The complexities and challenges of conserving common whelk (Buccinum undatum, L.) fishery resources: Spatio-temporal study of variable population demographics within an environmental context.

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7

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17   management, gonadosomatic index.

18

19   **Highlights**

20   - Size-at-maturity (SOM) is estimated for a number of whelk populations in the Irish Sea.

21   - A rationale for a standard methodology for estimating SOM in *B. undatum* populations is

22   presented.

23   - Environmental drivers of variable population demographics are investigated.

24

25   **Abstract**

26   The commercial fishery for common whelk (*Buccinum undatum* L.) has expanded significantly in the

27   Irish Sea since 1990 and continues to grow, particularly in Welsh waters and the Isle of Man territorial

28   sea, with landings throughout the region increasing by 227% between 2011 and 2016. Whilst whelk

29   populations are known to be vulnerable to localised overexploitation due to inherent life-history

30   parameters, fisheries remain relatively unrestricted by conservation measures in comparison to other

31   fisheries operating in the area. With the exception of the northernmost fishing ground between the Isle

32   of Man and Scotland (Point of Ayre), the size-at-maturity (L_{50}) estimate for populations sampled during

33   peak-aGSI (the months in which adjusted gonadosomatic index is highest) indicates that whelk are being

34   fished before the time at first spawning throughout the study area. A correlation was detected between

35   the size (total shell length) and depth, with smaller whelks found in deeper waters where there generally

36   is greater fishing effort, although effort data is not available at a resolution to investigate this relationship

37   quantitatively. No clear link between benthic infauna biomass and the average size (total shell length) or

38   reproductive capacity (aGSI) of whelk sampled throughout ICES Area VIIa was found, indicating that

39   the ecological energetics of whelk populations are more likely to be a function of scavenging

40   opportunities than predation on benthic communities. A mixed cohort analysis utilized length-based data

41   to infer a size-at-age relationship in the absence of direct age observations (e.g. statolith rings), with

42   whelk recruiting into the Isle of Man fishery five years after hatching. The evidence presented in this

43   study suggests that, prior to recommending a MLS that will adequately protect the spawning stock

44   biomass, L_{50} values should be adjusted for pre-spawning growth between the ideal time of assessment

45   (when aGSI values are at a peak) and the spawning season (when aGSI values decrease).

46

47   **1.0 Introduction**

48   The common whelk (*Buccinum undatum*, Linnaeus, 1758) is a neo-gastropod mollusc that is found in

49   the subtidal waters of the North Atlantic to depths of 1200 m (Ager, 2008). It is widely distributed on the

50   Atlantic continental shelf; from within the arctic circle (76° N) as far south as New Jersey, USA at the

51   western-most extent (38° N) (Van Guelpen et al., 2005; Borsetti et al., 2018). Populations are most

52   frequently observed in abundance in the northeast Atlantic, particularly in the waters of north-western

53   Europe, from the Celtic and Irish Sea through to the Skagerrak and Kattegat Bay, including northern

54   populations observed in Norwegian, Faroese and Icelandic waters (Ocean Biogeographic Information

55   System, 2017).

56

57   Whelk are opportunistic scavengers that feed mainly on carrion (Nasution & Roberts, 2004) and detect

58   feeding opportunities with a very acute chemo-sensory system (Himmelman, 1988). This allows whelks

59   to be commercially exploited by fishers, who typically use specifically designed baited traps. Inshore

60   whelk populations have been exploited by a mixed artisanal fishery in Europe since the early 20th century

61 (Dakin, 1912). Annual landings in England and Wales equated to 4500 t in 1911 (Dakin, 1912) and

62 European waters remain the principal area of fishing effort (FAO, 2017). The fishery has undergone

63 significant economic and geographical expansion in response to emerging Asian markets, with global

64 landings increasing from 7,000 t yr^{-1} to over 35,000 t yr^{-1} between 1990 and 2014 (FAO, 2017). The

65 effects of fishing mortality (F) on the phenotypic traits of *B. undatum* may be significant, especially

66 considering the expansion in commercial exploitation (Kuparinen & Merilä, 2007). Whelk are now

67 amongst the most economically important shellfisheries in the UK (Haig et al., 2015) with total UK

68 landings (21,606 t) equating to a value of £21.7 million in 2016 (MMO, 2017). Regionally, the Irish Sea

69 (ICES Area VIIa) has seen an estimated 227% increase in the total landed weight of whelk between 2011

70 and 2016 and is the source of approximately 10% of global landings for this species. The most substantial

71 increases in recorded landings in the region are from within the Isle of Man territorial sea (ICES rectangle

72 37E5) and Welsh waters (ICES rectangles 33E5, 34E5, 35E5) (IFISH2, 2017; Figure 1).

73

74 <Figure 1>

75 *Figure 1.* The spatial distribution of whelk (*Buccinum undatum*) landings in ICES Area VIIa by British
76 vessels in 2011 (A) and 2016 (B) by ICES Rectangle. Source: IFISH2 database.
77

78 Within ICES Area VIIa, management regimes are not consistent. Similar to many other jurisdictions in

79 the UK, whelk fisheries within Welsh waters are managed solely by a minimum landing size (MLS = 45

80 mm Total shell length; TSL) established by the European Union (EU), which has been shown to be

81 inadequate in several studies (Shelmerdine et al., 2015; Haig et al., 2015). However, Isle of Man fisheries

82 are subject to a MLS of 70 mm TSL, informed by Kideys et al. (1993) and the fishery now includes a

83 restricted number of species-specific licenses, each of which has effort (pot number) restrictions.

84

85 The phenotypic plasticity displayed by other marine gastropod populations can be closely related to

86 mortality and growth rates (Stearns & Koella, 1986), which vary spatially and temporally with fishing

87 pressure (Torrogolsa & Gimenez, 2010; Fahy et al., 1995). Whelks do not reach sexual maturity for

88 several years, have limited dispersal potential (Martel et al., 1986a) and display little adult movement

89 (Pálsson et al., 2014; Weetman et al., 2006). Therefore, populations are inherently vulnerable to high F

90 and are particularly susceptible to recruitment overfishing (Shrives et al., 2015) and severe localised

91 depletion (Nicholson & Evans, 1997). Environmental parameters have been shown to influence the

92 biological characteristics of populations, with size-at-maturity being negatively correlated to bottom-

93 temperature but positively correlated with depth (McIntyre et al., 2015; Haig et al., 2015). This is

94 unsurprising given that the common whelk is a boreal species, although no clear latitudinal relationship

95 has been observed (McIntyre et al., 2015) and local factors such as food availability and fishing presure

96 are likely to have an influence in maturation and growth (Martel et al., 1986b).

97

98 There is presently little scientific evidence to suggest that the current MLS of 45 mm used as the baseline

99 throughout the EU is an adequate fisheries threshold for sustainable exploitation. Shelmerdine et al.

100 (2007) suggests that management measures should be considered on a regional basis after demonstrating

101 significant differences in the biology of whelk populations sampled in Shetland and the south-coast of

102 England. Haig et al., (2015) shows that the size at maturity (L_{50}) can vary considerably between

103 populations over distances as small as 10 km (although application of management measures at this

104 spatial scale are acknowledged to be impractical). Complications arrise when trying to compare research

105 on size-at-maturity, as there is not currently a standard scientific methodology to determine this metric

106 (Haig et al., 2015).

107

108 This study combines published data (Haig et al., 2015) from Welsh waters with data collected in the Isle

109 of Man territorial sea. The aim was to compare spatial variation in size-at-maturity and also to determine

110 reproductive response to spatial, temporal and environmental parameters.

111

112 **2.0 Materials and methods**

113

114 *2.1 Field Materials (Fisheries Dependent Data)*

115 Nine fishers, registered in Wales (3), England (1) and the Isle of Man (5), each fished two identical whelk

116 pots once a month within the ICES area VIIa (Irish Sea). The fishers retained the entire pot contents,

117 including undersized bycatch and non-target species. The pots supplied to fishers were 36 litre Fish-tec™

118 'WHELKER' pots, described by fishers as being 'stand-up' pots due to their orientation (Haig et al.,

119 2015). The pots are made of thick plastic and are weighted with lead. The drainage holes in the base of

120 the pot measure 30 mm in diameter and the entrance to the pot is covered with a purse-pull mesh netting.

