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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Title:

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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Keywords: commercial fishery, size at maturity, mollusc, gastropod, reproduction, fisheries, management, gonadosomatic index.

Highlights

- Size-at-maturity (SOM) is estimated for a number of whelk populations in the Irish Sea.
- A rationale for a standard methodology for estimating SOM in *B. undatum* populations is presented.
- Environmental drivers of variable population demographics are investigated.

Abstract

The commercial fishery for common whelk (*Buccinum undatum* L.) has expanded significantly in the Irish Sea since 1990 and continues to grow, particularly in Welsh waters and the Isle of Man territorial sea, with landings throughout the region increasing by 227% between 2011 and 2016. Whilst whelk populations are known to be vulnerable to localised overexploitation due to inherent life-history parameters, fisheries remain relatively unrestricted by conservation measures in comparison to other

fisheries operating in the area. With the exception of the northernmost fishing ground between the Isle of Man and Scotland (Point of Ayre), the size-at-maturity (L_{50}) estimate for populations sampled during peak-aGSI (the months in which adjusted gonadosomatic index is highest) indicates that whelk are being fished before the time at first spawning throughout the study area. A correlation was detected between the size (total shell length) and depth, with smaller whelks found in deeper waters where there generally is greater fishing effort, although effort data is not available at a resolution to investigate this relationship quantitatively. No clear link between benthic infauna biomass and the average size (total shell length) or reproductive capacity (aGSI) of whelk sampled throughout ICES Area VIIa was found, indicating that the ecological energetics of whelk populations are more likely to be a function of scavenging opportunities than predation on benthic communities. A mixed cohort analysis utilized length-based data to infer a size-at-age relationship in the absence of direct age observations (e.g. statolith rings), with whelk recruiting into the Isle of Man fishery five years after hatching. The evidence presented in this study suggests that, prior to recommending a MLS that will adequately protect the spawning stock biomass, L_{50} values should be adjusted for pre-spawning growth between the ideal time of assessment (when aGSI values are at a peak) and the spawning season (when aGSI values decrease).

1.0 Introduction

The common whelk (*Buccinum undatum*, Linnaeus, 1758) is a neo-gastropod mollusc that is found in the subtidal waters of the North Atlantic to depths of 1200 m (Ager, 2008). It is widely distributed on the Atlantic continental shelf; from within the arctic circle (76° N) as far south as New Jersey, USA at the western-most extent (38° N) (Van Guelpen et al., 2005; Borsetti et al., 2018). Populations are most frequently observed in abundance in the northeast Atlantic, particularly in the waters of north-western Europe, from the Celtic and Irish Sea through to the Skagerrak and Kattegat Bay, including northern populations observed in Norwegian, Faroese and Icelandic waters (Ocean Biogeographic Information System, 2017).

Whelk are opportunistic scavengers that feed mainly on carrion (Nasution & Roberts, 2004) and detect feeding opportunities with a very acute chemo-sensory system (Himmelman, 1988). This allows whelks to be commercially exploited by fishers, who typically use specifically designed baited traps. Inshore whelk populations have been exploited by a mixed artisanal fishery in Europe since the early 20th century

(Dakin, 1912). Annual landings in England and Wales equated to 4500 t in 1911 (Dakin, 1912) and European waters remain the principal area of fishing effort (FAO, 2017). The fishery has undergone significant economic and geographical expansion in response to emerging Asian markets, with global landings increasing from 7,000 t yr^{-1} to over 35,000 t yr^{-1} between 1990 and 2014 (FAO, 2017). The effects of fishing mortality (*F*) on the phenotypic traits of *B. undatum* may be significant, especially considering the expansion in commercial exploitation (Kuparinen & Merilä, 2007). Whelk are now amongst the most economically important shellfisheries in the UK (Haig et al., 2015) with total UK landings (21,606 t) equating to a value of £21.7 million in 2016 (MMO, 2017). Regionally, the Irish Sea (ICES Area VIIa) has seen an estimated 227% increase in the total landed weight of whelk between 2011 and 2016 and is the source of approximately 10% of global landings for this species. The most substantial increases in recorded landings in the region are from within the Isle of Man territorial sea (ICES rectangle 37E5) and Welsh waters (ICES rectangles 33E5, 34E5, 35E5) (IFISH2, 2017; Figure 1).

