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Effect of temperature on the growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis within the Irish Sea

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2

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6

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16

17 **Abstract**

18 In response to increased demand in Asian markets, the commercial fishery for the common whelk
19 (*Buccinum undatum*, L.) has expanded in north-eastern Europe. In the Irish Sea region (ICES Area 20
20 VIIa), increased effort and landings have raised concerns about long-term stability of the fishery
21 amongst stakeholders. Fisheries in Welsh waters and the Isle of Man territorial sea are now subject to
22 an increased minimum landing size according to the best available scientific data. This study addresses
23 key knowledge gaps by investigating the size-at-age relationship of the species across the latitudinal
24 extent of the fisheries management region. Our findings show that growth parameters, modelled using
25 growth rings observed in the statolith, vary between populations and show a broadly latitudinal pattern.
26 Thermal-time (expressed as sea bottom temperature degree-days) showed a significant negative linear
27 relationship with the asymptotic size reach by whelk populations (L_{∞}), where whelk grew to a larger
28 maximum size in cooler waters. Other parameters, including maximum growth rates and the age at
29 which growth rate begins to decrease, showed clear trends with sea-bottom temperature but linear
30 modelling failed to detect significant relationships, where warmer waters increase the rate of growth in
31 the early life stages of whelk but cooler waters allow growth to continue until later in life. Whilst there
32 are substantial requirements to further validate and refine the relationship between growth and sea-
33 bottom temperature, extrapolation of these data to other regions in Northeast Europe may provide a

34 valuable tool in approximating important life-history characteristics in stock assessments, such as L_{∞} ,
35 age-at- L_{50} and age-at-recruitment.

36

37 **1.0 Introduction**

38 The common whelk (*Buccinum undatum*, Linnaeus, 1758) is a neo-gastropod mollusc that is found in
39 the subtidal waters of the North Atlantic to depths of 1400 m (Mercier & Hamel, 2008). The species is
40 widely distributed on the Atlantic continental shelf and is frequently found in densities that support
41 commercial fisheries in both Europe and America (Emmerson, et al., 2018; Borsetti, et al., 2018). A
42 small scale fishery has existed in Europe for over a century, with recorded annual landings in England
43 and Wales of 4500 t in 1911 (Dakin, 1912). European waters are the principal area of production (FAO,
44 2017) and the fishery has undergone significant economic and geographical expansion in response to
45 emerging Asian markets, with global landings increasing from 7000 t yr⁻¹ to over 35000 t yr⁻¹ between
46 1990 and 2014 (FAO, 2017).

47

48 Whelk are the 6th most economically important shellfish species in the UK, with total UK landings
49 (20,800 t) equating to a value of £22.7 million in 2017 (MMO, 2018). What was once a small-scale
50 inshore fishery is now characterised by a fleet increasing in average length and fishing capacity. For
51 UK vessels under 12 m in length, whelk has overtaken crab and lobster as the most important shellfish
52 species by volume caught in the ‘pot and trap’ sector (Lawrence, et al., 2017). For larger vessels (> 12
53 m) they now rank as the second most important by volume. The same data highlight that over the last
54 decade, the economic significance of whelk has also increased. Among the five most valuable species
55 from 2008 to 2017 in the ‘10-12 m pots & traps’ sector, catch data shows the relative economic
56 contribution of whelk increase by 10%, whereas, European lobster and edible crab value increased
57 merely by 5% and Nephrops decreased by half (SEAFISH Economics, 2018). Regionally, the Irish Sea
58 (ICES Area VIIa) has an estimated 447% increase in the total landed weight of whelk between 2000
59 and 2016 by British registered vessels, with the most significant increases being recorded in the Isle of
60 Man territorial sea (ICES rectangle 37E5) and Welsh waters (ICES rectangles 33E5, 34E5, 35E5)
61 (Emmerson, et al., 2018). In the Irish Sea, whelk are the third most valuable shellfish resource after
62 *Nephrops* and scallops (*Pecten maximus*), worth £8.5 million in 2017 at first-sale value (16.5% of the

63 total value of all species landed by UK vessels in ICES VIIa) (MMO, 2018). The value of whelks
64 landed into Wales by UK vessels was greater than all other species combined in 2017 (MMO, 2018).

65
66 The sustainability of whelk fisheries has been questioned by both fisheries scientists and industry
67 stakeholders (see Nicholson & Evans, 1997; McIntyre et al., 2015). It is clear, for example, that the
68 widely adopted EU minimum landing size (MLS) (45 mm total shell length; TSL) fails to protect
69 juvenile individuals (individuals below the size of functional maturity; L_{50}) from harvest in many
70 regions of the British Isles (Shelmerdine, et al., 2007; Haig, et al., 2015; Emmerson, et al., 2018). The
71 uncertainty, knowledge gaps and localised variation in basic biological parameters such as maturity
72 (Haig, et al., 2015; McIntyre, et al., 2015), fecundity (Valentinsson, 2002) and mortality
73 (Laptikhovsky, et al., 2016), combined with low resolution data on fishing effort and catch has meant
74 that a conceptual framework for stock assessments has not yet been developed. As a consequence, the
75 fishery is considered 'data-poor' and there are no biologically referenced catch or effort restrictions.
76 Fisheries management responses to apparent whelk population declines have therefore been
77 precautionary in approach when compared to management decisions for other commercially important
78 species (Fahy et al., 2000; Fahy et al., 2005; Shrives et al., 2015).

79
80 An understanding of size-at-age and longevity of exploited marine species are fundamental in most
81 stock assessment models. For effective fisheries management to take place, scientists must be able to
82 understand changes of stock size and structure in response to dynamic anthropogenic (primarily fishing
83 mortality) and environmental factors (Hilborn & Walters, 1992). Using a size-at-age relationship to
84 estimate parameters such as age-at-recruitment and age-at-first-spawning are especially valuable for
85 evaluating existing management measures that are typically defined using size based metrics, as in the
86 case of whelk fisheries. Modelling the growth parameters of a marine species allows scientists,
87 managers and industry to formulate informed harvesting strategies with a medium-to-long term
88 perspective.

89
90 A reliable assessment of age and longevity in whelk populations is problematic for fisheries scientists
91 (Hollyman, et al., 2017b), primarily due to the heterogeneity between populations even over small
92 spatial scales (Shelmerdine, et al., 2007; Haig, et al., 2015). Age determination of this species and
93 other marine gastropods has typically been estimated by counting the growth rings on the operculum,

94 an organic ‘shield’ on the posterior edge of the animals foot (Santarelli & Gros, 1985). However, issues
95 of precision, accuracy and reliability (see Kideys, 1996) has meant that the methodology is viewed as
96 suboptimal, with < 20% of samples displaying clear readable rings (Hollyman, 2017a). Novel
97 techniques examining the statolith, which are an accretory calcareous particle typically < 300 μm and
98 integral to the animals central nervous system, have been developed to assess age and growth of
99 gastropod molluscs (Barroso, et al., 2005; Chatzinikolaou & Richardson, 2007). This has led to a
100 significantly improved degree of accuracy, precision and reliability in determining the age and growth
101 parameters of whelk (Hollyman, et al., 2018). Observing annual periodicity of growth rings in the
102 statoliths of whelk has also been validated using controlled laboratory tank-rearing experiments
103 (Hollyman, et al., 2018a) and by direct chemical analysis of the calcium carbonate structures
104 themselves (Hollyman, et al., 2017b).

