Integrating laboratory experiments and biogeographic modelling approaches to understand sensitivity to ocean warming in rare and common marine annelids

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Abstract

Among ectotherms, rare species are expected to have a narrower thermal niche breadth and reduced acclimation capacity and thus be more vulnerable to global warming than their common relatives. To assess these hypotheses, we experimentally quantified the thermal sensitivity of seven common, uncommon, and rare species of temperate marine annelids of the genus *Ophryotrocha* to assess those species' vulnerability to ocean warming. We measured the upper and lower limits of physiological thermal tolerance, survival, and reproductive performance of each species along a temperature gradient (18, 24, and 30 °C). We then combined this information to produce curves of each species' fundamental thermal niche by including trait plasticity. Each thermal curve was then expressed as a habitat suitability index (HSI) and projected for the Mediterranean Sea and temperate Atlantic Ocean under a present day (1970-2000), mid- (2050-2059) and late- (2090-2099) 21st Century scenario for two climate change scenarios (RCP2.6 and RCP8.5). Rare and uncommon species showed a reduced upper thermal tolerance compared to common species, and the niche breadth and acclimation capacity were comparable among groups. The simulations predicted an overall increase in the HSI for all species and identified potential hotspots of HSI decline for uncommon and rare species along the warm boundaries of their potential distribution, though they failed to project the higher sensitivity of these species into a greater vulnerability to ocean warming. In the discussion, we provide elements and caveats on the implications of our results for conservation efforts.

Introduction

The recognition that organisms are unevenly distributed on Earth and that rarity is more frequent than commonness has laid the foundation for the empirical investigation of the causes of rarity and commonness and their consequences on large-scale ecological processes, species biogeography, and biodiversity conservation (Kunin and Gaston 1997). Rarity has been an important driver of species disappearance in past extinctions (Harnik et al. 2012; Calosi et al. 2019), and it is a widely used criterion in conservation biology and ecosystem management to assess the current levels of vulnerability and extinction risk of species (IUCN 2001). Narrow geographic ranges, restricted habitat specificity, small population size, and a combination of these factors make rare species more at risk of decline or extinction compared with their common relatives (Rabinowitz 1981; Calosi et al. 2008a). The common-rare species paradigm not only defines the structure, dynamics, and function of ecosystems but is also useful for projecting the current and future sensitivity of taxa and the impending reorganisation of biodiversity patterns in response to ongoing climate changes (Violle et al. 2017).

Among the attributes of rarity, geographic range size is considered a good predictor of species susceptibility to environmental perturbations (Harnik et al. 2012; Staude et al. 2020). The strict correspondence between the extent of the spatial occurrence of a species and the ecological requirements under which it can thrive gave origin to the *niche breadth–range size hypothesis* (Brown 1984), which postulates that species with broader ecological niches can persist across a wider range of environmental conditions compared to species with narrower ecological niches. This hypothesis bears important implications for our understanding of the mechanisms underpinning commonness and rarity (Calosi et al. 2010; Slatyer et al. 2013) and provides a framework for the prediction of the redistribution of biodiversity under climate change scenarios

45   (Sunday et al. 2011, 2012). Such implications are particularly relevant for ectotherms, which

46   constitute the vast majority of species on Earth (Longhurst 2010), and for which temperature is a

47   major abiotic driver of their past, present, and future distribution *via* its pervasive effect on basic

48   physiological mechanisms, such as thermal tolerance and energy metabolism (Gagné et al. 2020;

49   Bennet et al. 2021).

50   In recent decades, considerable effort has been devoted to finding a mechanistic link

51   between the thermal niche breadth and range size of marine species to predict their distribution

52   and abundance changes under ocean warming. The inclusion of species-specific physiological

53   constraints in niche-based models has helped improve our ability to generate more accurate

54   predictions of species range shifts and species losses in the face of ocean warming (e.g., Kearney

55   and Porter 2009; Cheung et al. 2015; Reygondeau 2019). However, quantitative information on

56   the geographic occurrence and distribution of species is often insufficient for most taxa and is

57   disproportionally deficient for marine species. For many marine invertebrates, for example,

58   assessments of rarity based solely on the geographic range size is challenged by patchy

59   distributions, overdispersion, and the colonisation of microrefugia that may be difficult to detect

60   (Chapman 1999; Benkendorff and Przeslawski 2008). Accordingly, whether the applicability and

61   predictive power of the concepts of commonness and rarity also hold true in these cases has yet to

62   be tested on a wider array of taxa whose geographic distribution is not comprehensively

63   characterised. Furthermore, most niche-model studies estimate the fundamental thermal niche of

64   a species based on its mean basal thermotolerance alone, and thus these models do not account for

65   acclimation through phenotypic plasticity that can broaden the thermal requirements necessary for

66   a species to thrive (Sunday et al. 2011). Further improvements to the predictive power of niche-

67   based models can thus be obtained by integrating, within the common-rare paradigm, the

68 assumptions of those climate-based hypotheses that link a species' thermal physiology and

69 geographic range size to its acclimation ability in order to predict ectotherms' sensitivity to ocean

70 warming. Among these hypotheses, the *climatic variability hypothesis* (CVH) posits that the

71 breadth of the thermal tolerance window of a species correlates positively with its latitudinal extent

72 (Stevens 1989). An extension of the CVH asserts that widespread species or species experiencing

73 higher levels of climatic variability (e.g., common species) should have a broader physiological

74 thermal tolerance and greater acclimation capacities (i.e., *Brattstrom rule*) when compared to less

75 extensively distributed species or species colonising more stable environments (e.g., rare species)

76 (Calosi et al. 2008a,b; Bozinovic et al. 2011; Magozzi et al. 2015).

77   In this study, we tested the possibility of using the concept of commonness and rarity to

78 assess the relative levels of thermal sensitivity of marine ectotherms with differing biogeographies.

79 To do so, we used seven species of temperate, interstitial annelids of the genus *Ophryotrocha*

80 Claparède and Mecznikow, 1869 (Dorvilleidae) characterised by different geographic range sizes

81 and abundances as case studies (Prevedelli et al. 2005; Simonini et al. 2009): *O. labronica* La

82 Greca and Bacci, 1962, *O. japonica* Paxton and Åkesson, 2010, *O. adherens* Paavo et al., 2000,

83 *O. puerilis* Claparède and Mecznikov, 1869, *O. diadema* Åkesson, 1976, *O. hartmanni* Huth, 1933,

84 and *O. robusta* Paxton and Åkesson, 2010. We specifically assessed whether the common or rare

85 status of these species was a good predictor of their vulnerability to ocean warming. To achieve

86 our goal, we first experimentally measured the physiological thermal tolerance limits, survival,

87 and reproductive performance of the studied species along a temperature gradient, i.e., 18, 24, and

88 30 °C. We then used the generated experimental data to build the fundamental thermal niche of

89 each species following the thermal habitat suitability index (HSI) concept developed by Helaouët

90 and Beaugrand (2009), taking into account the thermal plasticity of the measured traits. Finally,

91   we spatially projected the HSI values onto a present-day (1970-2000) scenario for ocean

92   temperatures and predicted their changes under mid- (2050-2059) and late- (2090-2099) 21st

93   Century scenarios of ocean warming. Two representative concentration pathways were chosen,

94   RCP2.6 and RCP8.5, representing a 'strong mitigation' and 'business-as-usual' climate change

95   scenario, respectively (IPCC 2013). Furthermore, to identify the putative ecological mechanisms

96   underpinning the differences between common and rare species, we explored the validity of the

97   *niche breadth–range size hypothesis* in the studied species and assessed whether their

98   physiological acclimation ability was related to their level of commonness or rarity as measured

99   by the extent of their geographic range size (*Brattstrom rule*). Tests were performed on laboratory

100   strains of each species originating from subtidal populations collected in the Mediterranean region,

101   a climate change hotspot where the average sea surface temperature is predicted to increase by

102   0.93 °C to 1.24 °C over the 2010-2039 period and by 3.45 to 4.37 °C over the 2010-2099 period

103   under the RCP8.5 scenario (IPCC 2013). Ocean warming is causing the 'tropicalization' of the

104   southeast Mediterranean basin due to the migration of alien tropical species from the Red Sea and

105   the 'meridionalization' of the northern parts of the basin due to the increased occurrence of

106   indigenous thermophilic species, jeopardizing the persistence of rare, endemic, and colder-tolerant

107   species (Coll et al. 2010).

108

109   **Material and Methods**

110   *Biology and thermal habitats of the studied species*

111   The seven studied species have a similar ecology, morphology, reproductive biology, and

112   dispersal ability. They are all interstitial generalist grazers found in organic-rich benthic habitats

113   and have an average adult body length that ranges between 3 and 12 mm (*O. adherens* and *O.*

puerilis, respectively). They reproduce semicontinuously, laying clutches of eggs inside a protective matrix or tube that are cared for by the parents until the eggs hatch, and the embryos undergo direct development (Simonini et al. 2009, 2010). Occurrence data for these species have been obtained mainly from the Northern Hemisphere. The coasts of the Shetland Islands (Scotland, UK, 60° 20' 49.05'' N, 1° 14' 8.38'' W; *O. hartmanni*) and Oahu (Hawaii, USA, 21° 19' 0.23'' N, 157° 57' 13.04'' W; *O. labronica*) are the most northerly and southerly latitude locations, respectively, where at least one of these species was found (Simonini et al. 2009). All species have been recorded in the subtidal zone (first 60-90 cm below the lower tide level) of shallow marine and brackish coastal waters (Simonini et al. 2010), where they showed different patterns of distribution, prevalence, and abundance across thermal regions and habitats (Prevedelli et al. 2005; Simonini et al. 2009). For example, the distribution range of *O. labronica*, the most ubiquitous and abundant of the seven species, extends from the temperate coasts of the North Atlantic Sea to the subtropical coasts of the Red Sea (Simonini et al. 2009) and comprises locations where minimum and maximum annual water temperatures can range between 5 and 30 °C, respectively (Massamba-N'Siala et al. 2011). In contrast, the known occurrence of the rare species *O. robusta* and *O. diadema* is limited to Mediterranean-like climates, specifically to locations where water temperatures do not exceed 27.5 °C.