<Figure 1>

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

Within ICES Area VIIa, management regimes are not consistent. Similar to many other jurisdictions in the UK, whelk fisheries within Welsh waters are managed solely by a minimum landing size (MLS = 45 mm Total shell length; TSL) established by the European Union (EU), which has been shown to be inadequate in several studies (Shelmerdine et al., 2015; Haig et al., 2015). However, Isle of Man fisheries are subject to a MLS of 70 mm TSL, informed by Kideys et al. (1993) and the fishery now includes a restricted number of species-specific licenses, each of which has effort (pot number) restrictions.

The phenotypic plasticity displayed by other marine gastropod populations can be closely related to mortality and growth rates (Stearns & Koella, 1986), which vary spatially and temporally with fishing pressure (Torrogolsa & Gimenez, 2010; Fahy et al., 1995). Whelks do not reach sexual maturity for several years, have limited dispersal potential (Martel et al., 1986a) and display little adult movement (Pálsson et al., 2014; Weetman et al., 2006). Therefore, populations are inherently vulnerable to high *F* and are particularly susceptible to recruitment overfishing (Shrives et al., 2015) and severe localised depletion (Nicholson & Evans, 1997). Environmental parameters have been shown to influence the biological characteristics of populations, with size-at-maturity being negatively correlated to bottom-temperature but positively correlated with depth (McIntyre et al., 2015; Haig et al., 2015). This is unsurprising given that the common whelk is a boreal species, although no clear latitudinal relationship has been observed (McIntyre et al., 2015) and local factors such as food availability and fishing presure are likely to have an influence in maturation and growth (Martel et al., 1986b).

There is presently little scientific evidence to suggest that the current MLS of 45 mm used as the baseline throughout the EU is an adequate fisheries threshold for sustainable exploitation. Shelmerdine et al. (2007) suggests that management measures should be considered on a regional basis after demonstrating significant differences in the biology of whelk populations sampled in Shetland and the south-coast of England. Haig et al., (2015) shows that the size at maturity (L_{50}) can vary considerably between populations over distances as small as 10 km (although application of management measures at this spatial scale are acknowledged to be impractical). Complications arrise when trying to compare research on size-at-maturity, as there is not currently a standard scientific methodology to determine this metric (Haig et al., 2015).

This study combines published data (Haig et al., 2015) from Welsh waters with data collected in the Isle of Man territorial sea. The aim was to compare spatial variation in size-at-maturity and also to determine reproductive response to spatial, temporal and environmental parameters.

2.0 Materials and methods

2.1 Field Materials (Fisheries Dependent Data)

Nine fishers, registered in Wales (3), England (1) and the Isle of Man (5), each fished two identical whelk pots once a month within the ICES area VIIa (Irish Sea). The fishers retained the entire pot contents, including undersized bycatch and non-target species. The pots supplied to fishers were 36 litre Fish-tec™ ‘WHELKER’ pots, described by fishers as being ‘stand-up’ pots due to their orientation (Haig et al., 2015). The pots are made of thick plastic and are weighted with lead. The drainage holes in the base of the pot measure 30 mm in diameter and the entrance to the pot is covered with a purse-pull mesh netting.

Fishers completed data-forms with details on the location (latitude and longitude), date, soak-time and bait used. Isle of Man (Manx) samples were collected for a period of 12 months beginning in January 2016, with samples also collected in a pilot study in the Isle of Man during 2015. The Manx samples were compared to Welsh data collected over a 14-month period beginning in April 2013 (Haig et al., 2015). The general locations of the samples are displayed by area code to maintain commercial confidentiality (see Figure 2). The pots were fished separately and attached to commercial fishing 'strings', which varied in length but typically anchor between 20 and 50 pots to the seabed along ropes 400–700 m in length. The pots were baited with a combination of dogfish (*Scyliorhinus canicula*) and edible crab carcass (*Cancer pagurus*) and were 'soaked' for 24–48 hours.

<Figure 2>

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

2.2 Laboratory Analysis

Pot samples were frozen after landing and later defrosted before laboratory dissections. The latitude and longitude were recorded and the sample was assigned to an area. All individuals were sexed (presence / absence of a penis), weighed (total wet weight; 0.001g) and measured (total shell length (TSL); 0.1 mm).