121   Fishers completed data-forms with details on the location (latitude and longitude), date, soak-time and

122   bait used. Isle of Man (Manx) samples were collected for a period of 12 months beginning in January

123   2016, with samples also collected in a pilot study in the Isle of Man during 2015. The Manx samples

124   were compared to Welsh data collected over a 14-month period beginning in April 2013 (Haig et al.,

125   2015). The general locations of the samples are displayed by area code to maintain commercial

126   confidentiality (see Figure 2). The pots were fished separately and attached to commercial fishing

127   'strings', which varied in length but typically anchor between 20 and 50 pots to the seabed along ropes

128   400–700 m in length. The pots were baited with a combination of dogfish (*Scyliorhinus canicula*) and

129   edible crab carcass (*Cancer pagurus*) and were 'soaked' for 24–48 hours.

130

131   <Figure 2>

132   *Figure 2.* A map of the Irish Sea showing the areas where whelk (*Buccinum undatum*) were fished during
133   the study in ICES Area VIIa. IOM = Isle of Man, ROI = Republic of Ireland.
134

135   *2.2 Laboratory Analysis*

136

137   Pot samples were frozen after landing and later defrosted before laboratory dissections. The latitude and

138   longitude were recorded and the sample was assigned to an area. All individuals were sexed (presence /

139   absence of a penis), weighed (total wet weight; 0.001g) and measured (total shell length (TSL); 0.1 mm).

140

141   A randomly selected subsamples of 30 individuals were taken from each pot-sample and further analysed.

142   The penis length (PL) was measured from the point of attachment to the body to the tip accounting for

143   natural curvature. Maximum and minimum shell width was recorded as shown in Haig et al. (2015).

144   Additionally, the subsamples were dissected and the animal was removed from the shell. The wet weight

145   of the flesh was recorded (0.01 g). The posterior lobe of the digestive gland, which is partially covered

146   by the gonad on the dorsal surface, was visually inspected and the degree of differentiation (% $_{GONAD}$; 0,

147   0.25, 0.5, 0.75, 1) between the two organs was used to assign one of five maturity stages shown in table

148   1 (Haig et al., 2015; Hollyman, 2017a)

149

150   <Table 1>

151

152 The digestive gland and gonad, which are encapsulated by the same membrane forming the integument,

153 were dissected away at the area where the anterior edge of the digestive gland meets the renal gland and

154 weighed. The gonadosomatic index (GSI) was calculated by expressing the weight of the removed whorl

155 mass (gonad and digestive gland) as a percentage of the wet flesh weight:

156

157 $$GSI\ (\%) = \frac{Gonad + Digestive\ Gland}{Total\ wet\ flesh\ weight}$$

158

159 Additionally, an adjusted gonadosomatic index (aGSI) was calculated by multiplying the above GSI

160 value by the estimated proportion of the whorl occupied by the gonad gland (% gonad) in an attempt to

161 focus analysis on reproductive patterns (as in Hollyman, 2017), where:

162

163 $$aGSI = GSI \times \%_{GONAD}$$

164

165 *2.3 Statistical Analysis*

166

167 All analysis was carried out in the statistical software programme R v 3.3.1 (R Core Team, 2014). Prior

168 to statistical modelling, shell measurement and weight data were tested for normality (Kolmogorov-

169 Smirnov test) and inspected visually using a Q-Q plot. Heteroscedasticity was tested using the Levene's

170 test and Cook's distance plot was used to check for outliers. Transformations were applied to data where

171 appropriate to achieve a normal distribution.

172

173 Significant deviation from the expected 1:1 ratio of sex ratio was tested using Chi-square test. Visual

174 assessment of the gonadal maturity stage (G) (table 1) was used to determine a binary factor of functional

175 maturity (immature or mature; see Table 1). Similarly, a binary factor indicating maturity in male data

176 was also calculated using a penis-length index (PL_i), whereby if the ratio of penis length:total shell length

177 is ≥ 0.5, the individual was considered behaviourally mature (PL_{50}) ((Koie, 1969; Fahy et al., 2005).

178

179 Size-at-maturity estimates, the size at which 50% of the population is mature according to either G or

180 PL_i, were made using the logistic regression model (Roa et al., 1999) reformulated by (Walker, 2005) to

181 give:

182

183   $$P_i = \left\{ 1 + e^{-\ln(19)\frac{TSL_i - TSL_{50}}{TSL_{95} - TSL_{50}}} \right\}^{-1}$$

184

185   where P_i is the proportion of the population that is mature at a given size, TSL_{50} and TSL_{95} refer to the

186   lengths at which 50% and 95% of the population are mature respectively. Model parameters were

187   estimated using generalized linear model with logit link function and a binomial error structure.

188   Confidence intervals were assessed by bootstrapping the model (1000 runs). The base R code for plotting

189   the maturity ogives was constructed by Harry (2013) and has been adopted by Haig et al. (2015) and

190   Hollyman (2017). The maturity estimates for both TSL_{50} and PL_{50} are considered for temporal and spatial

191   variation.

192

193   To investigate whether TSL was the only factor that had a significant effect on L_{50} estimates, data were

194   analysed using generalised additive models (GAMs) in R. Modelling was conducted with the package

195   'mgcv' (Wood, 2017). Models were fitted using a binomial error distribution and a logit link function.

196   Modelling attempted to employ a backward selection, reducing the complexity (number of parametric

197   terms) by comparing AIC values (a model with an AIC value two points lower than a comparable model

198   was preferred).

199

200   The PL_{50} estimates for a male population, by way of further validation, is considered against an iterative

201   search procedure on the relationship between TSL and PL, whereby PL is modelled against TSL using

202   piecewise regression. The model examines the linear morphological relationship (PL:TSL) and searches

203   for significant deviation from the linear model, indicating maturation (an increase in PL_i). The method

204   searches each potential inflection (c) within a predetermined range until it has found the point at which

205   the total residual mean standard error is minimised (Crawley, 2007). The model is described by the

206   following equation:

207

208   $$y_i = \left\{ \begin{array}{l} \beta_0 + \beta_1 CW_i < c \\ \beta_2 + \beta_3 CW_i \geq c \end{array} \right\}$$

209

210   where y_i is the TSL of individual i, c is a breakpoint (inflection) between linear relationships applying

211   above and below the value of TSL equal to c, and the parameter β parameters are the intercepts and slopes

212   of the two linear relationships.

213

214   Temporal spatial variation in aGSI were displayed visually using the 'ggplot2' package in R and

215   investigated using univariate techniques analyses of variance and covariance. Post-hoc analysis consisted

216   of Tukey HSD tests with visual display of temporal-spatial trends using boxplots. Similarly, frequency

217   histograms are used to display size-frequency data, which were used to make inferences on general

218   population structure. Variation in population structure (TSL distribution) over time and space was

219   investigated using the non-parametric Mann-Whitney U test or, if exploration revealed data to be

220   normally distributed, t-test was employed for comparisons.

221

222   Depth data was assigned to each pot-sample using a high-resolution bathymetry layer (1 m^2) downloaded

223   from EMODnet (EMODnet Bathymetry Consortium, 2017) . Since the possibility that whelk feed on

224   small infaunal animals cannot be excluded (Himmelman & Hamel, 1993), TSL and aGSI data were

225   plotted against estimates of benthic infaunal biomass (g m^{-2} of wet mass; g WM m^{-2}), modelled by

226   (Whiteley, 2013, p. 103), to observe any effect of benthic ecology on population structures and

227   reproductive biology.

