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Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster, *Crassostrea gigas*.

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ABSTRACT

Invasive non-native species and global warming are two of the greatest components of global ecosystem change. The Pacific oyster, *Crassostrea gigas*, is the worlds most cultivated shellfish and was introduced throughout the Northwest European Shelf (NWES) under the premise it could not complete its life cycle. Recent warming trends have changed this and wild populations can be found as far north as Nordic Scandinavia. Under the RCP8.5 concentration pathway, we predict the majority NWES coastline will be within *C. gigas*'s thermal recruitment niche by 2100. Given the widespread occurrence of current naturalised *C. gigas* populations, its large larval dispersal potential and a lack of feasible management solutions, *C. gigas* will likely undergo a considerable range expansion this century. The time taken to reach maturity is predicted to decrease by up to 60 days, which may lead to precocious spawning events, facilitating expansion further. *C. gigas* can form extensive reefs completely transforming native systems. This may compromise native biodiversity, protected habitats and commercial species. However, naturalisation can also deliver a number of beneficial ecosystem goods and services to human society. Whether naturalisation is deemed positive or negative will depend on biogeographic context, the perceptions of stakeholders and the wider management priorities.

INTRODUCTION

Anthropogenic warming is causing the redistribution of species at a global scale (Burrows *et al.*, 2011; Chen *et al.*, 2011; Poloczanska *et al.*, 2013). On top of this, humans have directly or indirectly transported species outside their native ranges. The resulting reordering of community structure can have serious ramifications throughout the wider food web that can threaten the intimate link between healthy ecosystem function and human society (Pecl *et al.*, 2017). These trends show no sign of abating as temperature rises are predicted to accelerate over the coming decades and invasive non-native species (INNS) eradication attempts are almost impossible after the fact (Norton, 2009; Coumou and Rahmstorf, 2012; Perkins *et al.*, 2012). As climate change and INNS introductions represent two of the biggest components of global ecosystem change, predicting when and where ecosystem restructuring will occur is one of the most pressing challenges in conservation and ecosystem management (Walther *et al.*, 2009; Butchart *et al.*, 2010; Bellard *et al.*, 2013).

Correlative species distribution models (SDMs) are the most utilised tool for predicting contemporary and future species distributions. They work by establishing statistical relationships between present day occurrences and underlying environmental variables (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Guisan and Thuiller, 2005). However, they assume contemporary distributions are in equilibrium with the surrounding environment, and as such, it is unknown how much of a species' fundamental niche is represented by its current distribution (Pearson and Dawson, 2003). This means they may perform poorly when extrapolating to invaded and novel regions or future climates (Dormann, 2007; Fitzzpatrck and Hargrove, 2009; Kearney *et al.*, 2010). Another limitation is that environmental variables are often entered as static long-term means, rather than instantaneous measures (Bateman *et al.*, 2012). This offers little information on dynamic fluctuations of species distributions associated with intra and inter-annual variations. To try and overcome these issues there has been an increasing call for predictions to incorporate underlying physiological mechanisms, based on cause-and-effect relationships (Kearney

83   and Porter, 2009; Buckley *et al.*, 2010, 2011; Evans *et al.*, 2015) and high resolution climatic

84   data that incorporates intra and inter-annual variability (Zimmermann *et al.*, 2009; Reside *et*

85   *al.*, 2010; Bateman *et al.*, 2012). In this way, the ability to predict future species distributions

86   may be significantly increased.

87   Aquaculture is the world's fasted growing food industry and will be fundamental in future

88   global food production (FAO, 2016). Just like in terrestrial farming, marine species have

89   purposefully been introduced outside of their native ranges due to their ability to grow and

90   survive well in a range of environments. Relocation of bivalves outside of their native ranges

91   has a particularly rich history and some species now have global distributions (McKindsey *et*

92   *al.*, 2007). The Pacific oyster, *Crassostrea* (also known as *Magallana*) *gigas* (Thunberg,

93   1793), is the world's most globalised bivalve (Ruesink *et al.*, 2005; Smaal *et al.*, 2018) and

94   has been introduced from its native range in East Asia to over 50 countries. In the NE

95   Atlantic, production is focussed along coastlines of the Northwest European Shelf (NWES),

96   where it was introduced under the premise that it could grow well but conditions were too

97   cold for the successful completion of its life cycle (Troost, 2010). Recent warming trends

98   have changed this, with warmer ocean temperatures during summer now facilitating

99   spawning and settlement in many regions (Thomas *et al.*, 2016). This has resulted in

100   naturalisation occurring as far north as southern England and the Skagerrak coasts of

101   Denmark and Norway (e.g. Spencer *et al.*, 1994; Dielderich *et al.*, 2005; Thomas *et al.*,

102   2016). When naturalised, *C. gigas* can reach high densities and form extensive reefs (e.g.

103   McKnight and Chudleigh, 2015). This can completely transform native habitats and have

104   profound impacts on resident communities (reviewed by Troost, 2010 and Herbert *et al.*,

105   2016). The NWES is also a region of intense socioeconomic importance for fish catches and

106   seafood production and has a network of coastal ecological protections to protect native

107   habitat and species. Therefore, future ecosystem restructuring will have profound

108   implications for commercial enterprise and ecosystem managers.

109 Here, we take a mechanistic approach to predict the expansion of *C. gigas'* reproductive

110 niche and shifting phenology across the NWES. Specifically, we use known physiological

111 thresholds for spawning and settlement, coupled with high-resolution inter-annual ocean

112 temperature data, to hind cast successful recruitment years (2000 – 2019) and then project

113 how this could change in 20-year time slices up to 2100. We also track the shifting pace in

114 potential spawning date associated with such ocean warming. In doing so, we aim to equip

115 ecosystem managers with the necessary information to make informed choices regarding

116 management strategies of *C. gigas* farms over the coming decades.