105

106 Body temperature (T_b) affects the behaviour and physiology of ectotherms (Huey & Stevenson, 1979;
107 Angilletta Jr., et al., 2002), including aspects such as locomotion (Bennett, 1980; Young, et al., 2006),
108 sensory input (Werner, 1976), and rates of feeding and growth (Navaro & Iglesias, 1995). Hollyman
109 (2017a) observed clear variation in growth rates and seasonality of growth in whelk across the British
110 Isles. Across this latitudinal range, warmer sea bottom temperatures in the south stunted L_∞ (the
111 theoretical average maximum size of the sampled population) and whelk in cooler waters to the north
112 were hypothesised to have a greater time-window within which shell growth could occur, maximising
113 L_∞ values. Variable growth rates were highlighted by Haig et al. (2015) as a potential key driver in
114 localised variation in size-at-maturity (L_{50}) and size-structure of whelk populations sampled in South
115 Wales. Haig et al. (2015) also hypothesised that these observations were likely a consequence of local
116 temperature regimes. Whelk experience a large range of sea temperatures across the geographical range
117 of the species (0 – 22 °C; Smith, et al., 2013). Physiological processes are bound by critical thermal
118 limits, beyond which the processes cease, defined as the critical minimum (CT_{\min}) and critical
119 maximum (CT_{\max}) T_b that permit performance (Angilletta Jr., et al., 2002). The thermal performance
120 curve of whelk is not known but typically may be asymmetric with maximum performance of
121 individuals occurring at some intermediate temperatures (Angilletta Jr., et al., 2002), otherwise known
122 as a *thermal preferendum* (Sharpe & DeMichele, 1977).

123

124 Degree-days are an increasingly popular method for explaining variation in growth and development of
125 marine organisms (Chezik, et al., 2014), despite only accounting for 5% of all temperature related
126 growth studies between 1980 and 2006 (Neuheimer & Taggart, 2007). Neuheimer and Taggart (2007)
127 found strong linear functions of the DD metric can explain > 92% of the variation in size-at-age data
128 among forty-one data sets representing species from a variety of marine and freshwater environments
129 as well as laboratory studies. Since the metabolic functioning of whelk, a boreal species, is expected to
130 decrease linearly from a *thermal preferendum*, we model temperature as a function of DD (Sharpe &
131 DeMichele, 1977; Angilletta Jr., et al., 2002).

132

133 This study presents a regional analysis of data from statolith samples collected in the Irish Sea,
134 specifically from within Welsh waters and the Isle of Man territorial sea. Spatial comparisons of the
135 size-at-age relationships are coupled with satellite-derived sea-bottom temperature data in an attempt to
136 empirically explain the relationship between temperature and growth parameters for this geographical
137 area.

138

139 **2.0 Materials and methods**

140 **2.1 Biological samples**

141 Whelk were collected by industry participants from exploited fishing grounds in both the Isle of Man
142 territorial sea and Welsh waters (Figure 1) using industry-standard Fish-tec[®] pots (see Emmerson et al.,
143 2018 for details). Samples were collected in the Isle of Man during autumn 2016, whilst samples in
144 Wales were collected through 2016 to spring 2017. The whelks were not ‘graded’ according to MLS to
145 ensure that the maximum range of size classes were available for analysis. They were stored in
146 freezers at -20°C upon landing. Precise spatial details of the sampling locations are not presented in
147 agreement with the participants’ requests to protect commercially sensitive data. After thawing, the
148 TSL of each whelk was measured to the nearest 0.1 mm using Vernier callipers.

149 <Figure 1>

150 Figure 1. A map of the Irish Sea showing the general locations where whelk (*Buccinum undatum*) were sampled. A
151 = Isle of Man, B = Amwlch, C = Nefyn, D = Bardsey Island, E = Carmarthen Bay and F = Swansea Bay.

152

153 **2.2 Statolith analysis**

154 One statolith from each specimen was extracted using the methodology described by Hollyman, et al.
155 (2018a). The statoliths were mounted onto separate microscope slides using Crystalbond™ 509
156 thermoplastic resin and imaged under a Meiji Techno MT8100 microscope with a Lumenera Infinity 3
157 microscope camera at 20x magnification. Extracted statoliths were visually assessed according to the
158 rankings described by Hollyman et al. (2018) (see figure 3 in Hollyman et al. (2018) for a visual
159 comparison of the quality and clarity rankings of statolith rings; StR) and only specimens ranked 3 or 4
160 were used for subsequent analysis. Photomicrographs were analysed using ImageJ v1.48 (Ferreira &
161 Rasband, 2012) to count and measure the width of each statolith ring (StR) starting with the hatching
162 ring (Figure 2). After initial training by PH, the agreement in age determination by StR between the
163 two readers was 89.2%.

164 <Figure 2>

165 Figure 2. An example of a photomicrograph of a statolith (sampled in the Isle of Man territorial sea, June 2016).
166 Red lines indicate the growth rings observed, with the centremost arrow showing the hatching ring. The blue arrow
167 at the extremity of the statolith structure shows the edge of the statolith and is not counted as an annual growth
168 ring.

169

170

171 **2.3 Temperature data**

172 Sea bottom temperature (SBT) data for each sampling location were extracted from the Global Ocean
173 Physics Reanalysis Products “GLOBAL-REANALYSIS-PHY-001-030”, which was acquired through
174 the Copernicus Marine Environmental Monitoring Service (CMEMS) (<http://copernicus.eu>).

175

176 The data provides global ocean eddy-resolving ($1/12^\circ$ horizontal resolution and 50 vertical levels)
177 reanalysis covering the altimetry era 1993-2016. It is based largely on the current real-time global
178 forecasting CMEMS system. Observations are assimilated by means of a reduced-order Kalman filter.
179 Along track altimeter data (Sea Level Anomaly), satellite Sea Surface Temperature, Sea Ice
180 Concentration and *in situ* temperature and salinity vertical profiles are jointly assimilated. The global
181 ocean output files are displayed on a standard regular grid at $1/12^\circ$ (approximately 8 km), with the
182 most relevant grid square to the sampling location being extracted from the overall time series.

183

184 The annual sum of degree-days (with a base temperature, T_0 , near to the minimum temperature in the
185 coldest extremes of the species; *B. undatum*: 0 °C) can be used to explore the relationship between

186 physiological processes and temperature. Degree-days are an expression of thermal-time (Chezik, et al.,
187 2014) or thermal opportunity for growth (Chezik, et al., 2015), where the degree-day for a single day
188 (DD; °C·days) is expressed as:

$$DD = \frac{(T_{Max} + T_{Min})}{2} - T_0$$

189 Equation 1.

190

191 Data were filtered to include SBT for the period 2010-2016. The time series of daily mean SBT data
192 for each location were then calculated as Annual Degree-Days (°C) (aDD) (equation 2). The number of
193 measurements for each region were equal.

$$aDD = \frac{\sum DD}{time_{years}}$$

194 Equation 2.

195

196 **2.4 Modelling growth and L_∞**

197 TSL-at-age data of each specimen was calculated using a formula calculated by Hollyman (2017a, p.
198 183), which estimates y (size TSL; mm) to be a function of x (statolith width; μm) such that:

$$y = 43.439x^{0.4259} (R^2 = 0.96, n = 1719)$$

199 Equation 3.

200 The measurements from each ring within each statolith sample were then modelled using equation 3 to
201 create an account of growth for each individual whelk. These data were analysed by location and
202 modelled using equation 4 to estimate the average size at each age (ring) within the sampled
203 populations.

204

205 This pre-analytical calculation was necessary to fill data gaps brought about by difficulties in sampling
206 small whelks under the 45 mm MLS, so that growth curves could be modelled with a greater goodness-
207 of-fit to size-at-age data. Importantly, this technique avoided the unrealistic application of $TSL \leq 0$ mm
208 at age t_0 (hatching), which would result in incorrect asymptotic estimates (Hollyman, et al., 2018).