228

229   Due to the time and resource constraints on the present study, age-analysis of the statoliths (as described

230   in Hollyman, 2017 and Hollyman et al., 2017) were not possible; however, the biological material for

231   this analysis has been retained and will be investigated in the future. Therefore, when frequency

232   histograms showed multi-modal distributions, length-frequency analysis within the mixed distribution

233   was investigated as a proxy for size-at-age analysis. Using the R packages 'MIXTOOLS v1.0.3' (Young

234   et al., 2017) and 'MIXDIST v0.5' (Macdonald & Du, 2012), the estimated mean and standard deviation

235   of the cohorts were calculated and exported to MS Excel. Within Excel, the data was modelled using the

236   LINEST function to estimate the coefficient values of the quadratic relationship along with the R^2 value.

237

238   **3.0 Results**

239

240   A total of 9,234 whelks were collected by fishers for the present study in ICES area VIIa with an average

241   sex ratio of 1.14:1 females to male, which was significantly different from the expected 1:1 ratio (χ^2 =

242   24.077, p < 0.001). The sex ratio varied temporally (Fig. 3).

243

244   <Figure 3>

245   *Figure 3*. The average sex-ratio (F:M) of whelk (*Buccinum undatum*) samples collected throughout the
246   study period ± standard deviation. The red dotted line represents the expected ratio of 1:1.
247

248   The sample size varied both temporally and spatially due to the fisheries dependent nature of the study

249   (see table 2), thereby restricting the number of statistical comparisons available. A total of 3,290

250   individuals were selected as subsamples and underwent dissection. Gonadal assessment ($\%_{GONAD}$) was

251   successfully recorded for 2,451.

252

253   <Table 2>

254

255   Linear regression on log transformed data revealed a significant relationship between total weight and

256   total shell length (R^2 = 0.952, p < 0.001) described using the equation $W = aL^b$, where a = 2.6 x 10^{-4} and

257   b = 2.795. Further analysis showed that this relationship did not have a significant interaction with sex

258   but there was a significant interaction with country (ANOVA; $F_{1,169.2}$=25.382; p < 0.001) (Figure 4a)

259   with the average whelk sampled in Welsh waters attaining more weight per mm TSL.

260

261   <Table 3>

262

263   The size distribution of whelk sampled within the Isle of Man territorial sea was significantly larger than

264   that of Welsh waters (Mann-Whitney U Test; p < 0.001), with the mean average being 77.7 ± 15.9 mm

265   TSL and 72.0 ± 18.1 mm respectively. TSL data for male and female whelk were not significantly

266   different in Wales, but were in the Isle of Man (Mann-Whitney U Test; p < 0.001). Significant spatial

267   variation was observed in the length distribution (TSL) of whelks throughout sampled areas in ICES

268   Area VIIa (ANOVA; $F_{9,\ 8687}$ = 266.3, *p* < 0.001; Figure 4d). Post-hoc Tukey HSD testing revealed

269   significant differences (p < 0.05) in the TSL distribution did not occur between all areas, as indicated by

270   the lettering in figure 4d.

271

272   <Figure 4>

273   *Figure 4*. a) The total shell length (TSL; mm) by total wet weight (g) relationship for whelk, *Buccinum*
274   *undatum*, in the Irish Sea (ICES Area VIIa). 4b & 4c) Length frequency histograms of the total shell
275   length distribution for whelks from Wales (4a) and Isle of Man (4b) in temporally pooled data, with
276   percentages above indicating the relative density of each 10 mm bin. The vertical (4b, 4c) and horizontal
277   (4d) red lines represent the current minimum landing size in each fishery jurisdiction. Figure 4d shows
278   the temporally aggregated TSL data for each survey area, displayed as boxplots. The letters above 4d
279   indicate a significant difference (p<0.05), whereby matching letters indicate no significant difference.
280   The white and grey boxplots represent Welsh and Isle of Man samples respectively.
281

282   Generalized linear models with a binomial distribution were applied to the aggregated dataset, which

283   includes all sampling events throughout the study, to produce a maximum likelihood estimate of

284   functional maturity (TSL_{50}) for the female (A), male (B) and combined sex (C; "Combined") populations

285   in the Irish Sea (Fig. 5).

286

287   <Figure 5>

288   *Figure 5*. Maturity ogives showing the functional maturity estimates of whelk (*Buccinum undatum*)
289   populations sampled in ICES Area VIIa during the study period. Three separate models were applied to
290   female, male and combined sex data. The hashed lines represent the 95% confidence intervals of the
291   model.
292

293   The narrow 95% intervals suggest a high level of confidence in the models applied to aggregated data,

294   which showed TSL to be a highly significant explanatory variable for maturity (p < 0.001 in all three

295   models). The smallest observed mature animal was observed at a size of 43 mm in Fishguard (West

296   Wales).

297

298   Environmental or seasonal variables that might influence the proportion of mature whelk were considered

299   further within general additive models, which were reduced in complexity according to a backward

300   selection. The simplest model was able to explain 44.3% of the deviance (adjusted-R^2 = 0.497) in the

301   data (AIC value =1894), described as;

302

303   $Maturity \sim TSL + Area + Month + Sex + s(Depth)$

304   Model 1

305   The modeled parametric coefficients are summarised in table 4. Note that "s" denotes an isotropic

306   smoother applied to depth data (s(Depth); edf=1.193, χ^2 = 1.362, p = 0.491).

307

308   <Table 4>

309

310   The results from the GAM showed that the most significant terms to influence the binary response

311   variable 'mature', were size, month, area and sex. In agreement with previous studies, size-at-maturity

312   estimates are therefore modelled using the GLM approach separately for males and females on a finer

313   temporal-spatial scale.

314

315   Considering that the month in which the sample is acquired has a significant effect on the response

316   variable 'mature', a rationale is required for determining the time-period during which data should be

317   modelled to estimate L_{50}. The objective is to minimise false classifications of an individual animals

318   maturity stage (Table 1). Gonadal state is most visibly clear during a time period when ovaries and testes

319   of mature animals are full, after having fully recovered from previous spawning. This period can be

320   determined by analysis of the variation in gonadosomatic index.

321

322   Analysis of covariance found that the pattern in adjusted-GSI (aGSI) varied significantly amongst mature

323   whelks, explained by sex ($F_{1,7081}=452.8$, $p < 0.001$), month ($F_{11,3525}=20.5$, $p < 0.001$) and area

324   ($F_{9,2646}=18.8$, $p=0.001$), with significant interactions also between month and area ($F_{37,1946}=3.36$, $p <$

325   0.001), month and sex ($F_{11,1148}=6.67$, $p < 0.001$) as well as area and sex ($F_{9,400}=1.02$, $p =0.002$). The

326   aGSI pattern for male and female populations samples, aggregated by month and country (Isle of Man

327   and Wales) are visually displayed in figure 6.

328

329   <Figure 6>

330   *Figure 6*. Boxplots showing the median average, IQ-range and 95% CIs of aGSI: A) mature male and
331   female populations of whelk (*Buccinum undatum*) sampled in Welsh waters and B) the Isle of Man
332   territorial sea by month. C) boxplot showing aGSI in each seasons (aggregated data) and D) aGSI of
333   whelk assigned to each maturity stage (table 1). Dots indicate outliers.
334

335   Mature female whelk sampled within the Isle of Man territorial sea show a distinct reproductive cycle,

336   with peak aGSI during July to September (Fig 6b). Welsh data within ICES VIIa reveales that whelk had

337   a greater temporal range of peak aGSI, spanning from June until November (Fig 6a) with much greater

338   variation.

339

340   Estimated aGSI varied significantly according to season (Fig 6c) (ANOVA; $F_{3,2996}$=23.91, $p < 0.001$),

341   with significant differences occurring between all seasons aside from between winter (December –

342   February) and spring (March – May) (Tukey *post hoc*, $p_{adj} < 0.001$) and peaking during summer (June -

343   August). Similarly, aGSI varied significantly between maturity stages (6d) (ANOVA; $F_{4,40587}$=487.7, p

344   < 0.001), with significant differences occurring between all maturity stages (Tukey *post hoc*, $p_{adj} < 0.001$)

345   with the exception of between '5; recovering' and '3; ripe' (Tukey *post hoc*, $p_{adj} = 0.99$) and '5;

346   recovering' and '4; spent' (Tukey *post hoc*, $p_{adj} = 0.32$), with 'ripe' whelk having the greatest average

347   aGSI value.