Assessment of species commonness-rarity status

We identified the level of commonness or rarity of the studied species using two of the three criteria suggested by Rabinowitz (1981): geographic range size and local population abundance. We measured geographic range size as the extent of occurrence (EOO) (Gaston and Fuller 2009), which was calculated with the tool GeoCAT (Bachman et al. 2011) using information

137 on the known global distribution of the studied species in the Northern Hemisphere (see Online

138 Resource 1, Fig. S1; Online Resource 2, Table S1). We calculated local population abundance as

139 the mean maximum number of individuals recorded in each sampled locality (Online Resource 2,

140 Table S1-S2). We then coded species as common (c), uncommon (u), or rare (r) following a

141 modified version of the 'proportion of species' method described by Gaston (1994). Species with

142 an EOO and local abundance higher than the third quartile of the EOO and abundance distribution

143 were considered common; *O. labronica* and *O japonica*. Species with an EOO or local abundance

144 between the first and third quartiles of the EOO and abundance distribution were categorised as

145 uncommon: *O. adherens* and *O puerilis*. Species with an EOO or local abundance below the first

146 quartile of the EOO and abundance distribution were considered rare: *O. hartmanni*, *O diadema*,

147 and *O. robusta* (Online Resource 1, Fig. S2).

148

149 *Specimen maintenance and experimental design*

150   The specimens used in our study came from laboratory cultures maintained for

151 approximately ten generations (approx. 1.5 years) under a constant temperature (24 °C) and

152 salinity (35; 40 ‰ for *O. hartmanni*, as this salinity guaranteed better performance), and a 12:12

153 h light-dark regime. Founder individuals were collected in Porto Empedocle (Italy; 37°18'N;

154 13°32'E) for *O. labronica, O. puerilis*, *O. adherens*, *O. robusta*, and *O. diadema* and in La Spezia

155 (Italy; 44°06'N; 09°49'E) for *O. japonica* and *O. hartmanni*.

156   For each species, we produced sixty reproductive pairs (parental generation) by pairing

157 sexually mature individuals that were haphazardly collected from the laboratory cultures and by

158 isolating them in a 20 mL glass bowl under the same conditions as the cultures of origin. When

159 the first egg mass was laid and the eggs hatched (F1 generation), the parents were removed and

160   the development of the F1 individuals was followed for approximately 20 d in *O. labronica*, *O.*

161   *japonica*, *O. diadema*, and *O. robusta*, 10 d in *O. adherens*, 35 d in *O. puerilis*, and 25 d in *O.*

162   *hartmanni*. These times corresponded to the late juvenile stage that precedes the full development

163   of oocytes in the coelomatic cavity of the individuals and were used as a temporal reference to

164   randomly assign broods to one of the three acclimation temperatures: 18, 24, and 30 °C, for a total

165   of twenty broods *per* acclimation temperature, thus ensuring that exposure to the acclimation

166   temperatures started at the same developmental stage under all treatments in all species. Two of

167   the acclimation temperatures, 18 and 24 °C, were chosen within the thermal range normally

168   experienced by all the tested species in their natural environment, while 30 °C was the highest

169   temperature recorded in the site colonised by the common species *O. labronica* (Massamba-

170   N'Siala et al. 2011). Exposure to 18 and 30 °C was achieved through the increase or decrease in

171   temperature, respectively, from the culture temperature of 24 °C at a rate of 1 °C h^{-1} (Massamba-

172   N'Siala et al. 2012) using a programmable incubator (Everlasting, AM SLIM 701 TNV,

173   Towcester, UK). At the end of this gradual pre-exposure, for each acclimation temperature, a

174   number of F1 individuals were randomly taken from the broods and assigned to one of two

175   experiments aimed at determining the physiological thermal tolerance limits (Experiment 1) and

176   measuring the survival and reproductive performance (Experiment 2) of the studied species. Each

177   of these experiments is described in detail in the following sections (see also Online Resource 1,

178   Fig. S3 for a schematic representation of the experimental design). During exposure to the

179   acclimation temperatures, the experimental replicates were isolated in 20 mL glass bowls placed

180   inside plastic containers and kept in programmable incubators (Everlasting, AM SLIM 701 TNV,

181   Towcester, UK) with a light-dark regime set at 12:12 h. Salinity (35 ‰) was kept constant

182   throughout the experiments. Artificial sea water was made by dissolving artificial sea salt (Reef

183   Crystals, Instant Ocean, St. Blacksburg, VA, USA) in distilled water. Sea water in the bowls was

184   changed every 3 d, and individuals were fed on the same day *ad libitum* with a solution of spinach

185   minced in sea water (Massamba-N'Siala et al. 2012).

186

187   *Experiment 1: Determination of physiological thermal tolerance limits*

188   Upper and lower physiological thermal tolerance limits were measured using as metric

189   *maximum* and *minimum* critical temperature limits (CT_{max} and CT_{min}), respectively (Lutterschmidt

190   and Hutchison 1997). CT_{max} and CT_{min} were defined as the temperature at which we detected

191   specific, sequential behavioural endpoints used as proxies to define the gradual physiological

192   impairment caused by exposure to suboptimal and lethal temperatures (Massamba-N'Siala et al.

193   2012, 2014). Endpoints were measured using a dynamic method (Lutterschmidt and Hutchison

194   1997), specifically by continuously observing the behaviour of individuals exposed to a constantly

195   increasing or decreasing temperature for CT_{max} and $CT_{min,}$ respectively, *per* unit of time (1 °C min^{-}

196   ^{1}), starting at the acclimation temperature to which individuals had been exposed for 7 d

197   (Massamba-N'Siala et al. 2012). Tests were performed on a subset of twenty individuals for CT_{max}

198   and twenty individuals for CT_{min} randomly taken from the broods after an exposure of 7 d to the

199   assigned acclimation temperature. We tested a maximum of five individuals per round inside a

200   borosilicate glass bowl (diam. = 3 cm, depth = 2 cm) immersed in a computer-controlled

201   recirculating ethylene glycol bath (VWR-I462-7017, Radnor, PA, USA). During each round, we

202   continuously measured the temperature of the seawater inside the glass bowl with a digital

203   thermometer (Testo 922, 2-channel Thermocouple Thermometer, Milano, Italy) equipped with a

204   precision fine wire thermocouple (T/C type K, Testo). The size of each individual was measured

205   before starting each round by counting the number of chaetigers, i.e., the segments bearing bristles

206 (Massamba-N'Siala et al. 2012). The temperatures at which the loss of locomotor control, onset

207 of spasms, and death (lethal temperature) occurred were measured on the same individual as

208 (sequential) endpoints to define CT_{max}. In contrast, the temperatures at which the onset of spasms

209 and chill coma occurred were the (sequential) endpoints measured to define CT_{min} (Massamba-

210 N'Siala et al. 2012, 2014). More specifically, loss of locomotor control was identified as the

211 occurrence of reversible arrhythmicity in locomotor activities. Lethal temperature was defined as

212 the temperature at which individuals no longer responded to poking and showed no recovery after

213 being cooled back to the corresponding acclimation temperature. The onset of spasms was defined

214 as when spasmodic, uncontrolled contraction of the entire body started. Finally, a chill coma was

215 defined as a reversible status where motionless individuals did not respond to prodding.

216   We quantified the physiological acclimation ability of the studied species following the

217 approach used by Calosi et al. (2008a). More specifically, we calculated the absolute difference

218 between the mean temperature at which an endpoint (a proxy for CT_{max} or CT_{min}) was measured

219 after acclimation at 24 and 18 °C (mean $CT_{max/min}$ [24 °C] – mean $CT_{max/min}$ [18 °C]).

220

221 *Experiment 2: Determination of survival and reproductive performance*

222   Individual survival and reproductive performance were measured for each species in

223 twenty pairs *per* acclimation temperature during 90 d of exposure to the assigned acclimation

224 temperature. Pairs were formed by haphazardly selecting and matching sexually matured

225 individuals taken from different broods within the same acclimation temperature to avoid

226 inbreeding (Massamba-N'Siala et al. 2011). We checked each pair daily to record the presence or

227 death of each individual and the number of eggs laid, which were counted and discarded. We

228 calculated survival as the percentage of days that an individual was alive over the total duration of

229   the experiment (90 d) and reproductive performance as the total fecundity, which was defined as

230   the total number of eggs *per* chaetiger laid by a pair (Massamba-N'Siala et al. 2011).

231

232   *Determination of a species' fundamental thermal niche*

233   Following the theoretical approach suggested by Helaouët and Beaugrand (2009; see also

234   Sunday et al. 2012; Pörtner et al. 2007), we used the experimental data on CT_{max}, CT_{min}, and total

235   fecundity to determine the shape of the fundamental thermal niche of the studied species. Curves

236   were built on four thermal ranges – for *critical tolerance*, *tolerance*, *growth*, and *reproduction* –

237   defined by the mean upper and lower limits for physiological thermal tolerance and reproduction

238   measured at each acclimation temperature and quantified in the temperature dimension as an HSI.