209

210 Using R (R Core Team, 2017), the size and age data for each observation were modelled using a non-
211 linear least squares regression model fitted with a gompertz growth curve (Tjørve & Tjørve, 2017),

212 which captures the sigmoidal relationship of growth in *Buccinum* and other marine gastropods more
213 than other models (see (Hollyman, 2017a) , whereby:

$$TSL_t = L_\infty e^{-e^{-k_G(t-T_i)}}$$

214 Equation 4.

215 TSL_t is the size of a whelk shell at time t , L_∞ is the theoretical average maximum size of the sampled
216 population, k_G is the growth-rate coefficient (which affects the slope), and T_i represents time at
217 inflection of growth (i.e. where the curve is orientated against the x-axis, or when growth begins to
218 slow).

219

220 The estimated coefficient value of L_∞ , k_G and T_i for each sampled population was then plotted against
221 aDD for each location. Further, aDD was also modelled against maturity (L_{50}) estimates taken from
222 existing literature (Haig et al., 2015; Hollyman, *unpublished data*; Emmerson et al., 2018). The
223 relationship between estimated coefficients and aDD were tested using linear regression to assess
224 whether any significant linear relationship exists.

225

226 3.0 Results

227 A total of 1,796 individual statoliths were examined (2,973 ring observations) with a size range from
228 25.9 mm to 109.4 mm TSL across six locations (figure 3). The oldest whelk sampled had 8 clear
229 growth rings (excluding the hatching ring).

230 <Figure 3>

231 Figure 3. Size-frequency histograms of whelk (*Buccinum undatum*) sampled at Amwlch (n=287), Bardesy Island
232 (n = 279), Isle of Man (IOM) (n = 185), Nefyn (n = 278), Saundersfoot (Carmarthen Bay) (n = 278) and Swansea
233 Bay (n = 304).

234

235

236 The pattern of growth of whelks differed significantly by location (figure 4, table 1). L_∞ ranged
237 between 59.9 mm in Swansea and 116.8 mm in Isle of Man samples. The variation in L_∞ follows a
238 broadly latitudinal trend, with the larger maximum size of whelk being observed in samples in the
239 northern Irish Sea. In contrast, the growth rate k_G decreased with increasing latitude, meaning that
240 whelks in the south grew at a faster rate (max = 1.04, Carmarthen Bay) than in the north (min = 0.44,
241 Isle of Man).

242

243 <Figure 4>

244 Figure 4. The modelled size-at-age relationship of *Buccinum undatum* by sample site in Welsh waters and the Isle
245 of Man territorial sea. Points represent mean TSL at Age \pm S.E.

246 <Table 1>

247

248 The satellite data show clear seasonal variability in temperature at each location (figure 5). The lowest

249 minimum temperature was in the Isle of Man (5.8 °C) and highest minimum temperature in Carmarthen

250 Bay (6.9 °C). The lowest maximum temperature was also recorded in the Isle of Man (16.5 °C), whilst

251 the highest maximum temperature was in Swansea Bay (18.4 °C) between 2010-2016 (figure 5).

252 <Figure 5>

253 Figure 5. The daily sea-bottom-temperature (SBT °C) at each location sampled for whelk in the Irish Sea for the
254 period 2010-2016.

255

256 The average aDD for each location varied between 4004 (Isle of Man, coolest) and 4267 (Swansea

257 Bay, warmest). This equates to an average daily difference of 0.72 °C between the warmest and coolest

258 locations.

259

260 When the size-at-age parameters are plotted against the average aDD value for each location, there are

261 clear negative trends in the data for all parameters with the exception of k_G which is positive (figure 6).

262 Linear regression analysis shows a significant effect of aDD on L_∞ ($R^2 = 0.72$, p-value = 0.03) and is

263 described by equation 5a. Linear regression was unable to model the effect of aDD on other growth

264 variables to the same statistical certainty, where $p = 0.07$ for K_G and T_i and $p = 0.11$ for L_{50} .

265 Extrapolating the significant linear model of L_∞ over the aDD data available presents a graphical

266 display of the estimated maximum TSL for whelk populations in the Irish Sea (figure 7).

267 **5a)** $L_\infty = 696 - 0.15 aDD; R^2 = 0.72, p = 0.03 *$

268 **5b)** $L_{50} = 317 - 0.06 aDD; R^2 = 0.63, p = 0.11$

269 **5c)** $K_G = -5.7 + 0.002 aDD; R^2 = 0.60, p = 0.07$

270 **5d)** $T_i = 21.7 - 0.001 aDD; R^2 = 0.59, p = 0.07$

271

Equations 5a – 5d.

272

273

274 <Figure 6>

275 Figure 6. Scatterplots showing the relationship between estimated L_{∞} , Growth rate (k_G), Age at Gompertz
276 inflection (T_i ; years) and functional maturity (L_{50}) of whelk (*Buccinum undatum*) and sea-bottom-temperature
277 (SBT) expressed as annual average degree-days (aDD) in the Irish Sea. The black lines represent the linearly
278 modelled relationships (equation 5a – 5d) while the grey area shows the standard error in the model. Error bars
279 around the point show the standard error in the parameter estimations. N.B no maturity data is available for
280 Carmarthen Bay samples.

281

282

283

284 <Figure 7>

285 Figure 7. The aDD- L_{∞} relationship for whelk, *Buccinum undatum*, extrapolated throughout the data range of
286 average annual sea bottom temperature (2010-2016) for ICES Area VIIa.

287

288 4.0 Discussion

289

290

291

292 Using growth rings observed in statoliths, the size-at-age relationship was modelled for whelk
293 populations in the Isle of Man territorial sea and Welsh waters using specimens harvested by
294 commercial fishers on exploited fishing grounds. The modelled growth parameters varied by location,
295 with a clear latitudinal trend of increasing asymptotic size with latitude in the Irish Sea. The largest
296 potential size (on average) of whelk populations varied from a maximum of 116.8 mm TSL (Isle of
297 Man) in the north to 59.9 mm TSL (Swansea Bay) in the south, a pattern analogous with observations
298 by Hollyman, et al. (2018) where samples were taken across a geographic range from Shetland to
299 Jersey. This pattern is also observed in the size-distribution data for Irish Sea whelk presented in
300 Emmerson et al. (2018). Whilst we observe large variation in size and growth of whelk over latitudinal
301 scales, similar levels of variation have been observed in size-at-maturity and population structure at
302 local levels, suggesting the growth of whelk may vary significantly over local scales (Haig et al., 2015).
303 Studies examining the life history of this species have consistently alluded to or hypothesised that sea-
304 bottom temperature is the fundamental environmental driver of variation (see Bell & Walker, 1998;
305 McIntyre et al., 2015; Hollyman, et al, 2018). This study is the first to test the relationship between
306 growth parameters and SBT using observed data from statoliths sampled throughout the latitudinal
307 extent of a fisheries management area together with SBT derived from modelled satellite data.

308

309 A significant negative linear relationship between temperature, expressed as aDD, and L_{∞} was found
310 for the species on a regional scale in the Irish Sea (ICES Area VIIa), where the average maximum size
311 of an individual within a population decreases with increasing average annual sea-bottom temperature.
312 The Swansea Bay area experienced the greatest aDD of 4267 between 2010 and 2015 with populations
313 showing L_{∞} of 59.9 mm TSL. Cooler waters in North Wales around the Llyn peninsula (aDD = 4174)
314 and Anglesey (aDD = 4017) meant whelk there reached a larger L_{∞} , 89.6 mm and 90.9 mm TSL
315 respectively. The coolest waters were in the Northern Irish Sea around the Isle of Man (aDD = 4004)
316 where whelk grow to the greatest maximum size observed in this study (L_{∞} = 116.8 mm TSL). The
317 variation in estimated size-at-age produced by the gompertz model (figure 4) was larger in the Isle of
318 Man sample than in other samples. Intra-site analysis showed that this increased variation resulted from
319 cross-sampling across several distinct whelk populations on the east coast of the Isle of Man, with
320 'Northeast' and 'East' sites exhibiting significantly different size structures (see Emmerson, et al.,
321 2018). Low sample size for each site prevented separate analysis of statoliths, highlighting the need for
322 spatially specific sampling at local scales, particularly where localised hydrographic and bathymetric
323 variations affect ambient temperature. Significant differences in growth rate between the northeast area
324 of the Isle of Man and the rest of the territorial sea have also been observed in king scallop populations
325 (Dignan, et al., 2014).