348

349   Considering the analysis above, the most appropriate subset with which to conduct spatial comparisons

350   of functional maturity L_{50} is during summer and autumn (Fig 6a, 6b) prior to the spawning season, which

351   is characterised by a low aGSI value. Again employing a GLM approach, L_{50} is calculated for male and

352   female whelk within each area, with data aggregated throughout the peak aGSI period. The results of the

353   analysis, together with the sample size are presented in table 5.

354

355   \<Table 5\>

356

357   Penis length was also assessed in order to estimate size at maturity using temporally aggregated data.

358   Logistic regression analysis estimated that the size at behavioural maturity for males (PL_{50}) for whelk in

359   Welsh waters is at a size TSL = 78 mm; however, iterative searches observed an 'inflection' in the

360   PL:TSL relationship at a size TSL = 68 mm. Similarly, for data aggregated from samples within the Isle

361   of Man, PL_{50} is estimated at a size 81mm, whereas an inflection in the PL:TSL relationship is observed

362   in the same data at a size TSL = 77. In both sets of data, an allometric change in the penis is observed

363   before PL_{50} is observed.

364

365   Neither the reproductive output (aGSI; Fig7a), nor size (TSL distribution; Fig 7b), showed a clear trend

366   with modelled benthic infaunal biomass. Nonetheless, statistical testing revealed a significant difference

367   in the size distribution (TSL; ANOVA, $F_{6,6838} = 53.17$, $p < 0.001$) and reproductive output (aGSI;

368   ANOVA, $F_{6,1552} = 575.2$, $p < 0.001$) of whelk in areas of varying benthic infaunal biomass. Post-hoc

369 Tukey HSD tests, indicated by the letter-text in Fig 7, highlight that although differences are observed

370 between group, there is no clear correlative pattern. Note that dissected whelk from areas with a benthic

371 infaunal biomass > 300 g WM m^{-2} did show an aGSI value approximately 100% greater than elsewhere;

372 however, a low sample size (n = 19) limits the confidence in the statistical result (Fig 7a; D*). In contrast,

373 depth (analysed here as a categorical variable), appears to have a negative relationship with both

374 reproductive output (aGSI) and average size (TSL). Average ovary weight (ANOVA; $F_{5,1743}$ = 16.15, p

375 < 0.001) and average size (ANOVA; $F_{5,8346}$ = 64.86, p < 0.001) varies significantly between depth

376 categories. Post-hoc Tukey HSD tests show that significant differences are generally observed between

377 groups with increasing depth (Figure 7c and 7d).

378

379 <Figure 7>

380 *Figure 7*. Reproductive output (aGSI %) and population structure (TSL; mm) displayed as boxplots
381 plotted across two grouped environmental parameters; Benthic infaunal biomass (g WM m^{-2}) and depth
382 (m). The letters indicate where post-hoc testing revealed significant differences in data, whereby
383 matching letters indicate no statistically significant differences between data.
384

385 A sample, from within the NORTH survey area in March 2016 (n = 427), showed a multi-modal

386 distribution (Hartigan's dip test for uni-modality; $D_{12.37}$ = 0.014, *p*-value = 0.83 [alternative hypothesis

387 accepted, i.e at least bimodal]) with between five and seven modal intervals (cohorts). Using a mixed-

388 population cohort analysis, summary statistics (mean and standard deviation) estimates for individual

389 cohorts may be indicative of the population size-at-age relationship (Fig. 8). The estimates suggest that

390 whelk in this area initially grow approximately 15 mm yr^{-1} with the rate of growth decreasing with age.

391 In the fifth year of growth, whelk reach the MLS (70 mm TSL). Since the sample was collected in March,

392 it is also assumed that individuals have undergone a full annual growth period since initial spawning (age

393 0).

394

395 <Figure 8>

396 *Figure 8.* a) A probability density histogram showing the multi-modal TSL distribution of whelk within
397 a single pot sample (NORTH-March 2016). The green lines show the probability function of the mixed
398 data and the red lines show the modelled distribution of each estimated modal interval. The red arrows
399 on the x-axis represent the mean value of the modal intervals; b) a scatter plot showing the estimated
400 size-at-age relationship modelled using the results of the multi-modal analysis. The points represent the
401 average value of each modal interval (red arrows in fig 8a) ± standard deviation. The quadratic term and
402 R^2 value are shown.
403

404 **4.0 Discussion**

405   The whelk fishery in the Irish Sea (ICES Area VIIa) has recently undergone significant expansion both

406   in terms of landings and effort (MMO, 2017), with landings increasing from 2,900 t yr^{-1} to over 6,700 t

407   yr^{-1} (+227%) between 2011 and 2016, with a similar trend observed globally (FAO, 2017). Our results

408   suggest that, with the exception of one site to the north of the Isle of Man, there is a risk of recruitment

409   overfishing as the average whelk recruits into the fishery (at 45 mm in Wales and 70 mm TSL in the Isle

410   of Man) before they have an opportunity to spawn. It is possible that fishing under the size at maturity

411   may already have resulted in recruitment overfishing in principal fishing grounds in the Irish Sea. This

412   may culminate in long-term stock depletion in a fishery that is increasingly valuable to coastal and island

413   economies in the Irish Sea (DEFA, 2017).

414

415   Routine stock assessments are absent throughout the vast majority of the whelk fishery distribution, with

416   the exception of the States of Jersey, which began annual data collection in 1996 using baited-pots (Morel

417   & Bossy, 2004; Shrives et al., 2015) and the inshore waters of Québec, where commercial fishery

418   performance indicators (catch per unit effort; CPUE) are assessed every three years (Brulotte, 2015).

419   There are methodological challenges in using capture data from baited-pots to estimate absolute or

420   relative population densities (Borsetti et al., 2018), considering the unknown effects of highly variable

421   environmental parameters such as tidal strength, season, bait-type and soak-time as well as the inherent

422   sex-specific or size-specific selectivity of whelk pots (McQuinn et al., 1988). An improved sampling

423   method may be to use dredge-based surveys. In a similar study, Borsetti et al. (2018) used a dredge-

424   based survey methodology, whilst acknowleding that gear-specific efficiency studies for dredges may

425   facilitate absolute abundance assessments in the future. However, in the absence of accepted methods to

426   conduct annual stock assessments, the sustainable prosecution of the whelk resources in the Irish Sea is

427   difficult to manage. Fisheries managers in the region now seek to manage whelk fishing with robust

428   evidence (DEFA, 2017; Welsh Government, 2017) and transition towards routine assessments of stock

429   health. The results presented in this paper detail important population parameters, such as size-at-

430   maturity, size-at-age and length~weight relationships ($W=aL^b$), which are essential components of

431   biomass estimates in several stock-assessment techniques. Moreover, the variation within national waters

432   (see table 3 and table 5) may also need to be considered if future stock assessments are attempted at a

433   finer spatial scale, which has been the advice from other studies (Shelmerdine et al., 2007).

434

435   The sex-ratio was significantly different to the expected 1:1 ratio, indicating that the catch efficiency of

436   static-gear is higher for females. This is particularly evident during late winter and spring, when females

437   are recovering from egg-laying and are likely to be attracted to baited pots to feed after spawning in order

438   to replenish energy reserves. Similar patterns were observed in data collected elsewhere in the region

439   (Hollyman P. R., 2017a, p. 40). The consistent removal of a higher proportion of females may result in

440   sex overfishing under a sustained level of heavy fishing pressure, which has been shown for other species

441   targeted by static-gear fisheries in the region (Emmerson et al., 2017). In order to protect spawning stock

442   biomass, the sex-dependent selectivity of gear, as well as the underlying biological and environmental

443   drivers, should be carefully considered in a management strategy that may include temporal fishery

444   closures (Hollyman, 2017, p. 294). The results from models presented here highlight that size-at-maturity

445   (L_{50}) and the reproductive cycle of whelks are vital elements of evidence for fisheries managers that wish

446   to initiate appropriate management measures to protect spawning biomass, such as MLS and temporal

447   closures to protect spawning.