239   This index ranges from 0 (when the environment is unsuitable for the species) to 1 (when the

240   environment is optimal for the species). First, we bounded the thermal niche of each species using

241   the maximum mean value of the upper lethal temperature and the minimum mean temperature at

242   which chill comas occurred from each acclimation temperature. The HSI at these two designated

243   points was set at 0.01, while an HSI below or beyond this range was set as 0. Following the same

244   approach, we set the *critical tolerance* range (HSI = 0.1) at the mean value of upper lethal

245   temperature and chill coma averaged across acclimation temperatures. We then retrieved the upper

246   and lower limits of the *tolerance* range (HSI = 0.3) using the minimum mean temperature at the

247   onset of spasms (CT_{min}) and the maximum mean temperature at the loss of locomotor control,

248   respectively, measured across acclimation temperatures. We set the range for *growth* (HSI = 0.5)

249   between the maximum mean temperature at the onset of spasms (CT_{min}) and the minimum mean

250   temperature at the loss of locomotor control. We obtained the limits for the *reproduction* range

251   (HSI = 0.8) from the curve of reproductive performance derived from the data on total fecundity.

252   We assigned an HSI value of 1 to the temperature at which the maximum number of eggs was

253   estimated to be produced. Finally, we applied a shape-preserving, piecewise cubic interpolation

254   using all defined HSI values to quantify the full extent of the thermal niche from -4 to 42.7 °C

255   (mean minimum and maximum global annual sea surface temperatures) every 0.1 °C. The

256   interpolated value at a query point was based on a shape-preserving, piecewise cubic interpolation

257   of the values at thirty-five neighbouring grid points using the function *interp1* from MATLAB's

258   statistical toolbox. If a threshold point had not been quantified experimentally (e.g., total fecundity

259   for *O. puerilis* (u) and *O. hartmanni* (r)), we extrapolated the HSIs by interpolation using the other

260   existing points.

261   We calculated the breadth of the fundamental thermal niche of the species as the difference

262   between the maximum and minimum temperatures that defined each of the four ranges used to

263   build the curves of the fundamental thermal niche.

264

265   *Thermal habitat suitability maps*

266   We extracted the yearly average sea surface and bottom temperature from the IPSL-CM5-

267   MR (Institut Pierre Simon de Laplace), GFDL-ESM2 M (Geophysical Fluid Dynamics

268   Laboratory), and MPI-ESM (Max Plank Institute) Earth system models (ESMs) from the Coupled

269   Model Intercomparison Project Phase 5 (CMIP5) website for two emission scenarios, RCP2.6 and

270   RCP8.5, and for the reference (1970–2000), mid- (2050-2059) and late- (2090-2099) 21st Century

271   periods. We computed average values for each geographic cell on regular 0.5° x 0.5° grids between

272   the ESMs for each year and each decade. Then, using the fundamental niche previously computed,

273   we retrieved the corresponding HSI values averaged for each grid cell using sea surface and bottom

274   temperatures. In this way, we calculated HSI values for each species in the North Atlantic and

275   Mediterranean regions at the different periods for the two RCPs. Since the studied species are

276   associated with coastal environments, HSI values located in the open ocean domain were set to 0

277   following the biogeographic raster of Reygondeau et al. (2013). In addition, to better visualise the

278   changes in HSI under the two RCPs, we plotted maps to show the mathematical difference between

279   the HSI values projected in the future scenarios and those calculated for the reference period.

280   Following the approach described above, we also calculated HSI values for each species based on

281   real temperature data for the North Atlantic and Mediterranean regions using the World Ocean

282   Atlas 2018 database (Locarnini et al. 2019) and for the Mediterranean Sea using the

283   MEDAR/MEDATLAS database (Fichaut et al. 2003). These maps showed a good match with

284   those obtained for the reference period (1970–2000) used in our projections (Online Resource 3,

285   Appendix 1; Online Resource 1, Fig. S4-S5; Online Resource 2, Table S3).

286

287   *Statistical analyses*

288   We tested the effects of species status (*Status*; three levels: c, u, r), species identity

289   (*Species(Status)*; seven levels, nested in *Status*), acclimation temperature (*T*; two levels: 18, 24

290   °C), and their interactions on CT_{max} and CT_{min} with generalised linear models (GLMs; family

291   Gaussian, identity link), using body size as a covariate. This analysis was performed for only two

292   of the three acclimation temperatures because none of the rare species and only one uncommon

293   species, *O. adherens*, survived a 7 d exposure to 30 °C. We then performed a second analysis with

294   GLMs (family Gaussian, identity link), using body size as a covariate, to test for the effect of

295   species identity (*Species*; three levels), acclimation temperature (*T*; three levels: 18, 24, 30 °C),

296   and their interaction on the CT_{max} and CT_{min} of the three species that survived the exposure to 30

297 °C: *O. labronica* (c), *O. japonica* (c), and *O. adherens* (u). For this latter analysis, there was no

298 replication for the species *Status*.

299 Due to technical problems, all the specimens of *O. puerilis* (u) and *O. hartmanni* (r) died before

300 being paired for the measurement of survival and reproductive performance. Consequently, we

301 used GLMs to assess the effect of species identity (*Species*; five levels), acclimation temperature

302 (*T*; three levels: 18, 24, 30 °C), and their interactions on survival (family quasipoisson, log link)

303 and total fecundity (family Gaussian, identity link) for the remaining species, as there was no

304 replication for species *Status*.

305 Post hoc tests were performed with Tukey's test using the R package *multcomp*. Since multiple

306 endpoints, used to define physiological traits (CT_{max} or CT_{min}), or multiple life-history traits

307 (survival and total fecundity) were measured on the same individual, we applied the Benjamini–

308 Hochberg correction for false positives to all *P*-values.

309 Preliminary analyses showed that none of the measured traits exhibited a phylogenetic signal ($\lambda \neq$

310 0, $P < 0.05$), which was estimated using Pagel's λ using the 'phylosig' function in the R package

311 *phytool* (for details, see Online Resource 3, Appendix 2; Online Resource 1, Fig. S6; Online

312 Resource 2, Table S4). Accordingly, we performed final analyses without applying any

313 phylogenetic correction.

314   We investigated the relationship between the physiological acclimation ability and

315 geographic range size for each proxy of CT_{max} and CT_{min} using a phylogenetic generalised least

316 squares multiple regression with the R package *ape*, using body size as a covariate. Using the same

317 technique, we assessed the relationship between niche breadth and geographic range size by fitting

318 linear models for the breadth of the fundamental thermal niche as a function of the EOO for each

319 of the four performance ranges previously identified: *critical tolerance*, *tolerance*, *growth*, and

320 *reproduction*. Assumptions of normality and homogeneity of variance were checked on the

321 residuals with the Shapiro–Wilk test and Levene test, respectively, and were met for all the

322 regression models.

323 We performed all statistical analyses using R software, version 4.0.0 (RStudio Team 2020; see

324 Online Resource 4 for R scripts).

325

326 **Results**

327 *Physiological upper thermal tolerance limits*

328 Mean CT_{max} (± SE) ranged between 33.19 ± 0.03 and 41.82 ± 0.02 °C in the group of

329 common species (*O. labronica and O. japonica*), between 27.28 ± 0.79 and 35.70 ± 0.05 °C in the

330 group of uncommon species (*O. adherens and O. puerilis*), and between 29.33 ± 0.04 and $36.58 \pm$

331 0.04 °C in the group of rare species (*O. hartmanni*, *O diadema*, and *O. robusta*) (Fig. 1a-c).

332 Common species had a significantly higher mean CT_{max} than their uncommon and rare congeners

333 both at 18 and 24 °C and for all endpoints (*Status* by $T_{(18,24 \, °C)}$: maximum deviance = 182.48, $P <$

334 0.001; Table 1a-c, Fig. 1a-c. See Online Resource 2, Table S5 for pairwise comparisons).

335 Uncommon species showed a slightly but significantly lower mean CT_{max} compared to the rare

336 species when measured as the loss of locomotor control (Fig. 1a) and lethal temperature (Fig. 1c)

337 following exposure to 18 °C. In all other cases, uncommon and rare species showed comparable

338 mean CT_{max} (Fig. 1a-c).

339 We found significant interspecific differences for all the endpoints used to define CT_{max}

340 (*Species*(*Status*) by $T_{(18,24 \, °C)}$: maximum deviance = 144.67, $P < 0.001$; Table 1a-c; Fig. 2a-c).

341 Mean CT_{max} generally increased with increasing acclimation temperatures for all species when

342 measured as the loss of locomotor control (Fig. 2a) and for all species except *O. japonica* (c) when

343 measured as the onset of spasms (Fig. 2b). This trend was less consistent in the measurement of

344 lethal temperature, for which three out of the five rare-uncommon species showed comparable

345 levels of mean CT_{max} at 18 and 24 °C (Fig. 2c). Mean CT_{max} was the highest in *O. labronica* (c),

346 followed by *O. japonica* (c) (Fig. 2a-c. See Online Resource 2, Table S6 for pairwise comparisons

347 and Table S7 for mean raw values). In general, *O. diadema* (r) and *O. robusta* (r) showed lower

348 mean CT_{max} than *O. japonica* (c). *Ophryotrocha hartmanni* (r) and *O. puerilis* (u) stood out for

349 having the lowest mean CT_{max} of all species (Fig. 2a-c). Finally, *O. adherens* (u) had among the

350 lowest mean CT_{max} when measured as the loss of locomotor control (Fig. 2a) and had mean CT_{max}

351 between those measured for *O. japonica* (c) and *O. robusta* (r) when measured as the onset of

352 spasms and the lethal temperature (Fig. 2a-c).