326

327 Other Gompertz growth coefficients (K_G and T_i), i.e. the maximum rate of growth and the point of
328 growth rate inflection, showed marginally non-significant linear relationships with aDD ($p = 0.07$ for
329 both coefficients). Increased sampling may change the outcome of these analyses, since visual
330 interpretation of the data (figure 6) shows that there is a trend between aDD and both K_G and T_i . The
331 maximum rate of growth (K_G) showed a strong positive correlative trend with aDD, where populations
332 of whelk in Swansea Bay and Carmarthen Bay (South Wales) had the highest coefficient value, 0.98
333 and 1.04 respectively. These values indicate that the warmer sea bottom temperature, whilst limiting
334 the maximum potential size of whelk, also accelerates the rate of growth of individual during early life-
335 stages. The slowest growth-rate coefficient value was observed in cooler waters around the Isle of Man
336 ($K_G = 0.44$). The point at which this gompertz growth rate begins to decrease from the maximum (T_i)
337 showed a negative correlative trend with aDD. Growth of whelks in warm waters such as Swansea Bay

338 begins to decrease at age 0.94 years, whereas in the Isle of Man growth rate begins to decrease at 2.81
339 years.

340

341 Whelk populations found at higher latitudes in the northern hemisphere generally have a larger
342 maximum body size than those living further south (Hollyman, 2017a), despite initial slower growth
343 rates. This is a common pattern among many ectotherms, such as the scallop *Pecten maximus*
344 (Chauvaud, et al., 2012). Chauvaud et al. (2012) observed that low annual growth rates in northern
345 populations are not due to low daily growth rates, but rather a fewer number of days (thermal window)
346 within which scallop growth could occur, which was also hypothesised in the case of whelk by
347 Hollyman (2017a). Chauvaud et al. (2012) also showed that, “despite initial lower annual growth
348 performance ... differences in asymptotic size (L_{∞}) as a function of latitude resulted from persistent
349 annual growth performances in the north and sharp declines in the south”. Classical growth models
350 have failed to capture this dynamic in long-lived ectotherms that have thermally constrained growing
351 seasons (Chauvaud, et al., 2012), such as whelk. The growth observed in the data for whelk in the Irish
352 Sea point to Bergmans rule, “a general trend of animal sizes to increase with latitude” (Blackburn, et
353 al., 1999). Clearly, higher ambient temperature drives rapid growth in whelk in the early life-stages of
354 the species with larger time-windows for growth, but they reach a smaller asymptotic maximum size
355 earlier in life. These patterns are captured in the behaviour of the gompertz curve, which explained
356 growth in *Buccinum* with a greater R^2 and goodness-of-fit values than other analyses (Hollyman, et al.,
357 2018). We also hypothesise that as well as being temperature drive, the time-window for growth
358 decreases with age in whelks, which is consistent with the notion that as they mature there is a trade-off
359 between growth and reproduction or defence, resulting in a decrease in the length of growing season
360 with age (Stearns, 1992; Lankford, et al., 2001). Chauvaud et al. (2012) were able to demonstrate with
361 scallops that the decrease in the length of growing seasons with age is more rapid at lower latitudes, a
362 hypothesis that may also be reflected in the data presented here.

363

364 It is important that data and models explaining species life-history are incorporated into fisheries
365 management where possible. Whelk fisheries in both the Isle of Man and Wales are considered “data
366 poor” though they are managed primarily with an MLS informed by size-at-maturity studies (Haig et
367 al., 2015; Emmerson et al., 2018). Viewing the analyses in this study in the context of other work on

368 whelk in Welsh waters and the Isle of Man (see Haig et al., 2015; Hollyman, 2017a; Emmerson et al.,
369 2018) suggests that, on average, populations reach functional maturity (L_{50}) by age 4. It may therefore
370 be possible to also estimate reproductive characteristics, upon which MLS is ideally referenced, using
371 solely temperature data if the temperature~growth parameters are further investigated and the
372 relationship is substantiated with additional data. Broadly speaking, management of whelk fisheries in
373 the Northeast Atlantic should follow a latitudinal pattern of increasing MLS with latitude. The EU
374 minimum conservation reference size (MCRS) of 45 mm TSL may well be sufficient to protect
375 spawning stock according to L_{50} estimates in parts of the English Channel (McIntyre, et al., 2015), but
376 it is insufficient in the Irish Sea where L_{50} has been shown to be up to 75 mm TSL (Emmerson, et al.,
377 2018). As whelk fisheries continue to expand throughout the British Isles, it is essential that
378 management is both evidence-based and regionalised.

379

380 Within the context of the Irish Sea region, a linear relationship sufficiently explains the variation in the
381 SBT- L_{∞} relationship ($p = 0.03$) and provides good cause to suspect the relationship can be explain other
382 growth coefficient factors (K_G and T_i). However temperature in the Irish Sea varies over a relatively
383 narrow range compared to the temperatures experienced by whelk over the full geographical extent of
384 the species. Whelk are highly eurythmic and have been reported to survive in temperatures from below
385 0 °C to above 22 °C (Smith, et al., 2013). We hypothesize a non-linear relationship between
386 temperature and L_{∞} of this species over its geographical distribution with asymptotic limits to the size
387 of whelk in populations as average SBT approaches the lower and upper critical thermal limits (Figure
388 8). Indeed, anecdotal evidence supports this hypothesis, such that preliminary observations in the
389 Orkney Islands (northern Scotland) show $TSL_{L_{\infty}} \approx 140$ mm at $aDD = 3,465$ (M. Coleman, *unpublished*
390 *data*). A broad-range study to explore this relationship would also reveal whether populations of whelk
391 exhibit ecotypic characteristics, where subpopulations may have undergone genotypic adaptations to
392 specific environmental conditions that affect life-history traits such as growth. It is possible that,
393 following successful validation of the DD~growth relationship in further studies by combining both
394 laboratory and field-based methodologies, the growth rate of this species can be modelled throughout
395 its distribution based solely on open source satellite-based temperature data. However, more work is
396 required to validate the relationship in the first instance.

397

398 <Figure 8>

399 Figure 8. A hypothetical illustration of the relationship between degree days ($^{\circ}\text{C}$) and L_{∞} for the common whelk
400 (*Buccinum undatum*).