448

449   The length frequency distribution shows significant spatial variation between country and between intra-

450   national fishing grounds. This is also important to policy-makers that need to consider the spatially

451   variable economic impact of a legislative change in MLS. Apart from a correlation between average

452   whelk size and water depth, other important environmental and ecological drivers remain poorly

453   understood for the species such as habitat type, sea bottom temperature and salinity. Benthic infauna

454   biomass, the foundation of the benthic food-web, was hypothesised to influence the mean size of whelk,

455   though no correlative relationship with TSL distribution was observed in the data. It remains possible

456   that benthic infauna biomass correlates with whelk population density, though further investigation is

457   needed to test this hypothesis. The indication that smaller whelk, with lower aGSI values (i.e. lower

458   relative weight of ovaries to total body weight), were caught in deeper waters suggests that there could

459   be habitat partitioning of life history stages driven by biological (food availability and reproductive

460   needs) and environmental (sea-bottom temperature and substrate type) preferences.

461

462   Increased temporal monitoring of population structure should reveal how whelks respond to both

463   environmental and anthropogenic factors, such as climate change as well as direct and indirect fishing

464   mortality. The population structure of whelk in the inshore grounds to the east of Douglas exhibit a

465 similar size range (TSL) to that reported by Kideys (1991), suggesting that the levels of fishing

466 experienced in recent years may not have impacted length frequency. This is notwithstanding the increase

467 in fishing effort in other sectors of the industry, which may have either positive or negative, direct or

468 indirect impacts on whelk populations. Within the Isle of Man territorial sea, the principal whelk grounds

469 are subject to heavy fishing pressure from scallop trawling (Shepperson et al., 2014). Bottom-towed, or

470 trawling gear, is known to impact other commercially fished species; for example, egg-bearing female

471 brown crabs are regularly caught as bycatch in the Isle of Man scallop gear (Ondes et al., 2016).

472 Conversely, trawling indirectly influences common whelk populations by providing additional food

473 resources in the form of damaged bivalves, echinoderms, and crustaceans following trawling disturbance

474 (Ramsey et al., 1998). The scavenging opportunities created by benthic disturbance may be a significant

475 energetic input for whelk populations considering the results presented in this study, that benthic infauna

476 biomass shows no clear correlation to whelk population parameters. Understanding this interaction would

477 be a positive step towards ecosystem-based management, a process which would require mapping of

478 commercial effort in order to quantify the cumulative impacts of indirect and direct interactions between

479 fisheries (Murray et al., 2008).

480

481 The analysis presented in this paper exhibits progress towards understanding the reproductive cycle of

482 whelk populations in the Irish Sea and, importantly, provides clear rationale for routine assessment of

483 maturity in this region and elsewhere. The methodology discussed, that maturity analysis should be

484 conducted during peak-aGSI, is in agreement with other recent work (Hollyman, 2017, p. 287). McIntyre

485 et al. (2015) attempted to minimize seasonal variability in their analysis of SOM in various English

486 locations by collecting samples during January – May. However, under the assumption that whelk

487 populations in the English Channel and North Sea also spawn in late winter, McIntyre et al. (2015) likely

488 overestimated L_{50} due to low aGSI values in the sampled whelk. Martel et al., (1986b) calculated GSI

489 values with eviscerated weight (total meat weight minus the weight of the testis, digestive gland and

490 seminal vesicle for males, and the total weight minus the weight of the ovary, digestive glans and pallial

491 oviduct for females) used as the denominator, in contrast to this study which used total meat weight.

492 Arguably, eviscerated weight would provide a more accurate GSI as the weight of reproductive organs

493 vary temporally. However, as Welsh data did not include eviscerated weight and in order to conduct a

494 regional comparison in the Irish Sea, the same methodology was adopted for Manx samples. This

495   demonstrates the need for the adoption of a standard assessment protocol to enable comparisons between

496   different studies, in different regions and in different countries. This will become increasingly important

497   to understand the broader scale impacts of increasing fishing pressure as well as climate change and

498   ocean warming. Sea surface temperature data strongly suggests that seasonal onset of maturity, as

499   indicated by an increase in aGSI values within a population (indicating the development and ripening of

500   gonadal organs) being linked to local temperature regimes. Historical sea-surface temperature (SST) data

501   for the Irish Sea region highlights a potential correlative relationship, considering that SST peaks in the

502   Isle of Man during July, August and September (exceeding 13 ℃), whereas peak SST from Welsh waters

503   shows a more prolonged temporal period within which temperature data exceeding 13 ℃, observed from

504   June until November (CEFAS, 2017). However, a greater temporal data-set of aGSI is necessary to

505   understand whether temperature may have a causative effect on aGSI observations. Benthic temperatures

506   would provide a more comprehensive picture, particularly if the water column is highly stratified. The

507   temporal patterns observed show that ovaries are most full during July to September in the Isle of Man,

508   which was also observed by Kideys (1991), and from June to November in Welsh samples.

509

510   Growth was assessed using mixed-modality analysis of length-based data. Identifying growth parameters

511   using direct observations made in laboratory or by investigating statolith ring analysis was outside the

512   scope of this study, although samples have been retained for analysis using the methods developed by

513   Hollyman et al. (2017). Nonetheless, the size-at-age model presented here provides some preliminary

514   detail on growth, which is an important consideration when interpreting L_{50} values, as well as potentially

515   modelling recovery rates of depleted populations and formulating advice for temporal datasets in size-

516   at-maturity. It is recommended that size-at-maturity estimates are repeated over a period of time relevant

517   to the life-history of a species (EU, 2010). In this case, the advice is to perform biennial assessments of

518   size-at-maturity and model the change in the mean average L_{50} of the current and previous assessment

519   (i.e a moving four-year average, a time-period which approximates to age of the average whelk beginning

520   to develop reproductive organs) (ICES, 2008). This method helps alleviate sampling variability,

521   maturity-stage uncertainty and significant changes in fishing practices; however, it may also mask

522   genuine changes in population parameters caused by environmental or anthropogenic factors (ICES,

523   2008). Acknowledging high spatio-temporal variability is especially pertinent for whelk, considering

524   current fishing pressure on brood stock, restricted movement of populations and changing temperature

525   regimes due to climate change.

526

527   When fitting a logistic curve to the maturity data, it does not always follow that output value (L_{50}) should

528   be the recommended MLS. It is important to account for additional information when available, such

529   seasonality and frequency of spawning events (including skipped spawning events as in gadoid species)

530   as well as fecundity-at-size estimates and eggs-per-recruit models (ICES, 2008). In the case of whelk in

531   the Irish Sea, the appropriate time for maturity assessment (i.e. peak-aGSI, when reproductive organs

532   exhibit the clearest distinction between mature and immature) is between June and September. However,

533   our results suggest that egg-laying occurs in late winter, during which time the assessed population is

534   expected to have grown beyond the L_{50} estimate. During that period in the Irish Sea, our data indicates

535   that a whelk may have increased TSL by 5-7 mm. For example, the logistic model applied to the

536   population sampled "North" of the Isle of Man in this study produced an L_{50} estimate of 67 mm TSL.

537   The size-at-age model (shown in figure 8b) estimates an individual is 4.5 years at that size. With an

538   additional 6 months growth until spawning, at age 5, that individual is estimated to be at a size 74 mm

539   TSL. It is therefore vital that growth is understood for this species on a regional basis, as L_{50} values are

540   likely to require a correction factor before being presented as evidence to inform MLS regulations.

541

542   **5.0 Conclusion**

543   This study provides the most comprehensive scientific evidence to date with which to manage and

544   conserve the common whelk resources within ICES Area VIIa. Additionally, we propose a clear rationale

545   for undertaking routine assessments biennially for size-at-maturity, which are biologically-referenced to

546   the time at which aGSI is at a peak in the population and visual classification of gonads is most accurate.

547   The evidence presented here suggests whelk are subject to fishing mortality before they have the

548   opportunity to lay eggs for the first time with the existing MLS regulations. Although no data is available

549   to indicate that populations are recruitment overfished, current understanding of whelk biology suggests

550   that a precautionary approach should be adopted in order to conserve resources in the light of this

551   additional evidence.