353   The lowest and highest mean (± SE) CT_{max} ranged between 34.34 ± 0.14 °C (*O. adherens*

354 (u)) and 42.66 ± 0.13 °C (*O. labronica* (c)), respectively, following exposure to 30 °C (Online

355 Resource 1, Fig. S7; Online Resource 2, Table S7 for mean raw values). Analyses performed on

356 the species that survived the exposure to 30 °C confirmed the previously observed patterns: *O.*

357 *labronica* (c) and *O. japonica* (c) showed higher mean CT_{max} than *O. adherens* (u) at all

358 acclimation temperatures for the loss of locomotor control, onset of spasms (*Species* by $T_{(18,24,30}$

359 $_{°C)}$: maximum deviance = 99.07, $P < 0.001$; Table 2a-b. See Online Resource 2, Table S8 for

360 pairwise comparisons) and lethal temperature (*Species*: deviance = 68.63, $P < 0.001$; Table 2c;

361 Online Resource 1, Fig. S8). Finally, mean CT_{max} also increased with increasing acclimation

362 temperature when 30 °C was included in the analysis. The only exception to this pattern was found

363 in the loss of locomotor control in *O. japonica* (c), for which no significant differences were

364 detected between CT_{max} measured at 24 and 30 °C (Online Resource 1, Fig. S7).

365

Physiological lower thermal tolerance limits

366

367   Mean ($\pm$ SE) CT_{min} ranged between -1.69 $\pm$ 0.02 and 8.08 $\pm$ 0.02 °C in the group of common

368   species, -2.07 $\pm$ 0.05 and 8.53 $\pm$ 0.07 °C in the group of uncommon species, and -2.40 $\pm$ 0.01 and

369   8.20 $\pm$ 0.02 °C in the group of rare species (Fig. 1d, e). The common species had slightly lower

370   mean CT_{min} compared to uncommon species when measured as the onset of spasms and had

371   slightly lower mean CT_{min} compared to both uncommon and rare species when measured as chill

372   coma following exposure to 24 °C. No significant difference in mean CT_{min} was found between

373   these three groups in any other cases (*Status* by $T_{(18-24 \, °C)}$: maximum deviance = 169.97, $P = 0.01$;

374   Table 1d,e; Fig. 1d,e. See Online Resource 2, Table S5 for pairwise comparisons).

375   CT_{min} varied differently among species depending on the acclimation temperature

376   (*Species(Status)* by $T_{(18,24 \, °C)}$: deviance = 117.91, $P < 0.001$; Table 1d,e; Fig. 2d,e). Mean CT_{min}

377   generally increased with increasing acclimation temperatures in all species. An exception to this

378   trend was observed in *O. labronica* (c), which showed comparable mean CT_{min} at 18 and 24 °C

379   when measured as the chill coma (Fig. 2e). In general, *O. adherens* (u) and *O. hartmanni* (r)

380   showed the highest mean CT_{min}, while *O. puerilis* (u) showed the lowest mean CT_{min} (Fig. 2d,e;

381   Online Resource 2, Table S6 for pairwise comparisons and Table S7 for mean raw values). The

382   remaining species showed intermediate mean CT_{min} that ranked differently across acclimation

383   temperatures depending on the endpoint considered (Fig. 2d,e).

384   The lowest and highest mean ($\pm$ SE) CT_{min} ranged between -0.63 $\pm$ 0.23 °C (*O. japonica*

385   (c)) and 12.45 $\pm$ 0.23 °C (*O. adherens* (u)), respectively, following exposure to 30 °C (Online

386   Resource 1, Fig. S7; Online Resource 2, Table S7 for mean raw values). *Ophryotrocha adherens*

387   (u) also had the highest mean CT_{min} following exposure to 30 °C (*Species* by $T_{(18,24,30 \, °C)}$: maximum

388   deviance = 72.94, $P < 0.001$; Table 2d,e. See Online Resource 2, Table S8 for pairwise

18

389 comparisons). Finally, mean CT_{min} generally decreased with increasing acclimation temperatures

390 in all three species and for all endpoints when exposure to 30 °C was included in the analyses

391 (Online Resource 1, Fig. S7).

392

393 *Survival and reproductive performance*

394 At 18 °C, uncommon and rare species showed a comparable mean survival to *O. japonica*

395 (c) (100% at all acclimation temperatures) and a higher mean (± SE) survival compared to *O.*

396 *labronica* (c) (76.78 ± 6.41%) (*Species* by $T_{(18,24,30\ °C)}$: deviance = 509.30, $P < 0.001$; Fig. 3a,

397 Table 3a. See Online Resource 2, Table S9 for mean raw values and Tables S10 for pairwise

398 comparisons). At 24 °C, the mean survival of *O. diadema* (r) and *O. robusta* (r) was comparable

399 to that measured in *O. japonica* (c), as well as comparable to that measured at 18 °C, while the

400 mean survival of *O. adherens* (u) was lower than that measured at 18 °C (49.79 ± 2.28%).

401 Survival of *O. labronica* (c) at 24 °C showed mean values comparable to those measured at 18

402 °C and were intermediate among those measured for *O. adherens* (u) and all the other species. At

403 30 °C, *O. japonica* (c) and *O. labronica* (c) (97.89 ± 1.77%) had comparable mean survival, and

404 both common species had a significantly higher mean survival than uncommon and rare species;

405 mean values for survival in the latter two groups ranged between 14.67 ± 2.57 and 11.32 ±

406 1.53% in *O. robusta* (r) and *O. adherens* (u), respectively (Fig. 3a).

407 *Ophryotrocha robusta* (r) was the most fecund species at 18 and 24 °C (60.39 ± 3.93 and

408 67.57 ± 10.16 eggs chaetigers[-1], respectively), followed by *O. adherens* (u) and *O. labronica* (c)

409 at 18 °C and by *O. adherens* (u), *O. labronica* (c), and *O. japonica* (c) at 24 °C (*Species* by $T_{(18,24,30}$

410 $_{°C)}$: deviance = 26027, $P < 0.001$; Fig. 3b, Table 3b. See also Online Resource 2, Table S9 for mean

411 raw values and Tables S10 for pairwise comparisons). The least fecund species were *O. japonica*

412   (c) and *O. diadema* (r) at 18 °C and *O. diadema* (r) at 24 °C. At 30 °C, *O. labronica* (c) showed a

413   mean total fecundity that was higher than *O. japonica* (c) (40.78 ± 6.75 and 27.79 ± 2.96 eggs

414   chaetigers^{-1}, respectively), and both common species were on average more fecund than the

415   uncommon and rare species. More specifically, *O. diadema* (r) and *O. robusta* (r) did not

416   reproduce, while *O. adherens* (u) had an extremely low mean total fecundity (0.56 ± 0.20 eggs

417   chaetigers^{-1}) (Fig. 3b).

418

419   *Acclimation ability, thermal niche breadth, and range size*

420   Physiological acclimation ability was not related to the geographic range size of the studied

421   species for all the analysed endpoints (Online Resource2, Table S11). Similarly, we found no

422   significant relationship between the breadth of the fundamental thermal niche and range size in all

423   the performance ranges considered (Online Resource 2, Table S12).

424

425   *Fundamental thermal niches and thermal habitat suitability*

426   The fundamental thermal niche of the studied species was represented by a unimodal, left-

427   skewed curve, where the thermal habitat suitability (HSI) increases with increasing temperatures

428   until it reaches a peak at the optimal temperature for reproduction and steeply descends thereafter

429   (Fig. 4). Common species extended their HSI towards higher temperatures for all functions and

430   maximised their reproductive performance under warmer conditions (25-27 °C) compared with

431   uncommon and rare species (21-23 °C), thereby intensifying the asymmetry of their curves (Fig.

432   4). In contrast, the left part of the curves unfolded within a narrower range of temperatures and

433   had no recognisable patterns in variation between species.

434   Projections based on the fundamental thermal niche of the studied species showed that HSI

435   values higher than 0.8 ranged between the 30th and 45th parallel latitudes when mapped in the

436   reference period (Online Resource 1, Fig. S9-S10). An overall increase in the HSI was observed

437   for all species under both RCP scenarios and was much more marked poleward, especially for *O.*

438   *labronica* (c) and *O. robusta* (r) (Fig. 5 and Online Resource 1, Fig. S11). In both the reference

439   and future scenarios, uncommon and rare species tended to possess higher HSI values (0.9-1) in

440   many more cells than their common relatives, particularly at the lowest latitude of their potential

441   distribution (Fig. 5 and Online Resource 1, Figs. S11). The HSI values decreased locally under

442   RCP 8.5 in some of the uncommon and rare species, specifically along the coasts of the Levantine

443   Sea (*O. hartmanni* (r)), the Sirte Gulf (Libya) (*O. puerilis* (u), *O. adherens* (u), and *O. hartmanni*

444   (r)), the Atlantic coasts of North Africa (*O. hartmanni* (r) and *O. adherens* (u)), and the southern

445   coasts of the USA (*O. puerilis* (u) and *O. hartmanni* (r)) (Fig. 5 and Online Resource 1, Fig. S11).