117 **METHODS**

118 **Predicting *M. gigas'* thermal recruitment niche**

119 Ocean temperature is the most important driver of bivalve fitness and dictates when and

120 where recruitment may occur (Giese, 1959; Philippart *et al.*, 2003; Zippay and Helmuth,

121 2012). While other drivers may interact with temperature to affect recruitment locally (e.g.

122 food availability Gourault *et al.*, 2019), temperature is the predominant driver at a regional

123 scale. Indeed, hindcasting approaches have effectively linked ocean warming with recent *C.*

124 *gigas* recruitment in previously unsuitable areas on the NWES (e.g. Thomas *et al.*, 2016).

125 Therefore, using known temperature-recruitment relationships for *C. gigas* is an effective

126 method to gain insight into future climate mediated range expansions at a regional scale.

127 In order for ectotherm development to progress from one stage to another, certain

128 cumulative heat exposure is required. Past an initiation threshold, ectotherm growth and

129 development increases linearly with temperature. Therefore, the time period needed to

130 achieve a given development stage will vary depending on the temperatures experienced by

131 an individual, and as such, development can be estimated in a cumulative stepwise manner

132 based on daily temperatures the organism experiences. As certain development stages,

133 such as spawning and larval development, have particular heat requirements, development

134 can be estimated based on accumulated degree-days over a given period. Total degree-

135 days are given by:

$$136 \qquad Total\ DD = \int_{day\,1}^{day\,365} (T - T_0)\ \ dt\ \ for\ T > T_0$$

137   Where *DD* is the number of degree-days, *T* is the ambient temperature in degrees Celcius

138   that the animal is exposed to, T_0 is a threshold temperature below which no

139   development/growth occurs.

140   For *C.* gigas, Mann, (1979) determined a threshold temperature (T_0) of 10.55°C below which

141   gametogenesis will not occur and a minimum accumulation of DD = 600°C above this level

142   to induce spawning. Whilst lower thermal requirments for spawning have been reported

143   (equivalent to 355 – 397 DD > 10.55 °C) these have been determined from individuals

144   obtained in spring when they may already be partially conditioned (e.g. Helm and Bourne,

145   2004; Rico-Villa *et al*., 1999). Mann, (1979) used individuals obtained in November, and as

146   such, they had not undergone any previous thermal conditioning before degree-day

147   estimates were derived. Therefore, we use Mann (1979)'s 600 DD requirments > 10.55 °C

148   as our threshold for spawning to occur. However, mature *C. gigas* gonads have also been

149   produced when individuals were conditioned for extensive periods at 8 °C (Fabioux *et al*.,

150   2005). This means our T_0 threshold may be too high, and as such, our estimations of *C.*

151   *gigas'* TRN are likey conservative. It should also be noted that many *C. gigas* populations

152   are intertidal, and as such, degree-day accumulation for such individuals may also be

153   affected by aerial temperatures not accounted for here.

154   Recruitment is dependent on larvae developing fully and settling, which has further heat

155   requirements. Based on four previous studies of larval development, Syvret et al. (2008)

156   estimated an additional 225°C degree-days are required for settlement to occur. Here, it is

157   assumed the larval phase shares the same 10.55 °C T_0 threshold required as

158   gametogenesis. How appropriate 10.55 °C is as a baseline for larval development is

159   unknown, as the majority of research has been conducted in hatcheries at high

160   temperatures. However, whilst settlement decreases in laboratrory settings at temperatures

161   < 15 °C (Gillespie *et al*., 2012), larvae have been observed in the field at temperatures as

162   low as 13 °C (Kulikova *et al.*, 2015). As our understading of the viability of larvae at lower

163   temperatrues in the field increases, the larval T_0 may need to be adapted slightly.

164   Here, we define *C. gigas*'s Thermal Recruitment Niche (TRN) to be 825°C degree-days

165   above 10.55°C (600°C for spawning and 225°C for larval development). To track *C. gigas's*

166   shifting phenology (i.e. the date at which spawning may occur) we use the spawning

167   threshold of 600°C degree-days above 10.55°C. To account for potential uncertainty in

168   reported degree-day estimates, we included a 10% uncertainty envelope in our analysis

169   (Figures S2 and S3).

170   **Climate data**

171   *Historic baseline*

172   Ocean bottom temperature data spanning the period 01/01/2000 to 31/12/2018 were derived

173   from the European North West Shelf Ocean Reanalysis system (available from

174   http://marine.copernicus.eu/services-portfolio/access-to-

175   products/?option=com_csw&view=details&product_id=NORTHWESTSHELF_REANALYSIS

176   _PHY_004_009; for a detailed description see

177   http://resources.marine.copernicus.eu/documents/PUM/CMEMS-NWES-PUM-004-009.pdf).

178   The regional ocean model is the FOAM AMM7 (Forecasting Ocean Assimilation Model, 7km

179   resolution Atlantic Margin Model) setup of NEMO (Nucleus for European Modelling of the

180   Ocean) version 3.6, together with the 3DVar NEMOVAR system (version 3) which

181   assimilates observations of sea surface temperatures together with vertical profiles of

182   temperature and salinity. Lateral open boundary forcing was derived from the GloSea5

183   global ocean reanalysis and at the Baltic margins from the CMEMS Baltic reanalysis.

184   Atmospheric forcing was derived from the ERA-Interim atmospheric reanalysis.

185   *Future temperature*

186   The future projection of ocean temperatures used a dynamical downscaling approach, i.e., a

187   high-resolution (7 km horizontal resolution) regional ocean model (ROM) was forced with

188   output from a low-resolution Global Climate Model (GCM) (~85 km horizontal resolution)

189   (see next paragraph and Hermans et al., 2020 for details). This approach has several

190   advantages: The GCM fails to capture small-scale topographical and climatological features

191   due to its low resolution and fixed depth levels which, are resolved by the ROM.

192   Furthermore, oceanographic processes important in shallow shelf sea areas, such as tidal

193   mixing or eddie dynamics, are resolved by the ROM.