401
402 It is anticipated that refinement of the aDD variable according to critical thermal limits of the species,
403 which are currently unknown, may result in the analytical models showing a statistical significance in
404 the temperature \sim growth relationship for all parameters. This study analysed the growth parameters of
405 whelk against a single aDD value (the average annual DD for the period 2010-2016), however further
406 investigations looking into the parameters that define DD over time (the maximum rate of increase in
407 DD (DDr), the point of inflection in DD (DDi) during the year) are warranted. That is to say, the
408 mechanistic effect of temperature on whelk may be such that aDD, which calculates the average annual
409 thermal input into the environment, has limited explanatory power. Instead, for example, it may be that
410 it is the *rate* of thermal input within specific season that provides greater statistical power in explaining
411 growth. In order to precisely analyse these hypotheses and to observe localised hydrographic
412 anomalies, temperature data would have to be generated from direct observations using temperature
413 loggers fixed to the seabed as opposed to the low resolution satellite data used in this study. Another
414 method that may further validate the temperature \sim growth relationship would be laboratory-based
415 studies, which control the temperature of the environment as a fixed variable in order to fully
416 understand the specific thresholds that drive and limit the energetic input into shell growth, as well as
417 the species specific *thermal preferendum*. In contrast to this study, which conducted a post-hoc analysis
418 using available temperature data, controlling for temperature as part of the experimental design would
419 add greater certainty to the relationship. The importance of understanding the environmental context of
420 sampling locations (fishing grounds) has been highlighted previously (Hollyman, et al., 2018). Indeed,
421 any specific *thermal preferendum* that exists to encourage energetic investment in shell growth for this
422 species would necessitate an experimental design that controlled for specific thermal parameters as
423 well as other confounding variables (e.g. food availability (Nasution & Roberts, 2004), predatory
424 pressure and aquatic chemistry). Given the opportunistic post-hoc nature of this study, and that the
425 analysis was performed on aggregated one-dimensional temperature data (aDD), it is encouraging that
426 a clear and significant relationship is observed (figure 7).

427

428 This study presents the first comparison of growth rates of sampled whelk populations throughout the
429 latitudinal extent of a fisheries management region (ICES VIIa), using data modelled from statolith
430 analysis. A linear trend was observed between SBT, expressed as aDD, and L_{∞} whereby warmer waters
431 limited maximum shell size. When extrapolated throughout the entire geographical extent of ICES
432 VIIa, the data broadly mirrors the reported parameters in other studies. Further verification of the
433 temperature ~ growth relationship for this species is required, combining both broad geographical
434 collaborations and controlled laboratory methodologies. Validating this relationship may lead to broad-
435 scale extrapolations throughout the species distribution, which would provide an incredibly valuable
436 and timely resource to fisheries managers who would otherwise depend on dedicated sampling studies
437 to understand the life-history parameters of whelk stocks, which are currently recognised as being data-
438 poor and potentially over exploited.

439

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449

450

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- 586
- 587

Table 1. Summary of results from growth models for each location, including parameter estimates for model coefficients, where L_{∞} is estimated maximum shell size, k_G is the growth-rate coefficient and T_i is the point of inflection in the model curve. Parameter statistical significance shown by p-value (***) = <0.001).

Model	Param	Est	S.E	t-value	sig.
Isle of Man	L_{∞}	116.8	4.77	24.5	***
	k_G	0.44	0.02	17.7	***
	T_i	2.81	0.11	24.5	***
Anglesey	L_{∞}	90.9	1.45	1.162.6	***
	k_G	0.72	0.03	22.2	***
	T_i	1.47	0.03	44.2	***
Nefyn	L_{∞}	89.6	1.19	74.9	***
	k_G	0.71	0.03	24.2	***
	T_i	1.59	0.03	55.9	***
Bardsey	L_{∞}	91.5	0.99	92.0	***
	k_G	0.74	0.03	26.2	***
	T_i	1.96	0.04	54.6	***
Carmarthen Bay	L_{∞}	81.9	1.49	54.9	***
	k_G	1.04	0.06	16.8	***
	T_i	1.14	0.04	30.3	***
Swansea	L_{∞}	59.9	1.77	33.7	***
	k_G	0.98	0.06	11.1	***
	T_i	0.94	0.08	13.5	***

Figure 1
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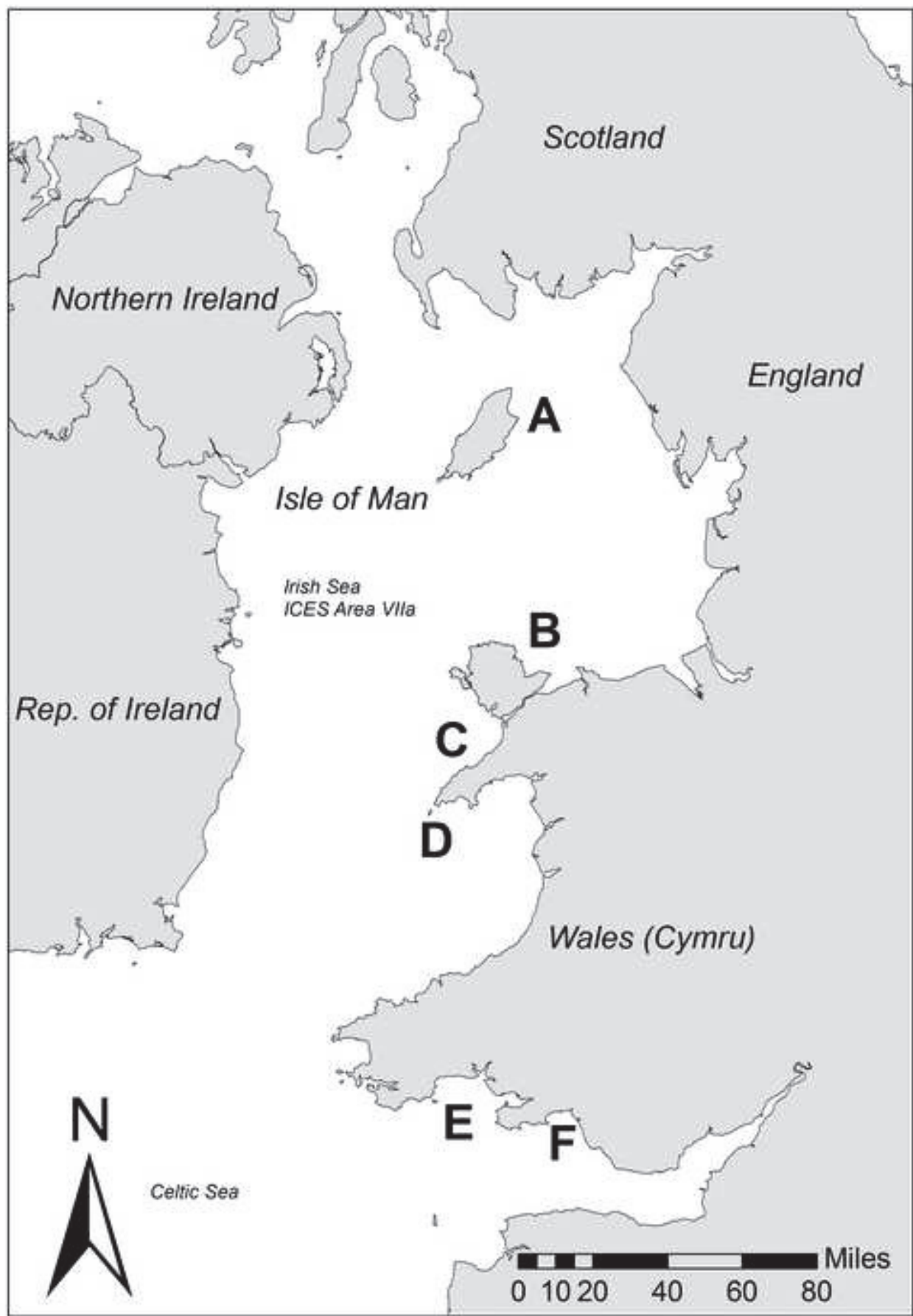