446

447   **Discussion**

448   Our study sheds light on a number of fundamental physiological and ecological

449   mechanisms explaining the commonness and rarity of temperate marine ectotherms, showing that

450   uncommon and rare species are more physiologically sensitive to elevated temperatures than

451   common species due to their lower physiological heat tolerance. Our simulations also suggest that

452   uncommon and rare species may be more prone to declines along the warm boundaries of their

453   potential distribution. However, the simulations fail to project these species' higher thermal

454   sensitivity into their overall greater vulnerability to ocean warming. Our results are consistent with

455   the known biogeography of the studied species and support the use of the dichotomous

456   commonness and rarity concept to assess macrophysiological patterns of thermal sensitivity in

457 ectotherm species. In addition, our results indicate that the predictive power of this conceptual

458 framework is less accurate when dealing with intermediate levels of rarity, for example, the

459 uncommon *versus* rare species in this case.

460

461 *Upper thermal tolerance: a driving factor in defining biogeographic differences*

462   We find strong support for the idea that common species possess a greater physiological

463 heat tolerance than their uncommon and rare congeners at all acclimation temperatures and for all

464 lethal and sublethal endpoints measured. In addition, common species outperformed uncommon

465 and rare species at the highest acclimation temperature, showing higher survival and reproductive

466 capacities. Similar results were obtained by Thibault et al. (2020), who found that *O. japonica* (c)

467 was able to persist for two generations at an elevated temperature (28 °C) thanks to the beneficial

468 adjustment of its energy metabolism, as characterised using a targeted metabolomics approach,

469 while *O. robusta* (r) faced a lethal increase in energy requirements before the first generation of

470 viable offspring could be produced. In contrast, no clear physiological or ecological patterns linked

471 to the biogeographical status of the studied species were found when cold tolerance was considered

472 or when survival and reproductive performance were measured and compared within the 18 to 24

473 °C range.

474   Our observations provide a mechanistic explanation of the known global, regional, and

475 local geographic distribution of the studied species. For example, the greatest heat tolerance of *O.*

476 *labronica* (c) accounts for its broadest geographic range size and its ability to persist in tidal and

477 subtidal waters where temperatures as high as 30 °C have been recorded (Massamba-N'Siala et al.

478 2011). Not surprisingly, *O. labronica* (c) has been the only species to date found in subtropical

479 waters, specifically along the coasts of the Northern Red Sea (Simonini et al. 2009). *Ophryotrocha*

480   *japonica* (c), a species originally from the North Pacific coasts, is the other most heat tolerant

481   species. Since it was first recorded in the Mediterranean Sea, this species was able to colonise the

482   same thermal regions as *O. labronica* (c) and now has the second largest range size extent among

483   the studied species (Simonini et al. 2009). In contrast, *O. hartmanni* (r), the least heat tolerant

484   species, is characterised by very low densities in subtidal waters (1-7 indiv.; Online Resources 2,

485   Table S1) but is among the most abundant macrobenthic species in the sediments of fish farms on

486   the North Atlantic coasts (Pereira et al. 2004), suggesting its preference for colder waters.

487   Similarly, *O. puerilis* (u) is among the most physiologically sensitive species to elevated

488   temperatures and it capitalizes on thermal habitats that better match its preference for colder

489   temperatures. For example, by colonising organic-rich sediments at higher depths (Taboada et al.

490   2017) or by reaching higher local densities during the coldest months of the year (Prevedelli et al.

491   2005).

492   Of course, several factors other than temperature can drive the spatial and temporal

493   distribution of marine species (Gagné et al. 2020). Different sensitivities to other abiotic factors

494   (such as salinity, oxygen, pH), biotic interactions, capacity and limitation to dispersal, habitat

495   preference, and colonisation history can prevent a species from fully realising its fundamental

496   thermal niche, contributing to a mismatch between the physiological thermal tolerance and

497   distribution range of a species (i.e., realised niche, Pulliam 2000; Arribas et al. 2012; Sánchez-

498   Fernández et al. 2012). For example, *O. diadema* (r), a species initially reported in the Pacific

499   coasts, and *O. robusta* (r), a species endemic to the Mediterranean Sea (Simonini et al. 2009),

500   display a greater physiological heat tolerance among rare species, but their known distribution is

501   limited to only two and eight known localities, respectively (Online Resource 1, Fig. S1). For these

502   species, upper thermal tolerance limits are expected to be major determinants of their colonisation

503   success in a new place. However, their recent colonisation history (for *O. diadema*) or the limited

504   chance of dispersion of the species of the genus *Ophryotrocha*, which usually passively occurs

505   through the ballast water of ships (Simonini et al. 2009), coupled with the absence of thermal

506   microrefugia along the dispersal trajectories due to the patchy occurrence of suitable habitats, may

507   play an important role in determining the rarity level of these annelid species.

508

509   *Macrophysiological and macroecological patterns for common and rare species*

510   Over the past decades, an increasing number of studies have attempted to use thermal

511   tolerance limits to search for macrophysiological and macroecological patterns that could inform

512   species vulnerability to climate change (e.g., Calosi et al. 2008a; Calosi et al. 2010; Bozinovic et

513   al. 2011; Sunday et al. 2011, 2012). Most documented patterns have produced hypotheses linking

514   the organismal thermal physiology and geographic range size. Among these hypotheses, the

515   *climatic variability hypothesis* (CVH) and its corollaries (e.g., *Brattstrom rule*) predict a positive

516   association between a species' geographic range size, physiological thermal tolerance, and

517   acclimation capacities (Bozinovic et al. 2011; Magozzi and Calosi 2015). In diving beetles of the

518   genus *Deronectes*, for example, heat and cold thermal tolerance were positively correlated with

519   range size, and restricted species were foreseen to be most at risk from global warming due to their

520   reduced acclimation capacities (Calosi et al. 2008a; Calosi et al. 2010). Our results provide partial

521   support for the CVH: a broader range size was associated with a greater physiological heat

522   tolerance in the two common species, but we report no quantitative link between the species range

523   extent and heat tolerance within the group of uncommon and rare species. In addition, no

524   relationship appears to exist between a species' range size and its physiological acclimation ability,

525   and upper and lower thermal tolerance limits increase and decrease with increasing acclimation

526   temperatures, respectively, in all species. The fact that we used strains originating from subtidal

527   temperate populations that are adapted to seasonal thermal changes may explain this result.

528   The existence of a relationship between a species' thermal tolerance breadth and its range

529   size is another mechanism suggested to explain differences in the distribution of common and rare

530   species (Brown 1984). The *niche breadth–range size hypothesis* has recently received empirical

531   validation (Slayter et al. 2013; Stuart-Smith et al. 2017), and numerous large-scale studies have

532   demonstrated the tight relationship existing between the width of the physiological thermal

533   tolerance window and the extent of geographic range boundaries across latitudinal gradients (e.g.,

534   Calosi et al. 2010; Compton et al. 2007; Sunday et al. 2011). In our study, the breadth of the

535   fundamental thermal niche failed to predict the extent of the range size. Our result contributes to

536   the ongoing debate around whether the *niche breadth–range size hypothesis* is universally valid

537   (e.g., Hirst et al. 2017). A mismatch between the scale at which niche breadth and range size are

538   measured could explain why our data provided no support for this hypothesis (Kambach et al.

539   2019).

540   The comparable or higher thermal sensitivity that uncommon species show compared to

541   rare species may (at least in part) help explain why our results provide weak or no support for the

542   tested hypotheses (*CVH*, *niche breadth–range size hypothesis*). On one hand, this highlights the

543   limitations of the approach used to categorise species into discrete biogeographical groups within

544   a *continuum* of forms, commonness and rarity, which are relative concepts. Rare-common species

545   cut-off points can, in fact, change depending on the level of rarity of other congeneric species, the

546   spatial and temporal scale of investigation, or following the inclusion of other criteria (Gaston

547   1994; Flather and Sieg 2007), potentially leading to different conclusions on the relative

548   differences in thermal sensitivity between uncommon and rare species. Currently, there are only a

549   few continuous indices of rarity, and the most used indices (in the terrestrial realm) are based on

550   exhaustive distributions (mostly from expert range maps) that are not available for marine

551   invertebrates. In fact, for this group of metazoans, gathering information on the criteria used for

552   categorising common and rare species (e.g., range size) is particularly challenging. The use of

553   more flexible categorisation approaches could help increase the accuracy with which closely

554   related species are arranged into intermediate levels of species rarity. This could be achieved by

555   including metrics that are generally considered less rigorous in predicting species distribution, such

556   species prevalence, i.e., the presence/absence ratio to the total number of sites collected (Jiménez-

557   Valverde et al. 2009). For example, the inclusion of information on prevalence among the criteria

558   used to define the common-rare status of our studied species would have made the distinction less

559   marked between *O. adherens* (u), *O. diadema* (r), and *O. robusta* (r), all of which had a prevalence

560   lower than or close to the first quartile (0.08) that defined the uncommon-rare species cut-off point

561   for this trait (Online Resource 2, Table S2). These observations were confirmed by the occurrence

562   data obtained for the studied species in the Mediterranean Sea, a region subjected to a more

563   extensive and systematic decadal collection effort and thus less biased by unbalanced sampling

564   compared to global distribution records (Simonini et al. 2009). On the other hand, we cannot

565   discard the possibility that species thermal physiology alone cannot provide a comprehensive

566   explanation of intermediate levels of rarity. As discussed above, temperature is not the only factor

567   influencing the geographic distribution of uncommon and rare species. The role of other abiotic

568   factors (e.g., Sunday et al. 2014), interspecific interactions (e.g., Godsoe and Harmon 2012), and

569   the number of dispersal opportunities (e.g., Grantham et al. 2003; Arribas et al. 2012) is worth

570   considering in future investigations of the mechanisms explaining rarity.