A randomly selected subsamples of 30 individuals were taken from each pot-sample and further analysed. The penis length (PL) was measured from the point of attachment to the body to the tip accounting for natural curvature. Maximum and minimum shell width was recorded as shown in Haig et al. (2015). Additionally, the subsamples were dissected and the animal was removed from the shell. The wet weight of the flesh was recorded (0.01 g). The posterior lobe of the digestive gland, which is partially covered by the gonad on the dorsal surface, was visually inspected and the degree of differentiation ($\%_{GONAD;}$ 0, 0.25, 0.5, 0.75, 1) between the two organs was used to assign one of five maturity stages shown in table 1 (Haig et al., 2015; Hollyman, 2017a)

<Table 1>

The digestive gland and gonad, which are encapsulated by the same membrane forming the integument, were dissected away at the area where the anterior edge of the digestive gland meets the renal gland and weighed. The gonadosomatic index (GSI) was calculated by expressing the weight of the removed whorl mass (gonad and digestive gland) as a percentage of the wet flesh weight:

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

Additionally, an adjusted gonadosomatic index (aGSI) was calculated by multiplying the above GSI value by the estimated proportion of the whorl occupied by the gonad gland (% gonad) in an attempt to focus analysis on reproductive patterns (as in Hollyman, 2017), where:

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

2.3 Statistical Analysis

All analysis was carried out in the statistical software programme R v 3.3.1 (R Core Team, 2014). Prior to statistical modelling, shell measurement and weight data were tested for normality (Kolmogorov-Smirnov test) and inspected visually using a Q-Q plot. Heteroscedasticity was tested using the Levene's test and Cook's distance plot was used to check for outliers. Transformations were applied to data where appropriate to achieve a normal distribution.

Significant deviation from the expected 1:1 ratio of sex ratio was tested using Chi-square test. Visual assessment of the gonadal maturity stage (*G*) (table 1) was used to determine a binary factor of functional maturity (immature or mature; see Table 1). Similarly, a binary factor indicating maturity in male data was also calculated using a penis-length index (PL_i), whereby if the ratio of penis length:total shell length is ≥ 0.5, the individual was considered behaviourally mature (PL_{50}) ((Koie, 1969; Fahy et al., 2005).

Size-at-maturity estimates, the size at which 50% of the population is mature according to either *G* or PL_i,, were made using the logistic regression model (Roa et al., 1999) reformulated by (Walker, 2005) to give:

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

where P_i is the proportion of the population that is mature at a given size, TSL_{50} and TSL_{95} refer to the lengths at which 50% and 95% of the population are mature respectively. Model parameters were estimated using generalized linear model with logit link function and a binomial error structure. Confidence intervals were assessed by bootstrapping the model (1000 runs). The base R code for plotting the maturity ogives was constructed by Harry (2013) and has been adopted by Haig et al. (2015) and Hollyman (2017). The maturity estimates for both TSL_{50} and PL_{50} are considered for temporal and spatial variation.

To investigate whether TSL was the only factor that had a significant effect on L_{50} estimates, data were analysed using generalised additive models (GAMs) in R. Modelling was conducted with the package 'mgcv' (Wood, 2017). Models were fitted using a binomial error distribution and a logit link function. Modelling attempted to employ a backward selection, reducing the complexity (number of parametric terms) by comparing AIC values (a model with an AIC value two points lower than a comparable model was preferred).

The PL_{50} estimates for a male population, by way of further validation, is considered against an iterative search procedure on the relationship between TSL and PL, whereby PL is modelled against TSL using piecewise regression. The model examines the linear morphological relationship (PL:TSL) and searches for significant deviation from the linear model, indicating maturation (an increase in PL_i). The method searches each potential inflection (c) within a predetermined range until it has found the point at which the total residual mean standard error is minimised (Crawley, 2007). The model is described by the following equation:

$$y_i = \left\{\frac{\beta_0 + \beta_1 CW_i < c}{\beta_2 + \beta_3 CW_i \geq c}\right\}$$

where y_i is the TSL of individual i, c is a breakpoint (inflection) between linear relationships applying above and below the value of TSL equal to c, and the parameter β parameters are the intercepts and slopes of the two linear relationships.