194   The ROM used here was the NWES configuration of the ocean model NEMOv3.6, AMM7

195   setup in configuration CO6 (see O'Dea *et al.*, 2017 and Hermans *et al.*, 2020 for details) and

196   has a horizontal resolution of 7 km. At the boundaries the ROM was forced with the GCM

197   MOHC-HadGEM2-ES (Collins *et al.*, 2011) using the RCP 8.5 concentrations pathway and

198   the model was run from 1972 to 2099. RCP 8.5 was selected to represent a worst-case

199   projection. Ocean bottom temperature was used to calculate the body temperature

200   experienced by oysters, as this is arguably more realistic than using sea surface

201   temperatures. Data were limited to 40 m to represent a maximum depth range for *M. gigas*

202   (FAO, 2007). Ocean bottom temperatures were extracted for the time period 2000–2099,

203   with 2000–2019 being used as the baseline period. The temperature data were bias

204   corrected against the NWES Ocean Reanalysis data (see section Historic Baseline for

205   details) using a reference period of 2000–2018. For the bias correction, a climatology of daily

206   temperatures over a year was calculated at each model grid point as the 7-day running

207   mean of 2000–2018 daily temperatures for both the NWES Ocean Reanalysis data and the

208   future RCP8.5 Northwest European Shelf simulation. The offset between the two

209   climatologies was subtracted at each grid point over the time span of the future simulation

210   for each year.

211   For our calculations of *M. gigas'* spawning threshold and TRN, we used daily climate data

212   (daily mean temperature) rather than seasonal means, maxima and/or minima. This

213   approach allowed us to capture spatial variability across the NWES together with intra- and

214   inter annual variability in the future projections and enabled cumulative degree-days to be

215   calculated on a daily basis. This means years where spawning and settlement can occur

216   were determined, as well as the precise date at which thresholds were exceeded. Instead of

217   only giving snapshot future projections at certain dates (e.g. 2050 or 2100), this approach

218   allows the progression, pace and intensity of potential future invasive characteristics to be

219   quantified.

220   **Individual shellfish sites**

221   To place our future projections of potential range expansion in an applied context and track

222   *C. gigas'* shifting reproductive phenology, nine representative shellfish sites were selected

223   (Figure 1; Table S1) where *C. gigas* is currently farmed or where wild populations are

224   established. These spanned eight countries throughout the NWES and covered a range of

225   climatic characteristics. For each site, we tracked the annual increase in total accumulation

226   degree-days, allowing us to determine the dates that thresholds were exceeded and the

227   expanding period over which degree-days could accumulate.

228   **RESULTS**

229   *Projected warming of ocean bottom waters*

230   The regional climate model projection, based on an RCP8.5 concentrations pathway, shows

231   increases in bottom seawater temperatures but with spatial variability across the NWES

232   (Figure 2). Ocean bottom temperatures are projected to increase most in the shallow areas

233   in the southern North Sea along the coastlines of northern France (excluding Brittany), The

234   Netherlands, northwest Germany, the west coast of Jutland (Denmark) and southeast

235   England. For the 2040–2059 timeslice, mean ocean bottom temperatures are projected to

236   increase by up to 1.3°C and by the end of the century (2080-2099) warming reaches up to

237   3.4°C in these regions. Bottom temperature changes are less pronounced along the

238   coastlines of southwest England, Wales and Ireland, where maximum changes reach 1.1°C

239   in the 2040–2059 timeslice and 2.8°C for the 2080–2099 timeslice. For the coasts of

240   Scotland and Northern Ireland, these values are are estimated to be lower at 0.7°C and

241   2.0°C, respectively.

242   The same patterns are reflected in the temperature changes at the representative shellfish

243   sites (Figure S1). Sites located along continental Europe and southeast England

244   (Wilhelmshaven, Agger Tange, Oostershelde, Whitstable and Cancale) all show temperature

245   increases exceeding 3.1°C by the end of the century. Lower temperature increases are seen

246   for Dungarvan, Bergen and Jura. For Jura, the temperature changes are nearly 1°C lower at

247   the end of the century than for the sites with the strongest warming. By ~2060, all sites have

248   exceeded at least 1°C of warming and 2.5°C by 2100, with respect to the 2000–2019

249   baseline period.

250   *Expansion of area within M. gigas's thermal recruitment niche*

251   Over the baseline period (2000–2019), the frontier of *C. gigas's* TRN was the Solway Firth in

252   Scotland, the Humber estuary in England, Ireland and Skagerrak coasts of Denmark.

253   Settlement thresholds ($DD > 825°C$) at the limits of *C. gigas's* TRN were exceeded

254   infrequently (< 3 out of 10 years), whereas coastlines of continental Europe (German Bight,

255   Southern Bight and English Channel) and Southern England were exceeded more often (> 7

256   out of 10 years) (Figure 3, Figure S2 and S3). Generally, *C. gigas*'s TRN was restricted to

257   coastal areas but offshore areas in the southern North Sea around the Southern and

258   German Bight were also suitable.

259   Under the RCP8.5 concentrations pathway, our simulation predicts the progressive

260   northwards expansion of *C. gigas*'s TRN to the end of the century. Limited expansion is

261   expected between 2020-2039 but during the 2040-2059 time slice *C. gigas*'s TRN will

262   encompass the majority of the Scottish Western Isles. This period also sees thresholds

263   move from infrequently exceeded (< 3 out of 10 years) to exceeded in the majority of years

264   (> 7 out of 10) around Ireland. *C. gigas*'s TRN encompasses the majority of Norway's North

265   Sea coast between 2060-2079 and the east coast of Scotland between 2080-2099. The

266   offshore island archipelagos of Shetland and Faroe remain unsuitable at the end of the

267   century.

268   For our representative sites, those situated in continental Europe (Cancale, France;

269   Oosterschelde, Netherlands and Wilhelmshaven, Germany) and southern England

270   (Whitstable) exceeded settlement thresholds every year over the baseline period (Figure 4).