Figure 2
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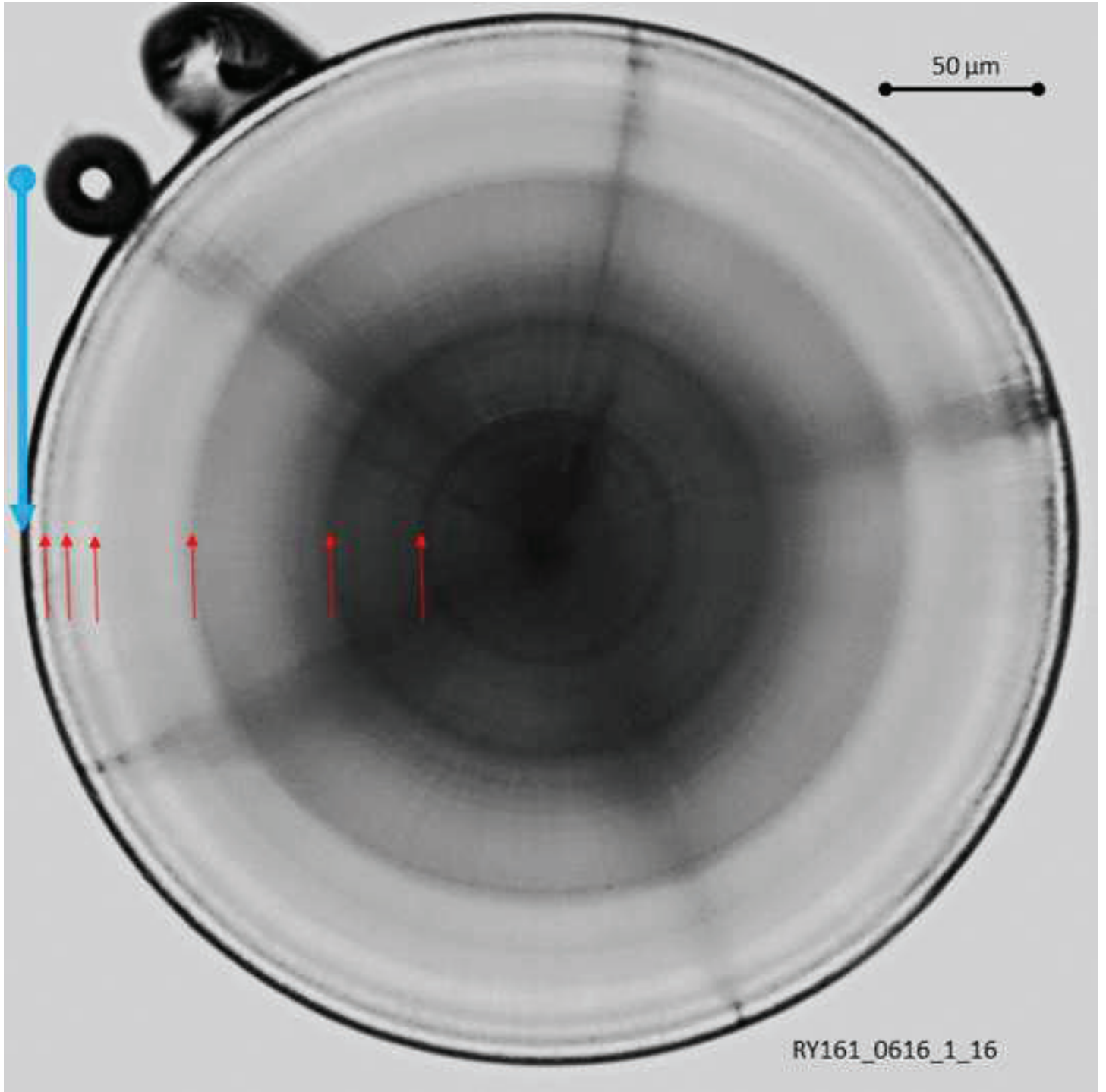


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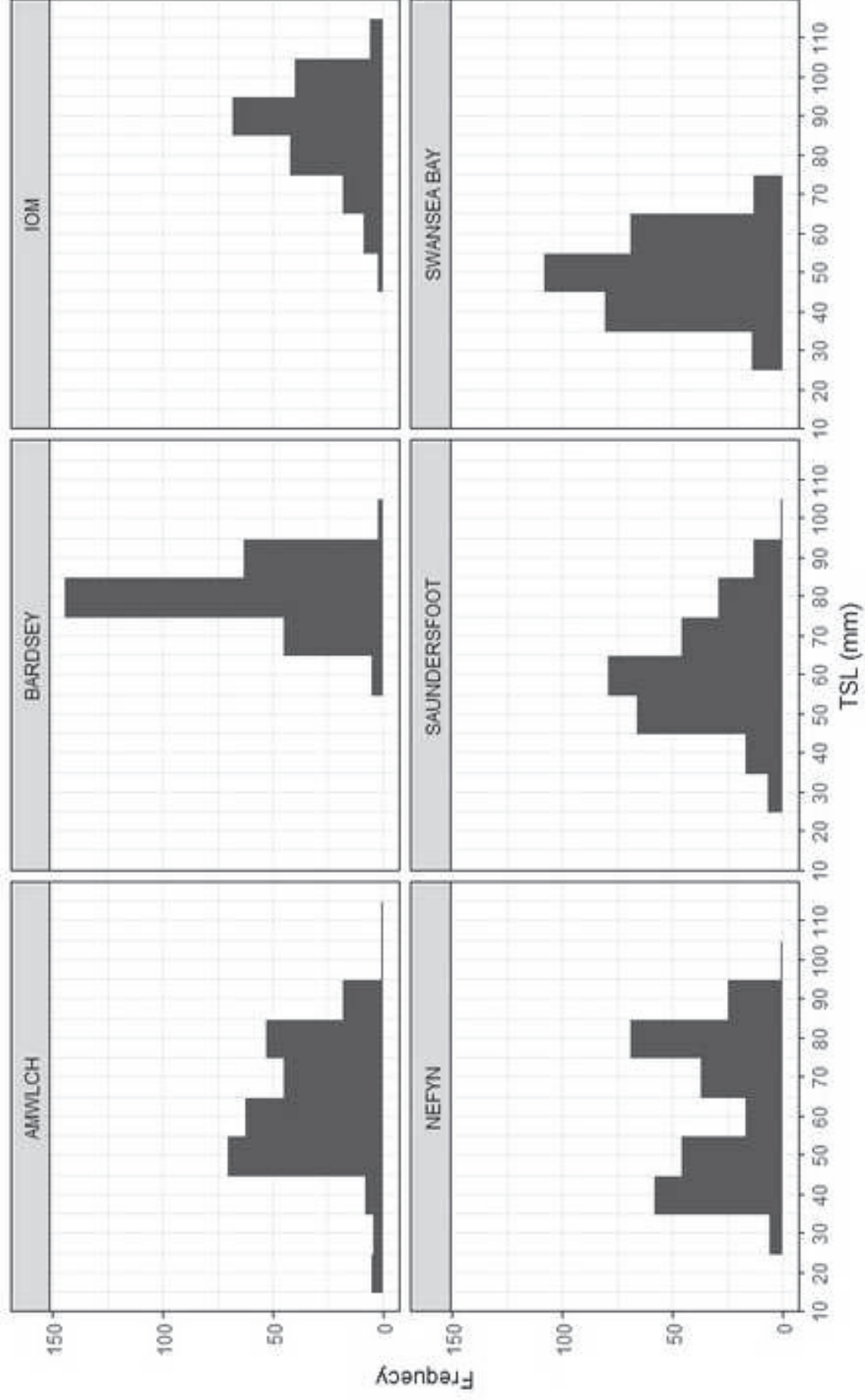


