here, exposure to ocean acidification and warming conditions led to species-specific changes
468 in the concentration of those minerals, with the mineral composition of *M. gigas* being
469 especially affected. A recent study found increased levels of Zn in *T. militaris* exposed to
470 ocean acidification and warming conditions, but without changes in other micro- and macro-
471 elements concentrations (Ab Lah *et al.*, 2018). Here, the reductions in Ca, Fe, and Se content
472 in *M. gigas* exposed to ocean acidification and warming to levels similar or lower than
473 *O. edulis*, coupled to the accumulation of Cu, represent a measurable change to its nutritional

474 value, which could have nutritional and safety implications. Copper, along with other trace
475 metals such as arsenic, copper and lead, can become toxic to marine organisms in high
476 concentrations (Götze *et al.*, 2014; Moreira *et al.*, 2016), and threaten human health through
477 seafood ingestion (Bhupander *et al.*, 2011; Han *et al.*, 1998). Since bivalves are filter feeders,
478 they readily accumulate metals present in the surrounding waters into their edible tissue (Lu
479 *et al.*, 2017; Raposo *et al.*, 2009). This process can be modulated by ocean acidification, for
480 instance enhancing the bioaccumulation of Cu in oysters (Belivermiş *et al.*, 2015; Götze *et al.*,
481 2014; Hawkins & Sokolova, 2017; Ivanina *et al.*, 2015; Ivanina *et al.*, 2016). While Cu
482 accumulation under ocean acidification and warming can come at metabolic costs to
483 organisms (Hawkins & Sokolova, 2017), the implications for human consumption are still
484 unclear. For instance, in Plymouth Sound where background levels are already high, further
485 bioaccumulation of potentially harmful minerals, such as Cu or Zn, in *M. gigas* could exceed
486 safe levels for consumption.

487

488

489 4.4 Implications for food security and aquaculture management

490 Our results suggest that the nutritional quality of *M. gigas*, but not *O. edulis*, is likely to be
491 affected by short-term warming and acidification of coastal seawater caused by CO₂
492 emissions. These changes include reduced proteins, lipids, energetic value, as well as changes
493 to their essential mineral contents. Oysters are seldom a major contributor to human diet,
494 however islands and countries with little agricultural land rely on wild-caught seafood and
495 aquaculture for protein (Cooley *et al.*, 2012). Should the changes observed in oysters be
496 widespread in seafood species, then the nutritional benefits of seafood to human health and
497 its role in food security may be further compromised (Cooley *et al.*, 2012; Ding *et al.*, 2017).
498 Given the need for additional and sustainable sources of proteins, the current exponential

499 expansion of the aquaculture industry is inevitable; nevertheless a careful evaluation of this
500 industry as well as the development of appropriate mitigations plans (Clements and Chopin,
501 2017) are needed to ensure that aquaculture is a wise investment in the face of ocean
502 acidification and warming. Diversifying the target species and promoting those currently
503 under-utilized may supplement the industry with ‘novel’ sources of protein. However, this in
504 practicality might face new challenges, such as selecting species that also thrive under
505 aquaculture conditions and avoiding selecting non-native species (Arismendi *et al.*, 2009),
506 and might require strategic management plans. In order to optimise protein supply and
507 secure socio-economic benefits of mollusc aquaculture, research needs to focus on
508 identifying and selecting native aquaculture species that are resilient to future climate
509 conditions, and able to retain their beneficial nutritional properties (Cooley *et al.*, 2012; Sato
510 *et al.*, 2018), without introducing new challenges.

511
512 Our results suggest *M. gigas* is at higher risk of reduction in nutritional quality than its native
513 counterpart *O. edulis* under future ocean acidification and warming scenarios. In the UK, a
514 reduction in the nutritional quality of oysters may not quickly be recognised by consumers,
515 but lower energetic reserves and condition of *M. gigas* may hold an economic relevance to
516 the aquaculture industry, since this species currently represents >90% of the production
517 (Humphreys *et al.*, 2014). Additionally, the biochemical composition can dictate meat
518 appearance, aroma, taste and texture (Cochet *et al.*, 2015; Fratini *et al.*, 2013), and any
519 changes in biochemical composition occurring because of ocean acidification and warming
520 can impact on the sensory quality (Lemasson *et al.*, 2017b). Therefore changes in
521 biochemical composition under ocean acidification and warming can influence the consumer
522 appeal for the product, reducing the demand for it and depressing its economic value (Cooley
523 *et al.*, 2012). As such, the UK aquaculture industry might need to reconsider the management

524 strategy for the future (Fernandes *et al.*, 2017; Jennings *et al.*, 2016) and consider a shift in
525 focus toward species more robust to climate change, such as *O. edulis*, in order to secure
526 future food provision and economic revenue.

527

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537

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541 **7 References**

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- 864

865 **Highlights: (3-5)**

- 866 • Ocean acidification and warming can reduce oysters nutritional quality
- 867 • Changes to nutritional composition were more pronounced in the introduced species
- 868 • Oysters displayed decreased protein, lipid, and carbohydrate contents
- 869 • Multifaceted implications for the aquaculture sector and future food security