552

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564

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699

700

701   <Table 1>

702

703   **Table 1.** The maturity-stage classifications of whelk (*Buccinum* undatum) as determined from visual
704   inspection of the reproductive organs.
705

	Stage	Description	Mature
1	Immature	Gonad non-differentiated from digestive whorl. Penis < 25 mm. VD not visible.	0
2	Developing	Gonad beginning to differentiate on anterior edge of whorl but is thin. Penis likely < 25 mm. VD may be visible.	1
3	Mature (ripe)	Ovary is fully differentiated from digestive whorl and full (3/4 of whorl volume). Penis > 25 mm and VD visible.	1
4	Mature (spent)	Ovary is fully differentiated from digestive whorl but flaccid (occupying ¼ of whorl volume). Penis fully developed and VD visible.	1
5	Mature (recovering)	Ovary is fully differentiated from digestive whorl, typically occupying > 1.2 whorl volume. Penis fully developed and VD visible.	1

706

707

708   <Table 2>

709   **Table 2.** The total number of whelks (*Buccinum undatum*) sampled via fisheries-dependent methods
710   (caught with scientific pots on commercial strings) in each month for all locations throughout the study
711   period (2013-2016). Italicised numbers represent data from Haig et al. (2015).

712

Area-code	Winter		Spring			Summer			Autumn			Winter
	J	F	M	A	M	J	J	A	S	O	N	D
2013												
ANGLESEY	-	-	-	-	91	-	87	-	68	152	212	-
LLYN	-	-	-	257	365	182	168	-	53	128	38	-
FISHGUARD	-	-	-	66	140	158	183	-	75	64	-	-
2014												
ANGLESEY	-	57	-	-	112	-	-	-	-	-	-	-
LLYN	-	-	-	69	332	-	-	-	-	-	-	-
FISHGUARD	-	88	27	-	-	-	-	-	-	-	-	-
RAMSEY	-	-	-	-	-	-	-	15	-	-	-	-
2015												
SOUTH	-	-	-	46	63	79	-	34	-	-	-	-
SOUTHEAST	-	-	42	-	-	-	-	-	79	-	-	-
EAST	22	50	-	-	-	-	-	-	-	45	-	-
2016												
SOUTHEAST	60	142	233	319	93	26	-	-	-	113	-	-
EAST	-	68	-	-	77	16	-	66	200	193	-	-
NORTHEAST	-	-	-	-	-	161	84	-	156	87	-	-
RAMSEY	-	-	-	175	57	-	-	-	-	-	-	-
NORTH	-	164	427	332	571	315	-	-	494	-	354	-
WEST	-	138	51	54	20	61	-	-	-	-	-	-

713

714

715

716   <Table 3>

717   **Table 3.** The estimated values of coefficients *a* and *b* for the Length~Weight relationship $W=aL^b$ for
718   whelk (*Buccinum undatum*) by area. The length weight relationship is applied to the current MLS in the
719   Isle of Man (70 mm TSL) to illustrate the variation.
720   <Table 3>

721

	Area	a	b	MLS_{IOM} (g)
WALES	ANG	8.616	2.900	40.7
	LLYN	7.152	2.562	41.9
	FSHGRD	8.365	2.831	39.0
ISLE OF MAN	SOUTH	8.775	2.909	35.9
	SOUTH-E	8.510	2.835	34.3
	EAST	8.120	2.750	35.3
	NORTH-E	9.457	3.056	34.1
	RAM	8.634	2.889	38.1
	NORTH	9.001	2.956	35.2
	WEST	8.762	2.919	38.2

722

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724   <Table 4>

725   **Table 4.** The estimated parameters, t-values, Std. Error and p-values for the preferred general additive
726   model describing the relationship between maturity as a binary factor (0,1; immature, mature) and
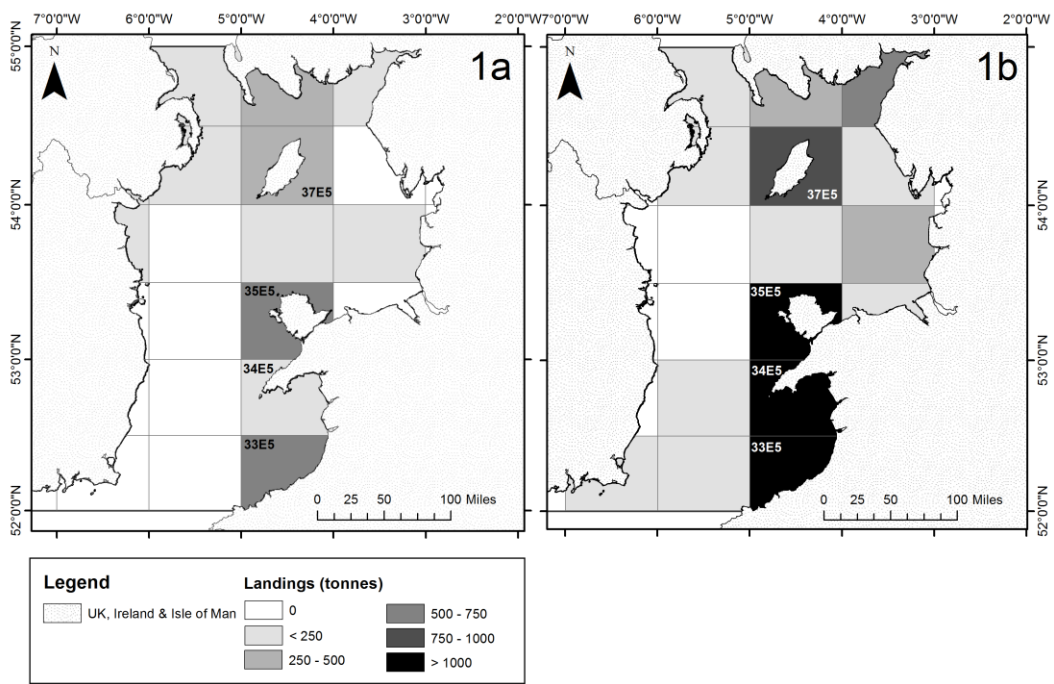727   explanatory variables. (Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '°', 0.1 '-').
728   <Table 4>

729

Parameters	Estimate	Std. Error	*t*-value	*p*-value
(Intercept)	-11.65	0.68	-17.21	< 0.001
TSL	0.17	0.01	24.43	< 0.001
Area-EAST	-1.01	0.33	-3.04	0.002
Area-FISHGUARD	-0.67	0.35	-1.95	0.051
Area-LLYN	-1.20	0.37	-3.23	0.001
Area-NORTH	-0.16	0.36	-0.45	0.651
Area-NORTHEAST	-1.29	0.39	-3.24	0.001
Area-RAMSEY	-0.79	0.52	-1.52	0.129
Area-SOUTH	-1.03	0.42	-2.44	0.015
Area-SOUTHEAST	-1.07	0.32	-3.33	< 0.001
Area-WEST	-2.73	0.40	-6.75	<0.001
FEB	1.06	0.35	2.99	0.003
MAR	0.60	0.36	1.66	0.097
APR	1.10	0.35	3.12	0.002
MAY	1.67	0.36	4.57	< 0.001
JUN	2.04	0.41	4.98	< 0.001
JUL	1.14	0.42	2.70	0.007
AUG	0.80	0.44	1.81	0.070
SEP	0.92	0.37	2.51	0.012
OCT	0.58	0.36	1.63	0.103
NOV	0.38	0.43	0.87	0.385
DEC	2.18	0.94	2.31	0.021
MALE	-0.34	0.12	-2.87	0.004

730
731

732   <Table 5>

733   **Table 5.** Functional maturity (L_{50}) estimates for male and female whelk (*Buccinum undatum*) by study
734   area within the Irish Sea (ICES Area VIIa) during the summer and autumn months (June to October).
735   Caution should be taken when considering samples with low sample size; *** = N too low to produce
736   an estimate, * = N sufficient to produce an estimate, but with low confidence.
737
738