271   For Agger Tange (Denmark) and Dungarvan (Ireland), settlement thresholds were only

272   exceeded infrequently (< 3 out of 10 years). For Grimstad (Norway), Bergen (Norway) and

273   Jura (UK) settlement thresholds were never exceeded during the baseline period.

274   The projections for Agger Tange show that the settlement threshold will be exceeded every

275   year (10 out of 10 years) by the middle of the century while this occurs in Dungarvan around

276   10 years later. The settlement thresholds will first be exceeded in Grimstad (Norway) from

277   2020, rising rapidly until they are exceeded in all years by 2060-2070. Jura (UK) and Bergen

278   (NOR) shared similar projections with thresholds not exceeded until the 2050's and rapidly

279   rising until thresholds are exceeded every year by 2099.

280   *Shifting phenology*

281   The period of the year during which populations can accrue degree-days increased

282   progressively towards 2100 (Figure 5). By 2099, the increase in days that exceed T_0 (>

283   10.55 °C) ranged from 54 (Wilmershaven, Ger) to 146 (Dungarvan, ROI). For Cancale

284   (France), Dungarvan (ROI) and Whitstable (UK), populations could accrue degree-days for

285   almost 100% of the year by 2100 (Figure 5; Table S2). Spawning thresholds were exceeded

286   in all years over the baseline period for all sites apart from Bergen, Grimstad and Jura where

287   they were exceeded 2, 9 and 1 times respectively. The mean date spawning could occur

288   varied considerably between sites (Table S3). Generally, spawning thresholds were

289   exceeded later at northerly sites and was reflective of the cooler conditions resulting in a

290   slower pace of degree-day accumulation. That said, Jura saw the latest date that spawning

291   thresholds were exceeded (mid November). The mean date the spawning threshold was

292   exceeded occurred progressively earlier up to 2099. By the end of the century, spawning

293   thresholds are predicted to occur between 27 (Cancale, F) and 60 (Dungarvan, ROI) days

294   earlier.

295   **DISCUSSION**

296   In this study, we have taken a mechanistic approach to predict the expansion of the area

297   within *C. gigas*' thermal recruitment niche (TRN) at its current naturalisation frontier on the

298   Northwest European Shelf. It is challenging to validate our simulations with historic spawning

299   and recruitment events as large-scale observation progammes are lacking. Moreover, just

300   because an area exceeds *C. gigas*'s TRN does not mean recruitment occurred in that year.

301   Indeed, in SE England, recruitment seems less frequent than our simulations would suggest

302   (Herbert *et al.*, 2012). Ultimately, such a fine scale understanding of annual recruitment will

303   require a deeper understanding of how ocean temperature interacts with other drivers to

304   affect recruitment locally. Nonetheless, in broad terms, our baseline predictions of area

305   within *C. gigas'* TRN align well with present day distribution records. Areas regularly

306   exceeding settlement thresholds correspond to locations where self-recruiting reefs are

307   found, along the coasts of continental Europe and southern England (Herbert *et al.*, 2016).

308   Settlement thresholds were exceeded less frequently further north and correspond to low

309   abundance wild populations reported around Ireland (Kochmann *et al.*, 2013) and the

310   Solway Firth in Scotland (Smith *et al.*, 2015). Whilst our simulations indicate settlement

311   thresholds were not exceeded along the Norwegian extent of our study, wild populations can

312   be found along Norway's Skagerrak and North Sea coasts (Wrange *et al.*, 2010; Anglès

313   d'Auriac *et al.*, 2016; Laugen *et al.*, 2015). For the Skagerrak, it may be that the

314   temperatures in the shallow inlets and bays are higher than our model suggests, allowing

315   settlement thresholds to be exceeded, or oyster larvae immigrated from warm source

316   populations such as Oslofjord (Norway), Sweden and continental Europe (Anglès d'Auriac *et*

317   *al.*, 2016). For Norway's North Sea populations, distances from these warmer donor sites

318   are likely too great and temperatures still too low for reproduction. Here, it has been

319 suggested that strong selection pressure and genetic isolation on a relic aquaculture

320 population near Bergen has facilitated natural selection lowering *C. gigas*' TRN here (Anglès

321 d'Auriac *et al.*, 2016). However, *in situ* monitoring of the reproductive biology of Norway's

322 Skagerrak and North Sea populations is required to determine the source of these

323 populations.

324 Under a future climate projected by a RCP8.5 concentrations pathway, we predict a

325 progressive poleward advancement of the area encompassing *C. gigas*'s TRN. By 2100,

326 Ireland, Scotland and Norway will see settlement thresholds move from never or rarely

327 exceeded, to exceeded in the majority of years. This will increase propagule pressure,

328 leading to higher abundances, and will ultimately result in poleward advancement of *C.*

329 *gigas*'s naturalised distribution. Given our predicted expansion of *C. gigas'* TRN, the

330 widespread nature of wild and farmed populations throughout the NWES and *C. gigas*' large

331 dispersal capacity (Shanks, 2009), it is likely the majority of coastline on the NWES will be

332 available for colonisation by 2100. Overall, this represents a habitat expansion of ~500 km^2

333 (area within *C. gigas* TRN) and a northward range expansion of 6° of latitude. However, it

334 should be noted that the RCP8.5 concentrations pathway represents a "worst-case scenario"

335 and if greenhouse gas emissions were to drop significantly in the coming decades then

336 ocean temperatures would warm at a slower rate (IPCC, 2013). This means that the

337 subsequent expansion of *C. gigas*' range could also be slower and less intense than shown

338 here. That said, current patterns of energy consumption show little evidence for such a

339 decline and this concentrations pathway is becoming increasingly more likely. Moreover,

340 given the inherent uncertainty in any of the IPCC scenarios the worst-case scenario is a

341 fundamental consideration for policy makers.