571

572 *Habitat suitability shift in common and rare species under ocean warming: conclusions and*

573 *caveats*

574   The unimodal, left-skewed curves of the fundamental thermal niche of the studied species

575   resembled the thermal performance curves used to describe the thermal sensitivity of biological

576   performances in ectotherms (Schulte et al. 2011). The level of asymmetry of these curves, as well

577   as the position of the thermal *optimum* relative to the mean of the environmental temperature, have

578   important implications for predicting species vulnerability to ocean warming. In fact, species

579   exposed to thermal conditions that are close to or above their thermal *optimum* for performance

580   are expected to have narrower or no safety margins to cope with increasing temperatures and,

581   consequently, be more at risk of population declines under ocean warming (Deutsch et al. 2008).

582   In our study, this prediction should have been relevant for *O. puerilis* (u), *O. adherens* (u), and *O.*

583   *hartmanni* (r) due to the closer proximity of their thermal *optimum* to their upper thermal limits

584   for reproduction, as confirmed (see below) by our simulations.

585   The spatial projections of the HSI captured the overall latitudinal range where this group

586   of annelids is found. This correspondence is better represented when the fundamental niche is

587   defined by the thermal range for reproduction ($0.8 < HSI < 1$) rather than the range for

588   physiological thermal tolerance ($0.1 < HSI < 0.5$). The former is in fact expected to provide a more

589   accurate approximation of the conditions that shape the ecological success of a species (Helaouët

590   and Beaugrand 2009). In both ways, *O. labronica* (c) is the only species shown to be a thermal-

591   range conformer: it exhibits a close match between its latitudinal range and its thermal tolerance

592   (Sunday et al. 2012). The idea of the presence of a 'hyper' performing species within the annelid

593   genus *Ophryotrocha* echoed what was observed in the widespread diving beetle *Deronectes latus*

594   Stephens, 1829 (Calosi et al. 2008a; Calosi et al. 2010) and the gammarid *Gammarus duebeni*

595   Lilljeborg, 1852 (Gaston and Spicer 2001). Both *D. latus* and *G. duebeni* are the most widespread

596   and physiologically tolerant species of their genus, supporting Gaston and Spicer's (2001) idea of

597   the existence of species that are jacks-of-all-trades and masters-of-all, further confirmed by

598   observations on the thermal metabolic performance and tolerance plasticity of the invasive

599   decapod Asian shrimp *Palaemon macrodactylus* Rath- bun, 1902 (Magozzi and Calosi 2015).

600   Conversely, all of the other species investigated in our study did not meet their potential

601   distribution range. The mismatch between the geographic range of a species and its potentially

602   occupied range based on its thermal physiology can reduce the accuracy with which projections

603   that are based only on temperature can generate predictions on range shifts (Aubry et al. 2017).

604   Our simulations foresee two trends of HSI shifts extensively documented in temperate

605   marine ectotherms in response to ocean warming: (i) range expansion towards higher latitudes and

606   (ii) range contraction at lower latitudes (Cheung et al. 2009; Morley et al. 2018). These patterns

607   varied depending on the common-rare status of the studied species. In the reference decades used

608   in this study, uncommon and rare species commonly lived closer to their thermal *optimum* for

609   reproduction and at many more sites than common species. This pattern is projected to intensify

610   at the end of the 21st Century, particularly at the lowest latitudes of the Atlantic and Mediterranean

611   regions, where uncommon and rare species are projected to live at their optimal temperatures for

612   performance in most localities, or above it in some regions at the warm edges of their potential

613   distribution under RCP8.5. Here, we identified hotspots of potential population decline for *O.*

614   *adherens* (u), *O. puerilis* (u), and *O. hartmanni* (r), the three species that showed narrower upper

615   safety margins for niche adjustment. Some of these areas, such as the Levantine Sea, are already

616   known for their high occurrence of extinction events of endemic species (Rilov 2016). It must be

617   noted, however, that such a scenario seems to be potentially relevant only for *O. adherens*, the

618   only species recorded in this area. Indeed, our projections suggest that ocean warming may have

619   an overall beneficial effect on the persistence of these annelid species, as indicated by the increased

620   HSI predicted for all the species across their potential distribution. Such predictions may be more

621   optimistic, as they were built on the thermal responses of strains subjected to laboratory

622   conditioning over multiple generations. Exposure to acute, severe conditions in subtidal habitats

623   can in fact exert a positive influence on an organism's thermal performance *via* the activation of

624   mechanisms regulating heat stress responses (Giomi et al., 2019). Consequently, we cannot rule

625   out the possibility that our studied species may be able to withstand warming waters more

626   efficiently in their natural habitat compared to an experimental setting. Nevertheless, the

627   magnitude of these considerations must be carefully examined in light of the limitations of the

628   methodological approach used and the ecology of the studied species. First, our simulations are

629   based on scenarios of ocean warming that rely on yearly averaged temperatures that do not

630   accurately predict the thermal conditions on which coastal species set their thermal *optima*

631   (Boersma et al. 2016; Stuart-Smith et al. 2017). This is particularly true in subtidal habitats, where

632   temperature can vary greatly at a short temporal scale and where the expected increase in the

633   frequency, intensity, and duration of extreme heat events may pose an additional challenge to the

634   persistence of less tolerant species. This highlights the importance of capturing the heterogeneity

635   of thermal conditions at a finer scale to identify the presence of microrefugia for thermally

636   sensitive species (Potter et al. 2013). However, temperature records that are more relevant to the

637   scale or habitat under investigation are often unavailable or not easily accessible to the scientific

638   community. Second, poorer dispersers are expected to have a lower probability of reaching new

639   suitable habitats and expanding their geographic range towards higher latitudes (Thomas et al.

640   2004). Species of the genus *Ophryotrocha* can actively disperse by drifting, though presumably

641   not for long distances given the presence of direct developing larvae. Scant dispersal abilities may

642   limit the potential poleward expansion projected for these annelid species, especially for

643   populations found in semi-enclosed basins such as the Mediterranean Sea. If tracking more

644   favourable thermal conditions is not an option, climate-driven local declines or extinction events

645   may be avoided through plastic or adaptive behavioural and/or physiological responses. Subtidal

646   organisms are known to possess physiological adaptations to cope with thermally stressful events,

647   either through acclimatisation or the evolution of higher thermal tolerance maxima and thermal

648   performance breadth (Tomanek 2010; da Silva et al. 2019). In our simulations, the inclusion of

649   species' physiological and reproductive thermal plasticity contributed to an expanded projected

650   thermal habitat suitability for all species but did not prevent the occurrence of HSI decreases in

651   some of the uncommon and rare species. This result suggests that the acclimation potential of a

652   species does not guarantee its persistence in a climate-change context, as previously reported by

653   other authors (e.g., Gunderson and Stillman 2015; Magozzi and Calosi 2015).

654   In conclusion, we provide general support for the possible use of the concepts of commonness and

655   rarity to predict the susceptibility to rapid environmental changes in temperate benthic

656   invertebrates, particularly in marine annelids, a ubiquitous and diverse group of metazoans that are

657   unrepresented in macroecological and macrophysiological studies. By combining experimental

658   observations and macroecological-physiological approaches, we found a greater thermal

659   sensitivity in uncommon-rare species compared to their common relatives, although information

660   on those species' geographic distribution was scant, patchy, or discontinuous. However, while the

661   experimental observations and simulations based on the common species' thermal performance

662   was in line with theoretical expectations, predictions on the fate of uncommon and rare temperate

663   species under ocean warming scenarios were less accurate and more susceptible to methodological

664   limitations. This highlights the need to develop an even more rigorous definition of the concept of

665   rarity and its intermediate levels for integration with scenarios of climate change that are more

666   relevant for the species under investigation if we want to more accurately predict the vulnerability

667   of 'elusive' taxa to climate change.

668 **Declarations**

675 **Conflict of Interest:** The authors declare that they have no conflict of interest.

676 **Ethical approval:** All applicable institutional and/or national guidelines for the care and use of

677 animals were followed [Canadian Council on Animal Care].

678 **Consent to participate:** Not applicable.

679 **Consent for publication:** Not applicable.

680 **Availability of data and material:** The datasets analysed during the current study were deposited

681 in Dryad with the doi: https://doi.org/10.5061/dryad.80gb5mksq.

682 **Code availability:** see Supplementary Information "MassambaNSiala_et_al_ESM4_Rscripts".

683 **Author contributions:** The experimental design has been conceived and planned by GMN.

684 Experimental measurements were carried out by GMN with the support of RS and DP. GMN

685 conducted statistical analyses with advice from RS and PC. Data modelling was conceived by

686 GMC, GR, WWC, PC and performed by GR. GMN wrote the first draft of this manuscript

687 supported by PC. All authors contributed to the final version of the manuscript.