Temporal spatial variation in aGSI were displayed visually using the 'ggplot2' package in R and investigated using univariate techniques analyses of variance and covariance. Post-hoc analysis consisted of Tukey HSD tests with visual display of temporal-spatial trends using boxplots. Similarly, frequency histograms are used to display size-frequency data, which were used to make inferences on general population structure. Variation in population structure (TSL distribution) over time and space was investigated using the non-parametric Mann-Whitney U test or, if exploration revealed data to be normally distributed, *t*-test was employed for comparisons.

Depth data was assigned to each pot-sample using a high-resolution bathymetry layer (1 m^2) downloaded from EMODnet (EMODnet Bathymetry Consortium, 2017) . Since the possibility that whelk feed on small infaunal animals cannot be excluded (Himmelman & Hamel, 1993), TSL and aGSI data were plotted against estimates of benthic infaunal biomass (g m^{-2} of wet mass; g WM m^{-2}), modelled by (Whiteley, 2013, p. 103), to observe any effect of benthic ecology on population structures and reproductive biology.

Due to the time and resource constraints on the present study, age-analysis of the statoliths (as described in Hollyman, 2017 and Hollyman et al., 2017) were not possible; however, the biological material for this analysis has been retained and will be investigated in the future. Therefore, when frequency histograms showed multi-modal distributions, length-frequency analysis within the mixed distribution was investigated as a proxy for size-at-age analysis. Using the R packages 'MIXTOOLS v1.0.3' (Young et al., 2017) and 'MIXDIST v0.5' (Macdonald & Du, 2012), the estimated mean and standard deviation of the cohorts were calculated and exported to MS Excel. Within Excel, the data was modelled using the LINEST function to estimate the coefficient values of the quadratic relationship along with the R^2 value.

3.0 Results

A total of 9,234 whelks were collected by fishers for the present study in ICES area VIIa with an average sex ratio of 1.14:1 females to male, which was significantly different from the expected 1:1 ratio (χ^2 = 24.077, $p < 0.001$). The sex ratio varied temporally (Fig. 3).

<Figure 3>

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

The sample size varied both temporally and spatially due to the fisheries dependent nature of the study (see table 2), thereby restricting the number of statistical comparisons available. A total of 3,290 individuals were selected as subsamples and underwent dissection. Gonadal assessment ($\%_{GONAD}$) was successfully recorded for 2,451.

<Table 2>

Linear regression on log transformed data revealed a significant relationship between total weight and 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 b = 2.795. Further analysis showed that this relationship did not have a significant interaction with sex but there was a significant interaction with country (ANOVA; $F_{1,169.2}$=25.382; $p < 0.001$) (Figure 4a) with the average whelk sampled in Welsh waters attaining more weight per mm TSL.

<Table 3>

The size distribution of whelk sampled within the Isle of Man territorial sea was significantly larger than that of Welsh waters (Mann-Whitney U Test; $p < 0.001$), with the mean average being 77.7 ± 15.9 mm TSL and 72.0 ± 18.1 mm respectively. TSL data for male and female whelk were not significantly different in Wales, but were in the Isle of Man (Mann-Whitney U Test; $p < 0.001$). Significant spatial variation was observed in the length distribution (TSL) of whelks throughout sampled areas in ICES Area VIIa (ANOVA; $F_{9,\ 8687}$ = 266.3, $p < 0.001$; Figure 4d). Post-hoc Tukey HSD testing revealed significant differences ($p < 0.05$) in the TSL distribution did not occur between all areas, as indicated by the lettering in figure 4d.

<Figure 4>

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

Generalized linear models with a binomial distribution were applied to the aggregated dataset, which includes all sampling events throughout the study, to produce a maximum likelihood estimate of functional maturity (TSL_{50}) for the female (A), male (B) and combined sex (C; "Combined") populations in the Irish Sea (Fig. 5).

<Figure 5>

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

The narrow 95% intervals suggest a high level of confidence in the models applied to aggregated data, which showed TSL to be a highly significant explanatory variable for maturity ($p < 0.001$ in all three models). The smallest observed mature animal was observed at a size of 43 mm in Fishguard (West Wales).