	Area	Sex	L_{50} (mm)	N
WALES	ANGLESEY	♂	63.6	71
		♀	65.6	78
	LLYN	♂	71.8	80
		♀	71.3	86
	FISHGUARD	♂	62.5	102
		♀	65.5	89
ISLE OF MAN	SOUTH	♂	71.1 *	38
		♀	63.9 *	34
	SOUTH-E	♂	71.9	57
		♀	73.1	68
	EAST	♂	74.9	100
		♀	72.3	96
	NORTH-E	♂	75.0	145
		♀	71.6	132
	RAM	♂	NA***	5
		♀	NA***	5
	NORTH	♂	64.7	82
		♀	67.3	79
	WEST	♂	65.5 *	23
		♀	75.1 *	21

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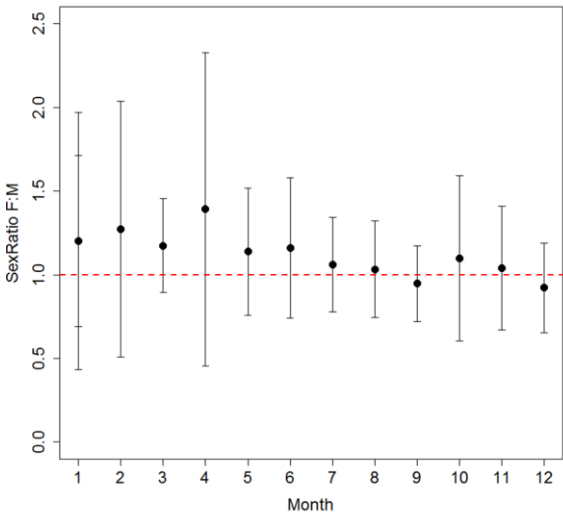
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742   Fig 1

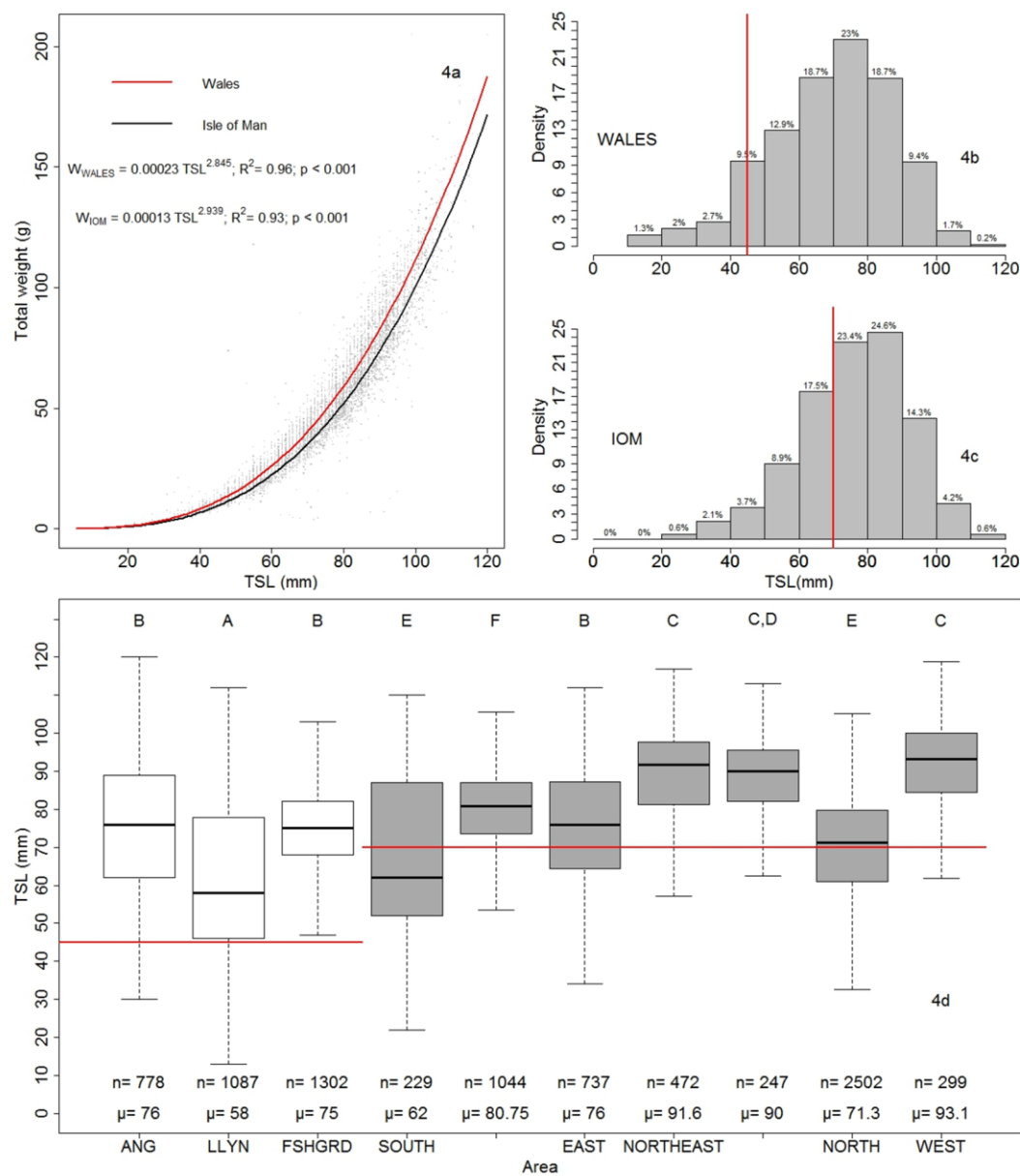743

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745   Fig 2
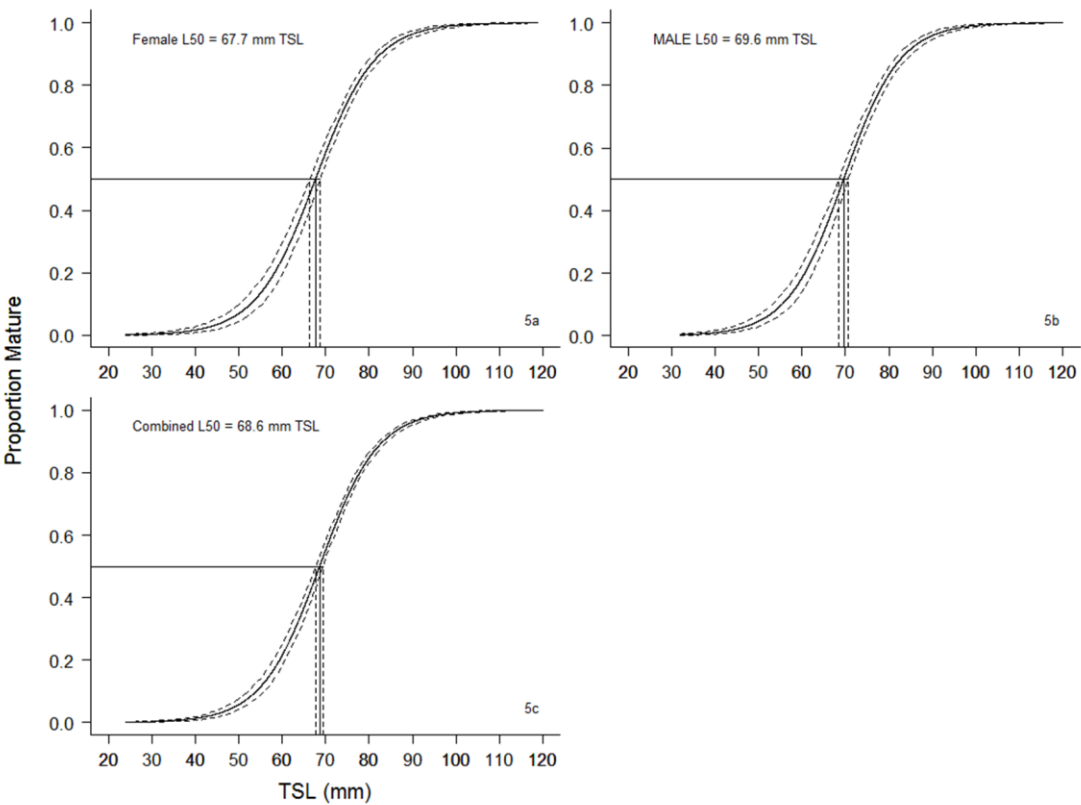