342 Expansion of *C. gigas* can have significant negative impacts on a wide range of habitats (e.g

343 mussel-beds, Kochmann *et al.*, 2008; salt marshes, Escapa *et al.*, 2004; rocky shores,

344 Krassoi *et al.*, 2008; seagrass beds, Wagner *et al.*, 2012; polychaete reefs, Dubois *et al.*,

345 2007; mud flats, Trimble *et al.*, 2009), and as such, poses a serious concern for managers

346   responsible for the resilience of these ecosystems. As an ecosystem engineer, *C. gigas* can

347   completely transform coastal systems and reduce habitat heterogeneity across different

348   substrates (Herbert *et al.*, 2016). This is a particular concern where transformed habitats are

349   protected for their ecological status, or are of commercial interest. For example, many

350   mudflats and rocky reefs are protected under the EU habitats directive

351   (Directive 92/43/EEC), while oysters can completely transform commercial mussel beds

352   (Markert et al., 2010). The options available to managers to prevent *C. gigas* naturalisation

353   are limited to farming sterile oysters or eradication of wild populations (Nell, 2002; McKnight

354   and Chudleigh, 2015), both of which are likely to be undermined by the widespread nature of

355   large source populations and *C. gigas*' extensive dispersal capacity (e.g. Lallias *et al.*, 2015;

356   Robins *et al.*, 2017; Angles d'Auriac *et al.*, 2017). As these interventions are unlikely to

357   prevent expansions, there may need to be a change in attitudes of managing *C. gigas,* away

358   from that of traditional INNS (Hobbs *et al.*, 2006; Truitt *et al.*, 2015).

359   In some ways, *C. gigas* naturalisation may benefit or safeguard coastal ecosystems of the

360   NWES. Historically, NWES coastlines included dense populations of native European

361   oysters, *Ostrea edulis,* but overfishing and disease decimated populations resulting in a 95%

362   decline in abundance since the 1950s (Thurstan *et al.,* 2013; Smyth *et al.*, 2020). This

363   decline has resulted in altered benthic assemblages across Europe and has undoubtedly

364   shifted ecosystem function. Where they coexist, *O. edulis* generally occupies the subtidal

365   and *C. gigas* the interidal but they harbour similar epifaunal assemblages (Zwerschke *et al.*,

366   2016) and can provide similar regulating services (Zwerschke *et al.*, 2020). Therefore, whilst

367   there is currently a considerable focus on restoration efforts for *O. edulis* across Europe

368   (Pogoda *et al.,* 2019), *C. gigas* naturalisation may help restore coastal communities and

369   ecosystem function in a similar manner to the previous state. Moreover, as ocean warming

370   threatens functionally similar native cool-water bivalves (Jones *et al.*, 2010; Fly *et al.*, 2015)

371   (e.g. *O. edulis* and the blue mussel, *M. edulis*), naturalisation may also safeguard the

372   delivery of provisioning and regulating ecosystem goods and services in the future (Troost,

373 2010; Christianen *et al.*, 2018). In some countries (e.g. The Netherlands), acceptance of *C.*

374 *gigas* as a "naturalised" species occurred decades ago (Drinkwaard, 1999), and there is

375 increasing discussion on managing *C. gigas* expansion as a natural resource in countries

376 where expansions have occurred more recently (e.g. UK – Herbert *et al.*, 2012; Scandinavia

377 – Laugen *et al.*, 2015, Mortensen *et al.*, 2019). Ultimately, whether the impact of *C. gigas*

378 expansion is deemed positive or negative will depend on biogeographical context (e.g.

379 proximity to vulnerable sites) and the priorities of ecosystem managers.

380 On top of an expansion of *C. gigas*' TRN, we also predict warming will impact *C. gigas*'

381 phenology. We show that the time needed to exceed the required cumulative heat exposure

382 for spawning (600°C degree-days) across the NWES may decrease by 27 – 60 days by

383 2099. This is a similar rate (~5 days per decade) as the 8 day shift in spawning date

384 observed for *C. gigas,* at Bourgneuf Bay, France, between 1988 and 2003 (Thomas *et al.*,

385 2016). Such earlier spawning may widen *C. gigas*'s recruitment window, increase propagule

386 pressure and facilitate its expansion further. However, it should be noted that in addition to

387 cumulative heat exposure for gonad development, spawning is also dependent on

388 exceedance of a threshold water temperature (between 16-23°C depending on site location -

389 Pouveau *et al.*, 2006; Castaños *et al.*, 2009; Gillespie *et al.*, 2012; Norgard *et al.*, 2014) and

390 often another enviromental trigger (e.g. tidal temperature shcoks – Mills, 2016, high

391 phytoplankton abundance – Ruiz *et al.*, 1992, hydrodynamic flow – Bernard *et al.*, 2016).

392 Moreover, once spawned the duration of the larval phase can be affected by quality and

393 quantity of microalgal food (Rico-Villa *et al.*, 2006). Therefore, whilst cumulative thermal

394 exposure for spawning and settlement may be reached, reaslised recruitment dates will also

395 be dependant on specific water temperatures, other environmental triggers and larval diet.

396 *C. gigas* has a global distribution with climate-mediated naturalisation occurring from

397 aquaculture introductions in North America (Andrews, 1979), South America (Escapa *et al.*,

398 2004), South Africa (Robinson *et al.*, 2005) and Australia (Ayres, 1991). Therefore, our

399 approach will be of interest to ecosystem managers at *C. gigas*' naturalisation frontiers

400   across the globe and given the simplicity of our approach can be easily implemented.

401   However, caution should be taken when trying to predict where exactly *C. gigas* reefs may

402   form. Here, a deeper understanding of how ocean temperature interacts with other drivers is

403   required. At a regional scale, recent approaches, incorporating dynamic energy budget

404   theory, show food availability is also fundemental in *C. gigas'* spawning (Thomas *et al.*,

405   2016). Therefore, a more accurate understanding of *C. gigas'* range expansion will be

406   gained as high-resolution phytoplankton forecasts become available. On a local scale,

407   availability of suitable substrate, local food-web dynamics and connectivity to source

408   populations will be fundamental in predicting where specific reefs may form. It is also

409   important to consider factors that may slow a realised range expasnion despite an expansion

410   of *C. gigas'* TRN. In particular, high summer temperatures, coupled with post-spawning

411   stress and pathogens can make *C. gigas* vulnerable to "summer mortality syndrome", where

412   severe (> 90 %) and rapid (~weeks) population crashes can occur (e.g. Mortensen *et al.*,

413   2016). *C. gigas* larvae and small recruits are also vulnerable to a range of predators (birds,

414   crabs, gastropods and sea stars) that that may also control its recruitment (e.g. Faasse and

415   Lighthart, 2009). Other aspects of climate change (e.g. ocean acification) or local stressors

416   (e.g. nutrient loading) may also interact with ocean warming in unforeseen ways. Thus, *C.*

417   *gigas*'s realised expansion will be more complex than the simplification of its thermal window

418   presented here. Nonetheless, our approach is useful tool to anticipate ecological change at a

419   regional scale and serves as an effective early warning for managers. This should be used

420   to facilitate discussion regarding the best way forward to adapt to this expansion.