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Table. 1. Results of the analysis of deviance for the effect of species *Status* (common, uncommon, rare), species identity (*Species(Status)*) and acclimation temperature (*T*: 18 and 24 °C), and their interactions on the upper (a-c) and lower (d-e) physiological thermal tolerance limits (CT_{max} and CT_{min}, respectively) of the species of the genus *Ophryotrocha*. Degrees of freedom (Df), deviance residuals (Dev. Res.), degrees of freedom residuals (Df Res.), deviance (Dev.), and *P*-value with Benjamini-Hochberg correction for false positives (*P*(BH)) are provided

CT_{max}

a) Loss of locomotor control

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			245	2154.10	
Body size	1	423.98	244	1730.12	8.25E-16
Status	2	733.80	242	996.32	8.25E-16
T	1	553.52	241	442.80	8.25E-16
Species(Status)	4	229.63	237	213.17	8.25E-16
Status*T	2	30.69	235	182.48	5.70E-11
Species(Status)*T	4	37.80	231	144.67	7.31E-12

b) Onset of spasms

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			245	1866.57	
Body size	1	763.69	244	1102.88	8.25E-16
Status	2	730.77	242	372.11	8.25E-16
T	1	80.46	241	291.65	8.25E-16
Species(Status)	4	166.39	237	125.26	8.25E-16
Status*T	2	4.49	235	120.76	0.01
Species(Status)*T	4	24.51	231	96.26	1.55E-11

c) Lethal temperature

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			245	*2258.59*	
Body size	1	927.17	244	1331.42	1.10E-15
Status	2	1013.09	242	318.33	1.10E-15
T	1	5.10	241	313.24	0.0009
Species(Status)	4	216.27	237	96.97	1.10E-15
Status*T	2	4.32	235	92.65	0.008
Species(Status)*T	4	5.93	231	86.71	0.008

CT_{min}

d) Onset of spasms

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			245	776.64	
Body size	1	37.04	244	739.60	5.50E-16
Status	2	7.55	242	732.05	0.001
T	1	362.48	241	369.57	5.50E-16
Species(Status)	4	194.45	237	175.12	5.50E-16
Status*T	2	5.15	235	169.97	0.01
Species(Status)*T	4	52.07	231	117.91	5.50E-16

e) Chill coma

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			245	728.72	
Body size	1	139.63	244	589.09	3.67E-16
Status	2	27.03	242	562.06	3.67E-16
T	1	87.33	241	474.73	3.67E-16
Species(Status)	4	301.06	237	173.68	3.67E-16
Status*T	2	25.60	235	148.07	3.67E-16
Species(Status)*T	4	68.19	231	79.89	3.67E-16

Table. 2. Results of the analysis of deviance for the effect of species identity (*Species*), acclimation temperature (*T*: 18, 24 and 30 °C), and their interaction on the upper (a-c) and lower (d-e) physiological thermal tolerance limits (CT_{max} and CT_{min}, respectively) of the species of the genus *Ophryotrocha* that survived the exposure to 30 °C (*O. labronica*, *O. japonica*, *O. adherens*). Degrees of freedom (Df), deviance residuals (Dev. Res.), degrees of freedom residuals (Df Res.), deviance (Dev.), and *P*-value with Benjamini-Hochberg correction for false positives (*P*(BH)) are provided

CT_{max}

a) Loss of locomotor control

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			164	1547.8	
Body size	1	108.61	163	1439.19	4.95E-16
Species	2	550.98	161	888.20	4.95E-16
T	2	680.52	159	207.69	4.95E-16
Species*T	4	108.62	155	99.07	4.95E-16

b) Onset of spasms

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			164	446.19	
Body size	1	41.85	163	404.34	2.2E-15
Species	2	244.45	161	159.88	2.2E-15
T	2	74.4	159	85.49	2.2E-15
Species*T	4	9.39	155	76.10	0.002

c) Lethal temperature

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			164	626.63	
Body size	1	95.52	163	531.10	1.98E-15
Species	2	462.47	161	68.63	1.98E-15
T	2	23.64	159	44.99	1.98E-15
Species*T	4	0.53	155	44.46	0.76

CT_{min}

d) Onset of spasms

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			164	971.49	
Body size	1	71.39	163	900.10	4.95E-16
Species	2	52.99	161	847.11	4.95E-16
T	2	717.89	159	129.22	4.95E-16
Species*T	4	56.28	155	72.94	4.95E-16

e) Chill coma

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			164	619.58	
Body size	1	239.21	163	380.38	4.95E-16
Species	2	116.78	161	263.60	4.95E-16
T	2	168.80	159	94.80	4.95E-16
Species*T	4	32.35	155	62.44	4.95E-16

Tab. 3. Results of the analysis of deviance for the effect of species identity (*Species*), acclimation temperature (*T*: 18, 24 and 30 °C) and their interaction on a) survival and b) total fecundity of five of the seven studied species of the genus *Ophryotrocha*. Degrees of freedom (Df), deviance residuals (Dev. Res.), degrees of freedom residuals (Df Res.), deviance (Dev.), and *P*-value with Benjamini-Hochberg correction for false positives (*P*(BH)) are provided

a) Survival

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			212	5541.00	
T	4	776.82	208	4764.20	1.1E-15
Species	2	2003.03	206	2761.20	1.1E-15
Species*T	8	2251.90	198	509.30	1.1E-15

b) Total fecundity

Source	Df	Dev. Res.	Df Res.	Dev.	*P*(BH)
Null			212	107387	
T	4	25142	208	82245	1.1E-15
Species	2	28465	206	53780	1.1E-15
Species*T	8	26027	198	26027	1.1E-15

Figure legend

Fig. 1 Difference in (a-c) upper and (d-e) lower physiological thermal tolerance limits (CT_{max} and CT_{min}, respectively) among common (c, green border), uncommon (u, orange border) and rare (r, dark-red border) species of the genus *Ophryotrocha* following 7 d of exposure to 18 and 24 °C (white and grey fill, respectively). The boundary of the box closest to zero indicates the 25th percentile, a horizontal line and a black diamond symbol inside the box mark the median and mean, respectively, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers. Capital letters indicate differences between species according to their common, uncommon, and rare status within acclimation temperature. An asterisk indicates differences between acclimation temperatures within status. Statistical significance: $P < 0.05$. Sample size: $14 \leq N \leq 20$

Fig. 2 Difference in (a-c) upper and (d-e) lower physiological thermal tolerance limits (CT_{max} and CT_{min}, respectively) between species of the genus *Ophryotrocha* following 7 d of exposure to 18 and 24 °C (white and grey fill, respectively). Common (c), uncommon (u), and rare (r) species are indicated with green, orange, and dark red borders, respectively. See Fig. 1 for the description of the box plots. Capital letters indicate differences among species within acclimation temperature. An asterisk indicates differences between acclimation temperatures within status. Statistical significance: $P < 0.05$. Sample size: $14 \leq N \leq 20$. lab = *O. labronica*; jap = *O japonica*; adh = *O. adherens*; puer = *O. puerilis*; hart = *O. hartmanni*; diad = *O. diadema*; rob = *O. robusta*

Fig. 3 Difference in a) survival and b) total fecundity between species of the genus *Ophryotrocha* measured during 90 d of exposure to 18, 24 and 30 °C (white, grey, and black fill, respectively). Common (c), uncommon (u), and rare (r) species are indicated with green, orange, and dark-red

borders, respectively. See Fig. 1 for the description of the box plots. Capital letters indicate differences among species within acclimation temperature. Lowercase letters indicate differences among acclimation temperatures within the same species. Statistical significance: $P < 0.05$. Sample size: $10 \leq N \leq 22$. lab = *O. labronica*; jap = *O japonica*; adh = *O. adherens*; diad = *O. diadema*; rob = *O. robusta*

Fig. 4 Relationship between temperature and the habitat suitability index (HSI) defining the fundamental thermal niche of the common (green lines), uncommon (orange lines), and rare (dark red lines) species of the genus *Ophryotrocha*. Curves were interpolated across different levels of physiological impairment (CT_{min} and CT_{max}) and reproductive *optima*. CC = chill coma; LT = lethal temperature; OS = onset of spasms (CT_{min}); LLC = loss of locomotor control; $T_{optimal}$ = optimal temperature for reproduction. Subscripts *min*, *mean* and *max* refer to the minimum, mean or maximum values among the means calculated at each acclimation temperature for the traits considered