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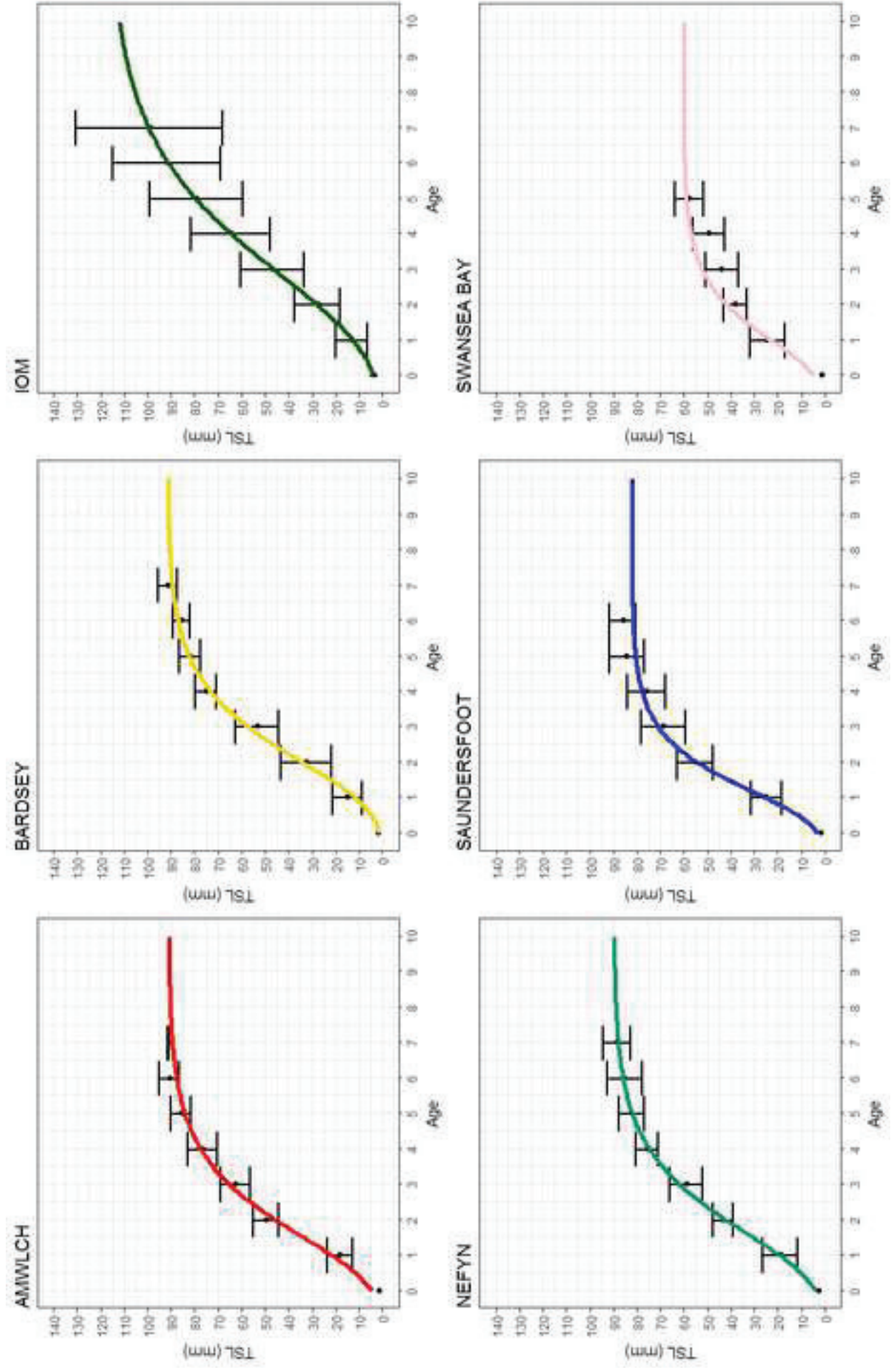


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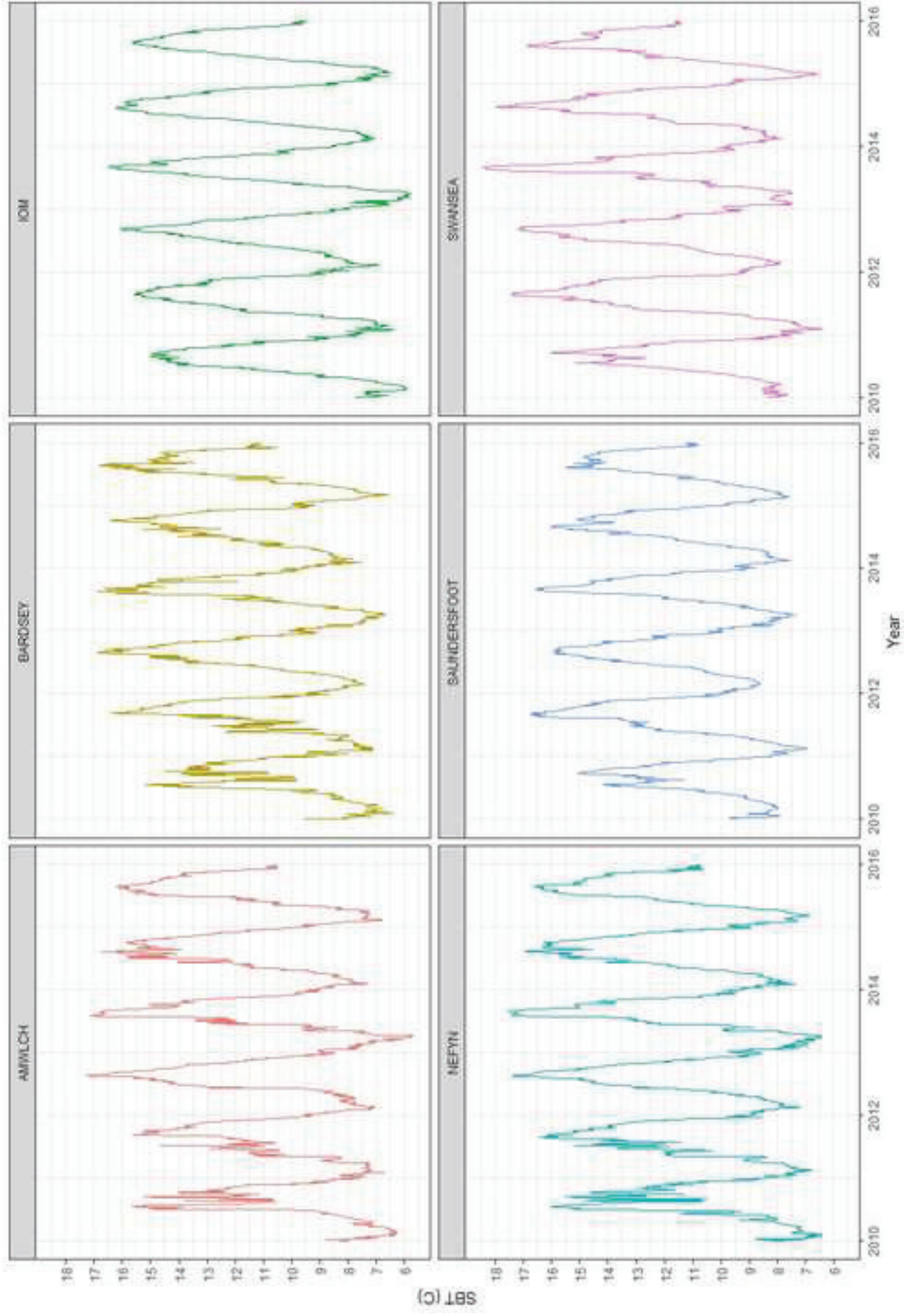