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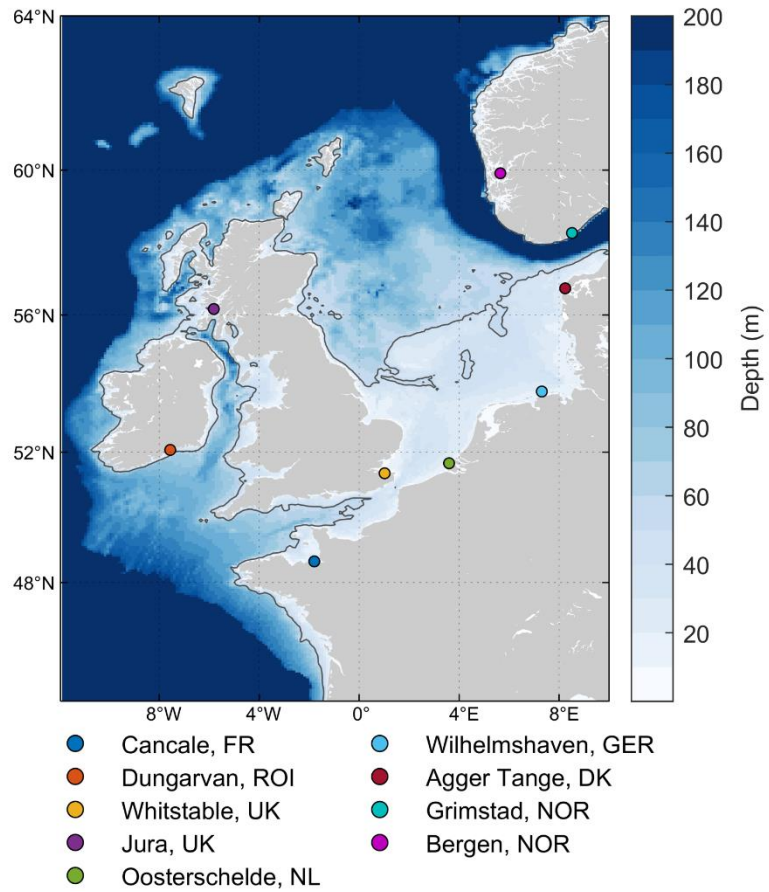689 bulletin, 111: 305-310.

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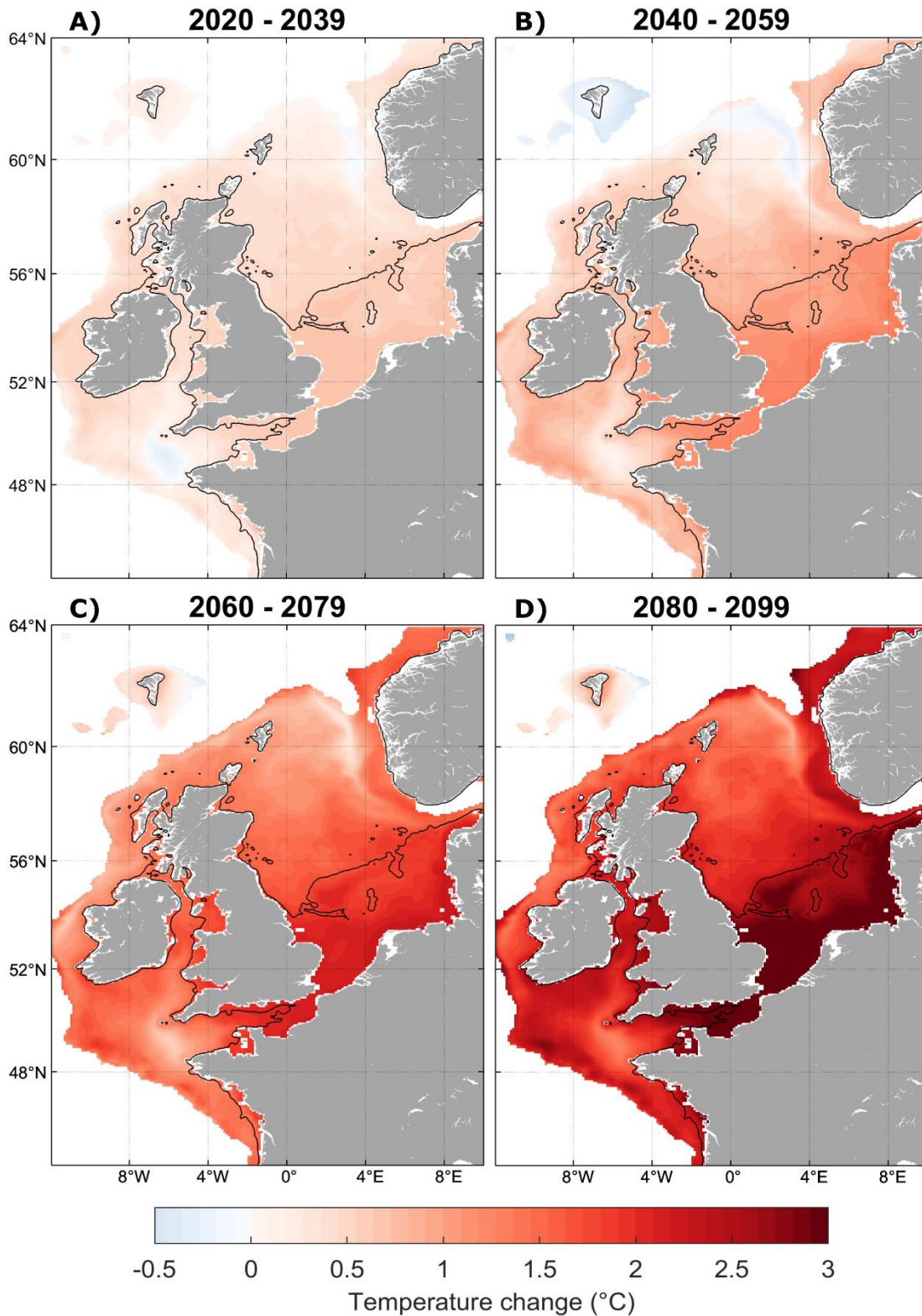
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Figure 1. Bathymetry and location of representative *M. gigas* sites within the Northwest European shelf. The
black line represents the 40 m depth contour, *M. gigas*' maximum viable depth.