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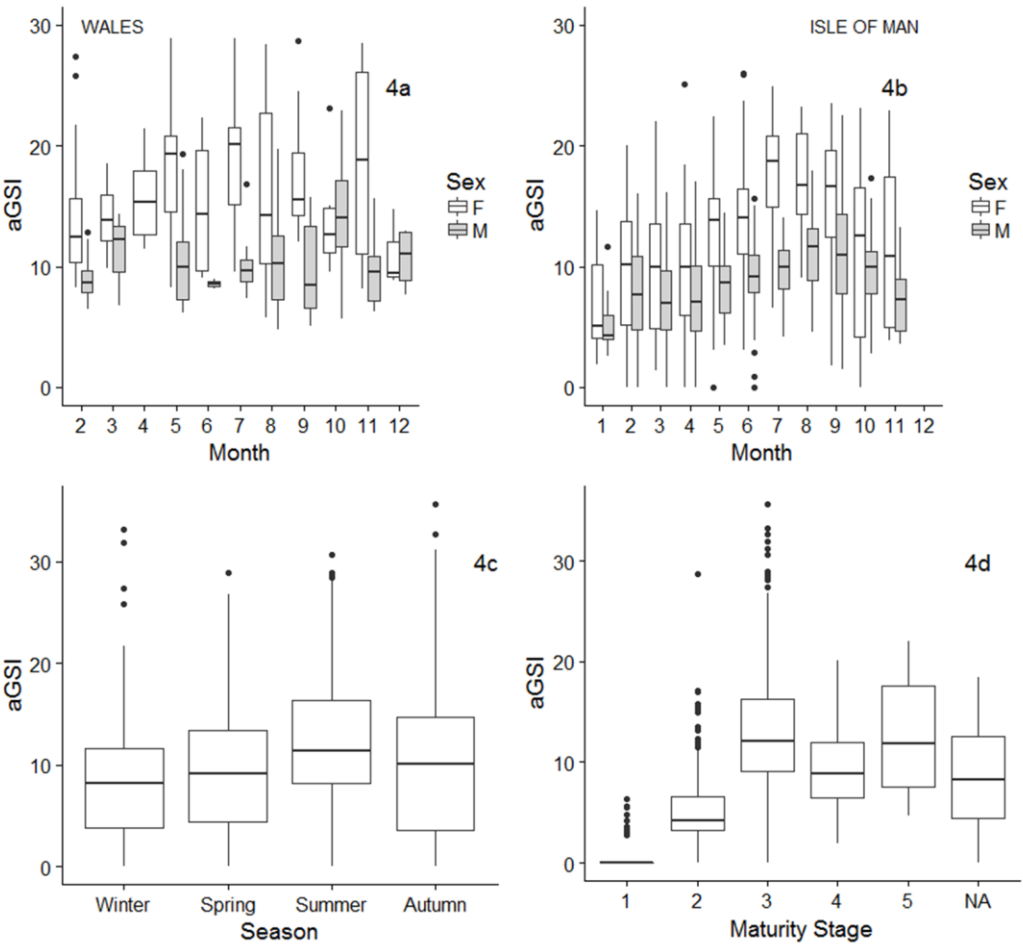
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748   Fig 3

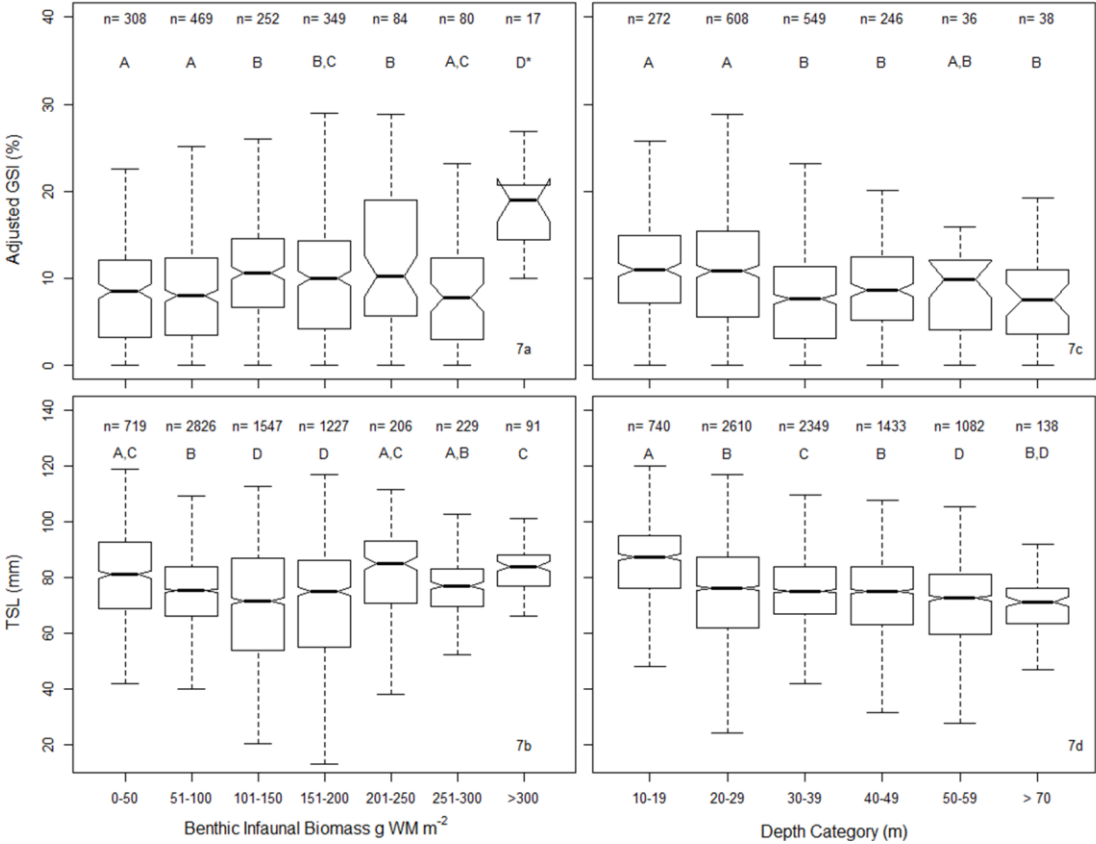749

750

751   Fig 4

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753

754   Fig 5

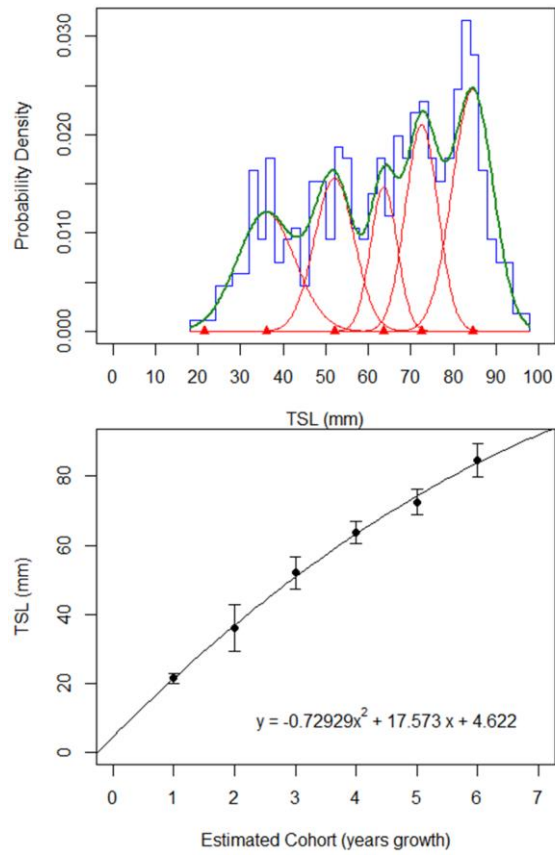755

756

757   Fig 6

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760   Fig 7

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763   Fig 8

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