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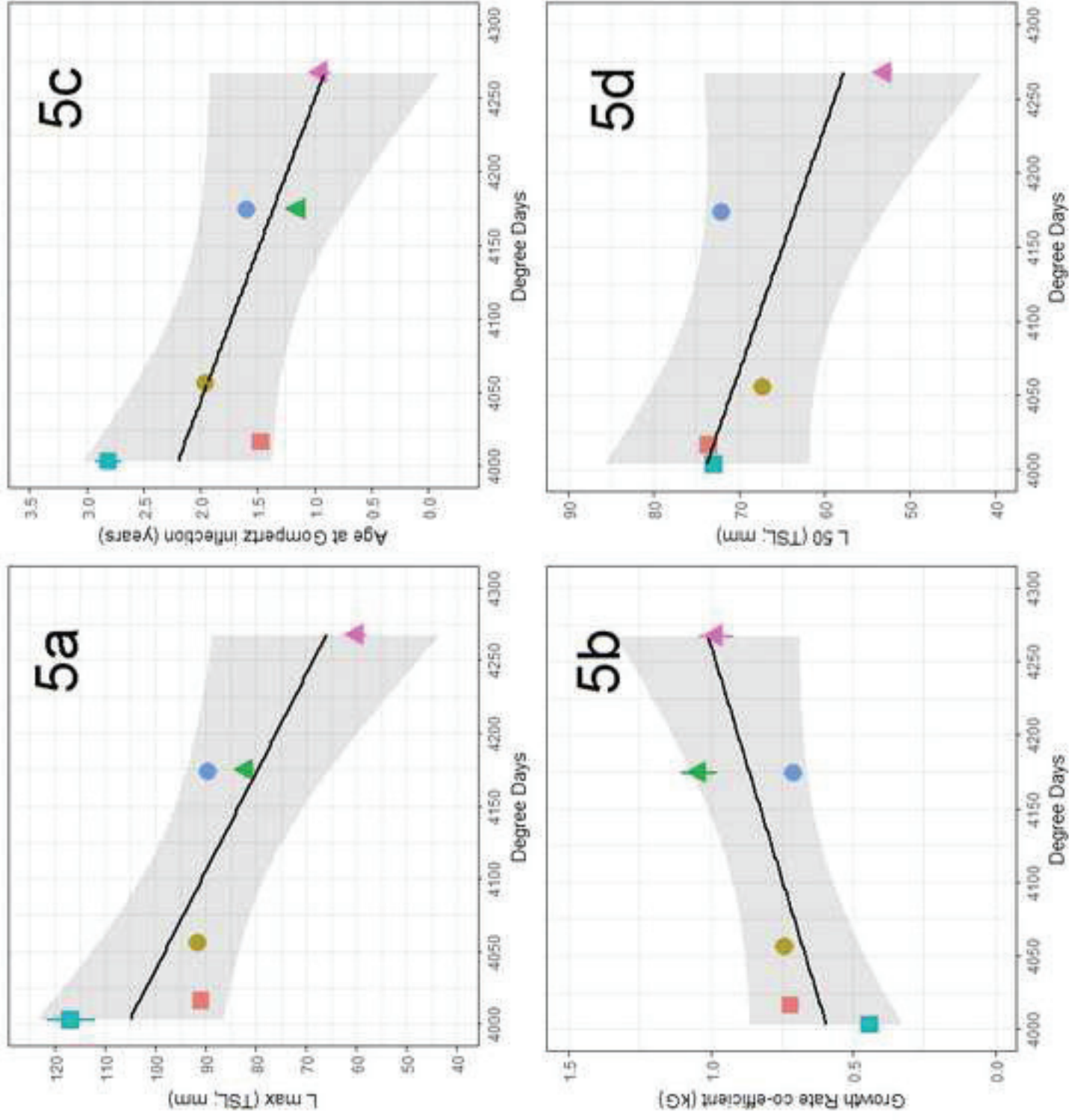
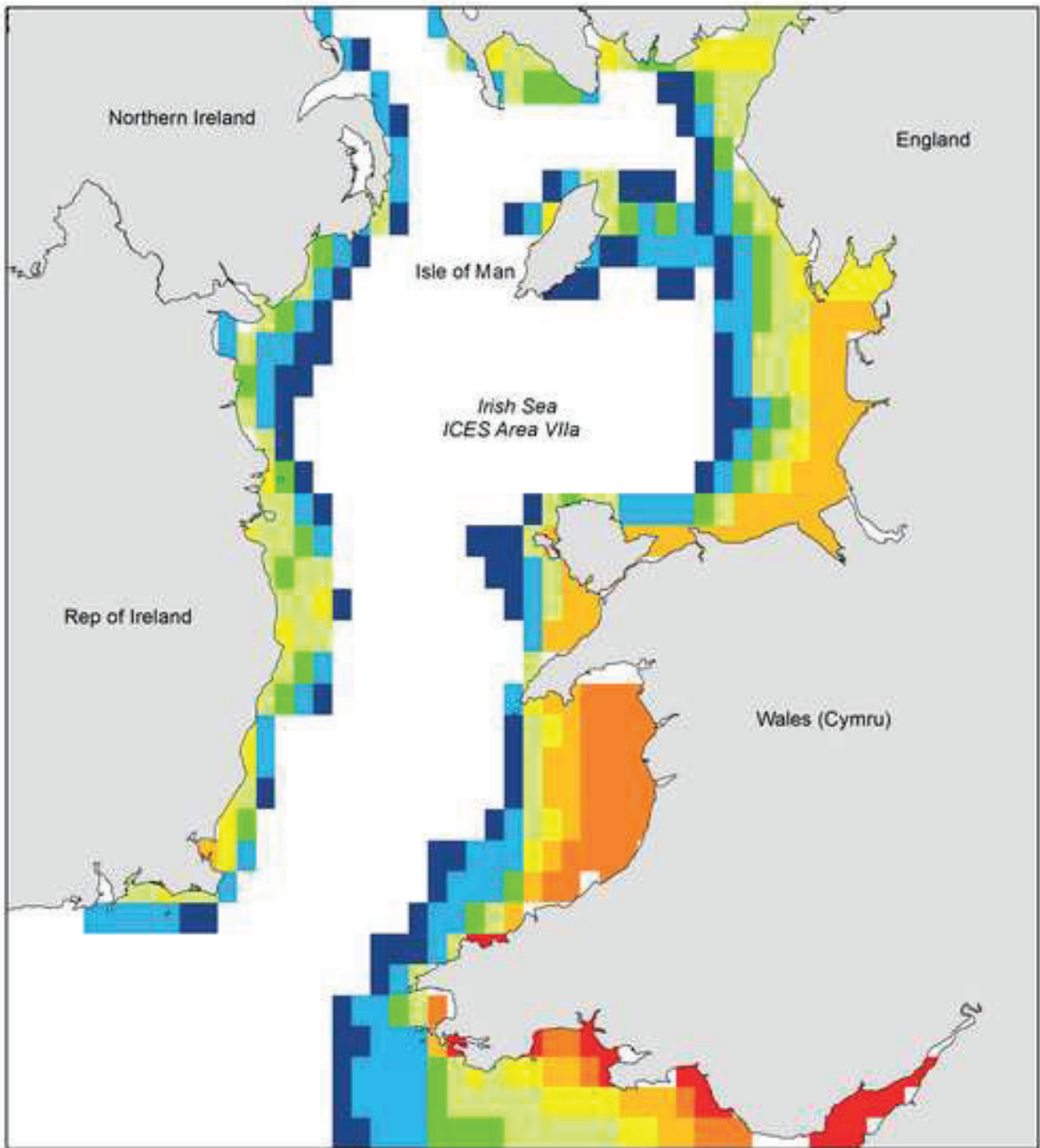


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Legend

United Kingdom
Republic of Ireland
Isle of Man

Lmax

< 60	90 - 100
60 - 70	100 - 110
70 - 80	110 - 120
80 - 90	> 120
	No Data

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