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Figure 2. Projected change in ocean bottom water temperatures compared with the baseline period 2000-2019, under an RCP8.5 concentrations pathway, across the Northwest European Shelf in 20 year mean time slices up to 2100. Temperature changes up to a depth of 350 m are shown. The black line denotes the 40 m depth contour which is the maximum viable depth for *C. gigas*.
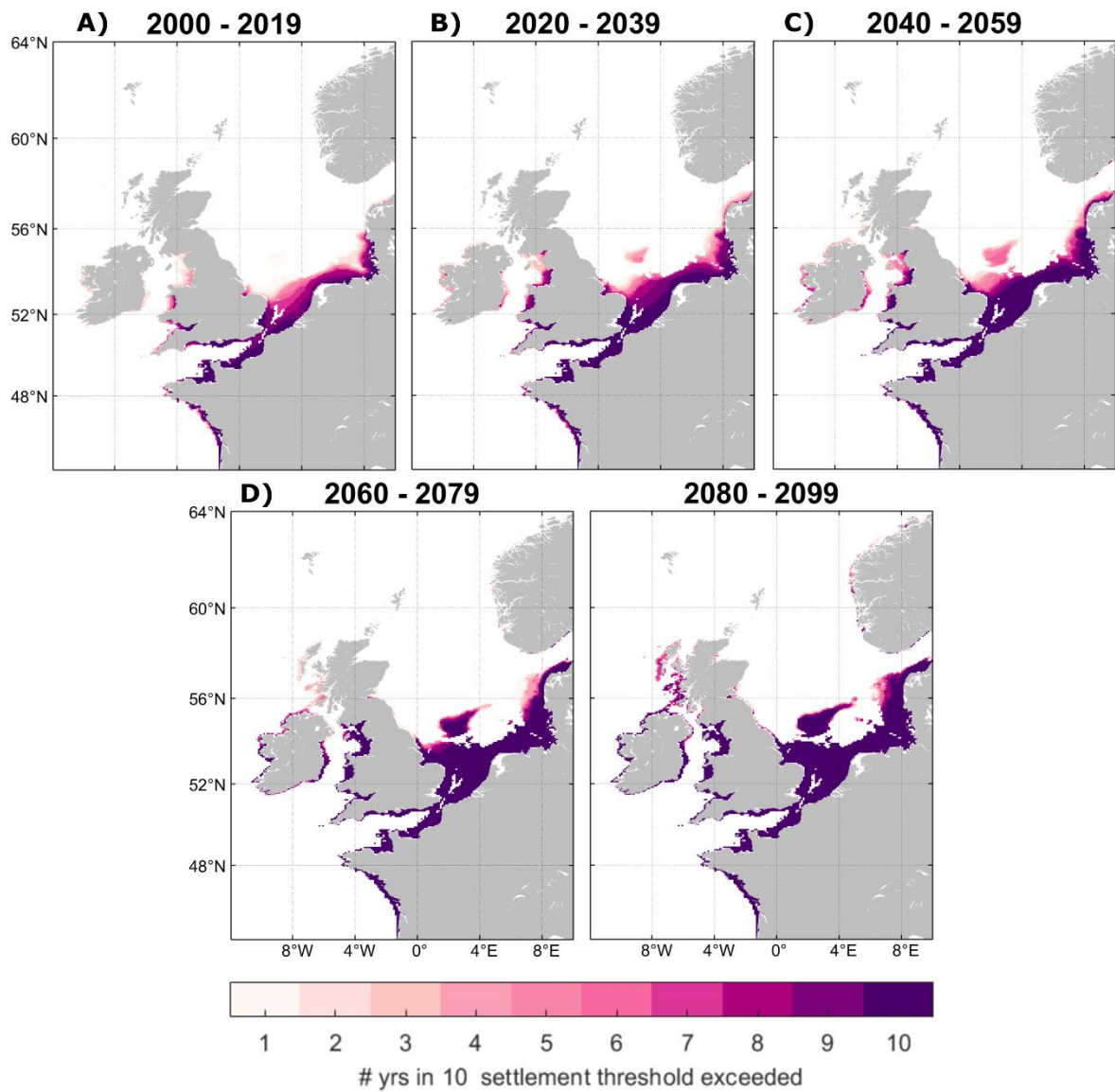
Figure 3. Proportion of years *M. gigas* settlement thresholds (825 degree days above 10.55°C) are exceed for present day baseline period (A: 2000–2019) and future (B-E: 2020–2099) time periods, across the northwest European Shelf. Data limited to 40 m (maximum viable depth of *C. gigas*).
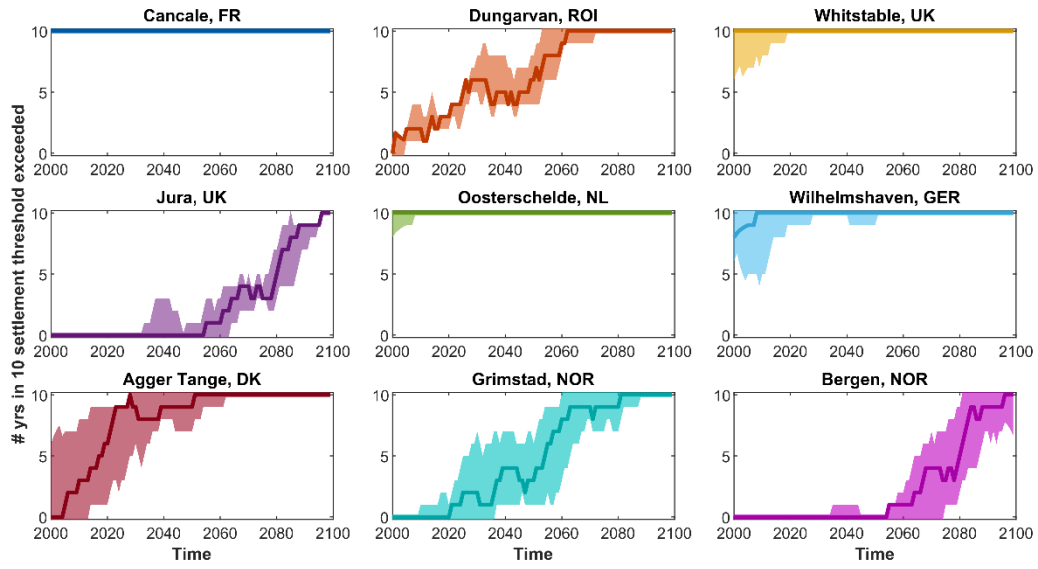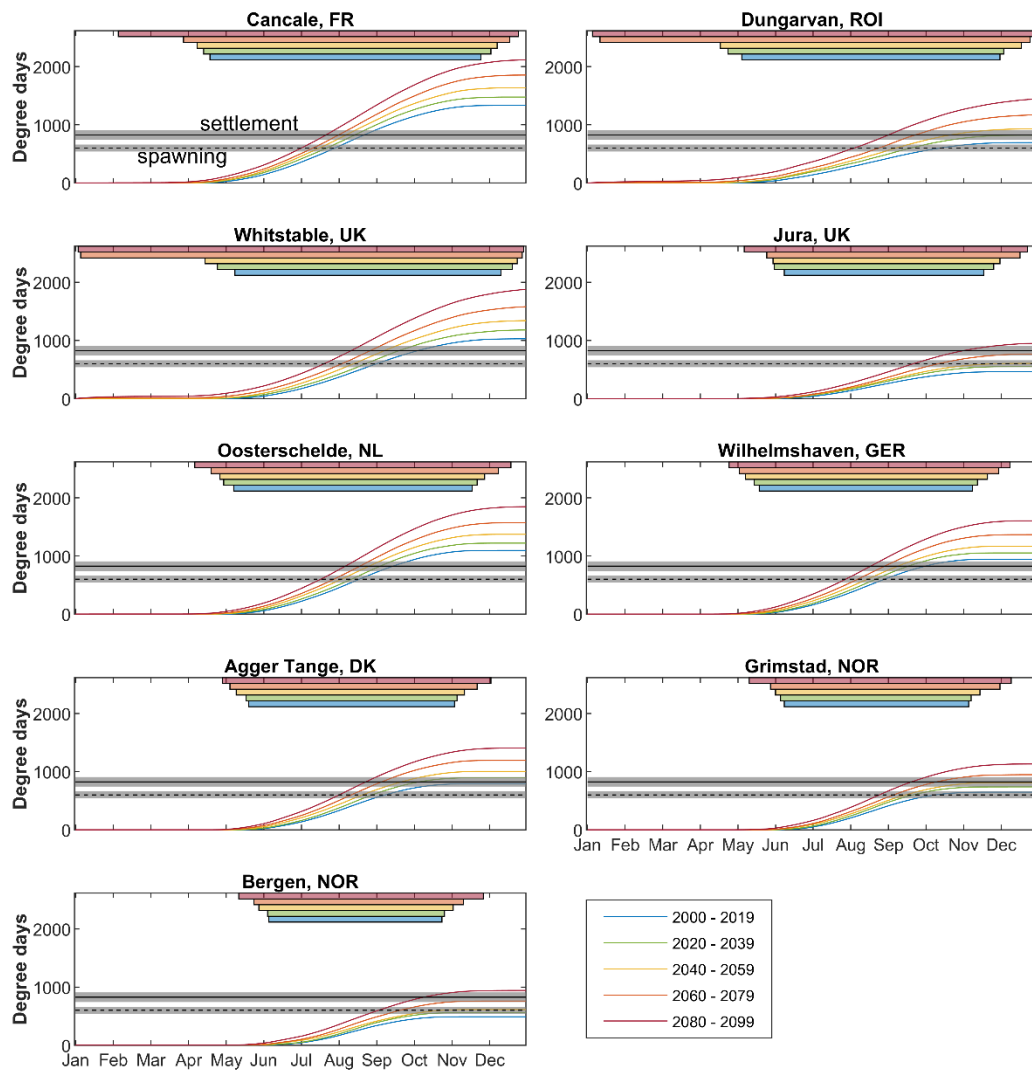
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Figure 4. Number of years out of 10 years settlement thresholds (825°C degree days above 10.55°C) areexceeded at nine European *C. gigas* population sites from 2000–2100. Shaded area represents +/- 10% degree day uncertainty envelope. For site location see Figure 1.

Figure 5. Shifting pace toward maturity in *C. gigas* across nine European oyster populations. Line plots show the date at which thresholds are exceeded. Perforated line = spawning threshold (600°C degree days above10.55°C) and solid line = settlement threshold (825°C degree days above 10.55°C). Bar plots show the period over which degree days can be accrued (> 10.55°C). Shaded area represents +/- 10% degree day uncertainty envelope. For site location see Figure 1.

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