Fig. 5 Maps of the difference in the thermal habitat suitability (HSI) between the mid- (2050-2059) and late- (2090-2099) 21st Century scenario, and the present day (1970-2000) scenario under the RCP8.5 scenario in the North Atlantic and Mediterranean regions, obtained for the common (c), uncommon (u), and rare (r) species of the genus *Ophryotrocha*. Black arrows indicate areas characterized by HSI decreases
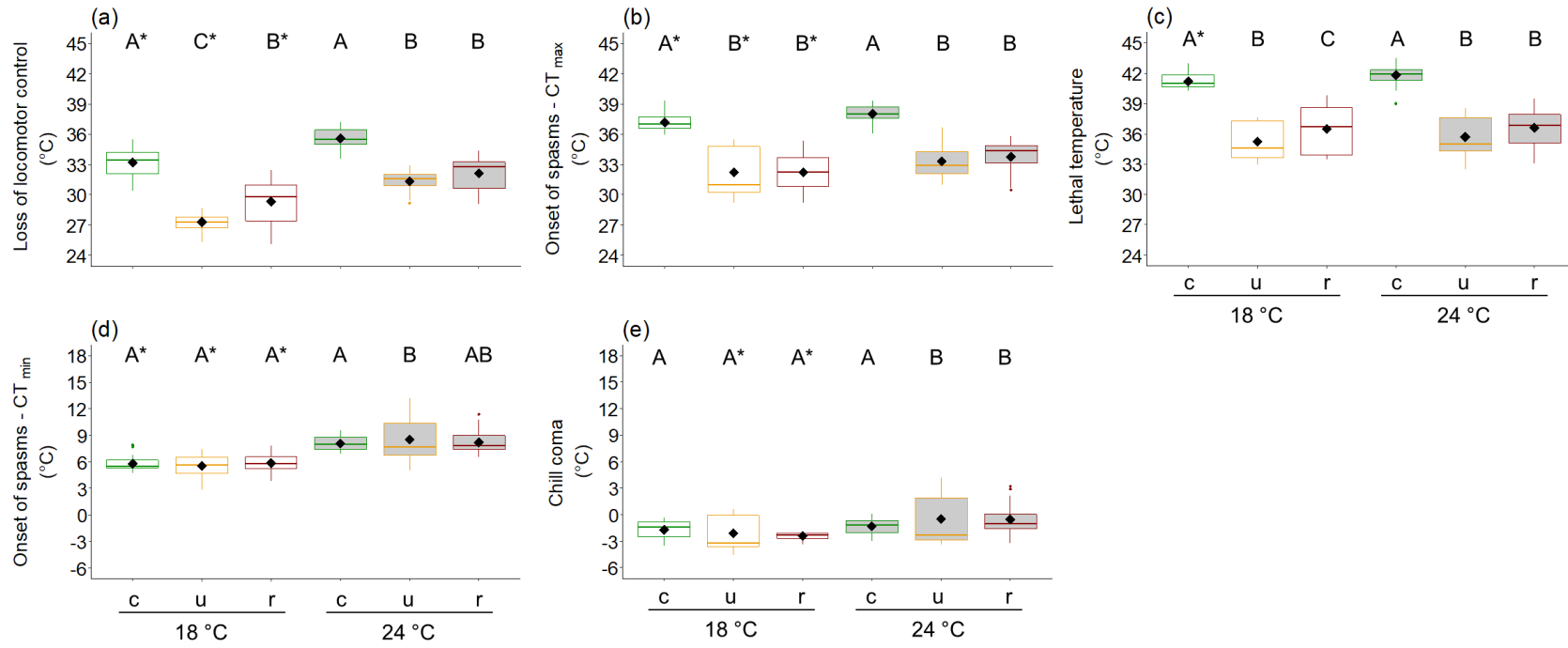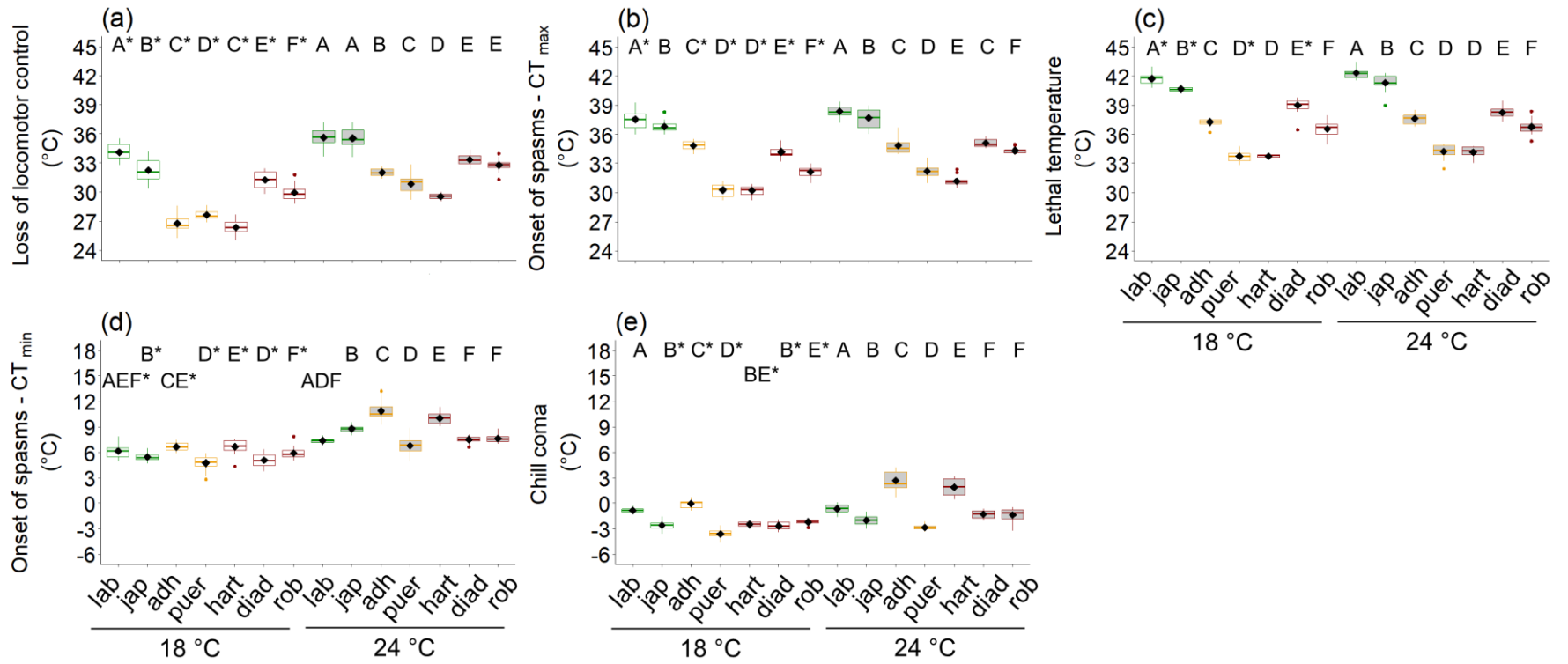
Figure 1.

Figure 2.
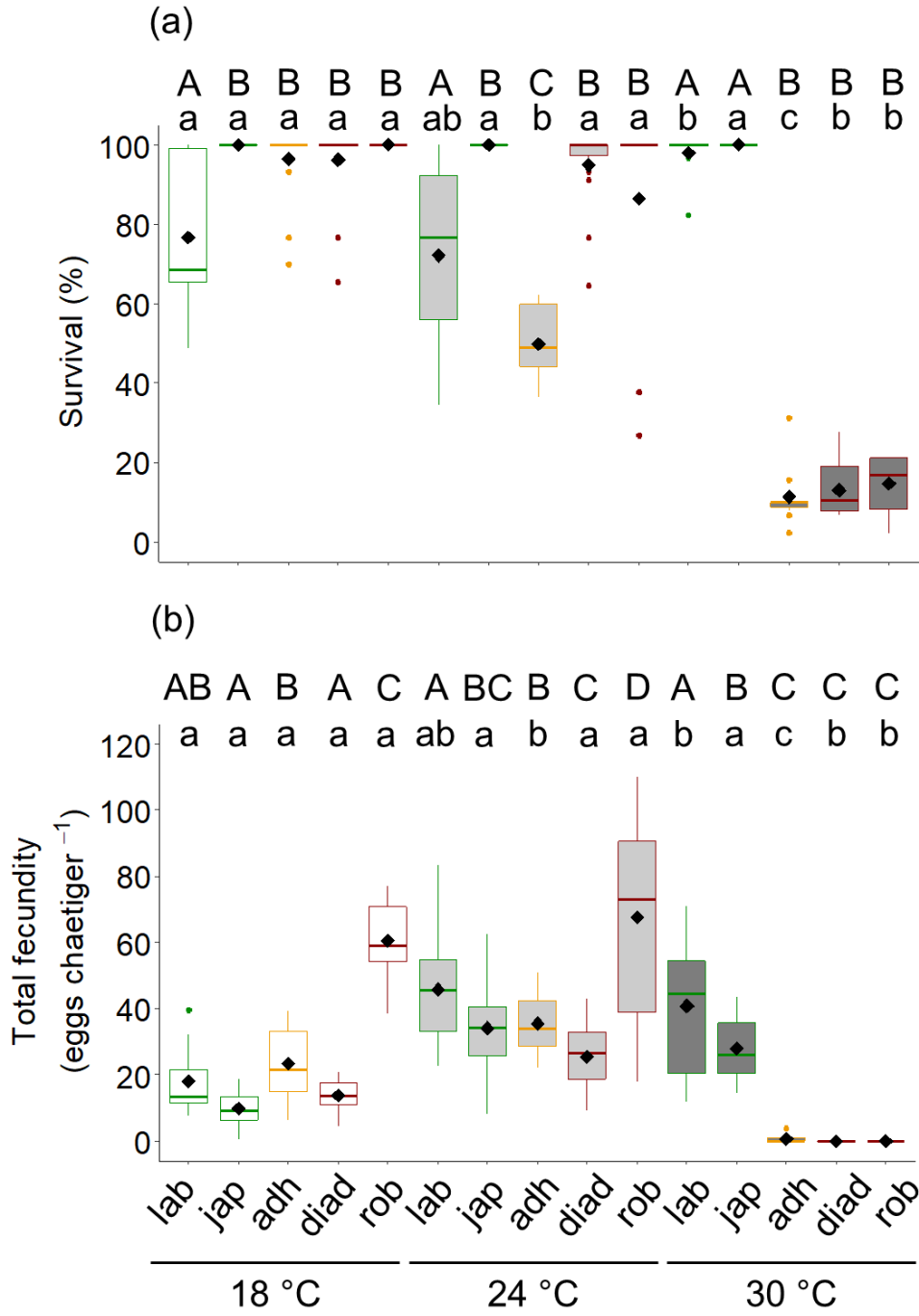
Figure 3.

Figure 4.

Figure 5.