Environmental or seasonal variables that might influence the proportion of mature whelk were considered further within general additive models, which were reduced in complexity according to a backward selection. The simplest model was able to explain 44.3% of the deviance (adjusted-$R^2 = 0.497$) in the data (AIC value =1894), described as;

$$Maturity \sim TSL + Area + Month + Sex + s(Depth) \qquad \text{Model 1}$$

The modeled parametric coefficients are summarised in table 4. Note that "s" denotes an isotropic smoother applied to depth data (s(Depth); edf=1.193, $\chi^2 = 1.362$, p = 0.491).

<Table 4>

The results from the GAM showed that the most significant terms to influence the binary response variable 'mature', were size, month, area and sex. In agreement with previous studies, size-at-maturity estimates are therefore modelled using the GLM approach separately for males and females on a finer temporal-spatial scale.

Considering that the month in which the sample is acquired has a significant effect on the response variable 'mature', a rationale is required for determining the time-period during which data should be modelled to estimate L_{50}. The objective is to minimise false classifications of an individual animals maturity stage (Table 1). Gonadal state is most visibly clear during a time period when ovaries and testes of mature animals are full, after having fully recovered from previous spawning. This period can be determined by analysis of the variation in gonadosomatic index.

Analysis of covariance found that the pattern in adjusted-GSI (aGSI) varied significantly amongst mature whelks, explained by sex ($F_{1,7081}$=452.8, p < 0.001), month ($F_{11,3525}$=20.5, p < 0.001) and area ($F_{9,2646}$=18.8, p=0.001), with significant interactions also between month and area ($F_{37,1946}$=3.36, p < 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 aGSI pattern for male and female populations samples, aggregated by month and country (Isle of Man and Wales) are visually displayed in figure 6.

<Figure 6>

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

Mature female whelk sampled within the Isle of Man territorial sea show a distinct reproductive cycle, with peak aGSI during July to September (Fig 6b). Welsh data within ICES VIIa reveales that whelk had a greater temporal range of peak aGSI, spanning from June until November (Fig 6a) with much greater variation.

Estimated aGSI varied significantly according to season (Fig 6c) (ANOVA; $F_{3,2996}$=23.91, p < 0.001), with significant differences occurring between all seasons aside from between winter (December – February) and spring (March – May) (Tukey *post hoc*, p_{adj} < 0.001) and peaking during summer (June - August). Similarly, aGSI varied significantly between maturity stages (6d) (ANOVA; $F_{4,40587}$=487.7, p < 0.001), with significant differences occurring between all maturity stages (Tukey *post hoc*, p_{adj} < 0.001) with the exception of between '5; recovering' and '3; ripe' (Tukey *post hoc*, p_{adj} = 0.99) and '5; recovering' and '4; spent' (Tukey *post hoc*, p_{adj} = 0.32), with 'ripe' whelk having the greatest average aGSI value.

Considering the analysis above, the most appropriate subset with which to conduct spatial comparisons of functional maturity L_{50} is during summer and autumn (Fig 6a, 6b) prior to the spawning season, which is characterised by a low aGSI value. Again employing a GLM approach, L_{50} is calculated for male and female whelk within each area, with data aggregated throughout the peak aGSI period. The results of the analysis, together with the sample size are presented in table 5.

<Table 5>

Penis length was also assessed in order to estimate size at maturity using temporally aggregated data. Logistic regression analysis estimated that the size at behavioural maturity for males (PL_{50}) for whelk in Welsh waters is at a size TSL = 78 mm; however, iterative searches observed an 'inflection' in the PL:TSL relationship at a size TSL = 68 mm. Similarly, for data aggregated from samples within the Isle of Man, PL_{50} is estimated at a size 81mm, whereas an inflection in the PL:TSL relationship is observed in the same data at a size TSL = 77. In both sets of data, an allometric change in the penis is observed before PL_{50} is observed.

Neither the reproductive output (aGSI; Fig7a), nor size (TSL distribution; Fig 7b), showed a clear trend with modelled benthic infaunal biomass. Nonetheless, statistical testing revealed a significant difference in the size distribution (TSL; ANOVA, $F_{6,6838}$ = 53.17, p < 0.001) and reproductive output (aGSI; ANOVA, $F_{6,1552}$ = 575.2, p < 0.001) of whelk in areas of varying benthic infaunal biomass. Post-hoc

Tukey HSD tests, indicated by the letter-text in Fig 7, highlight that although differences are observed between group, there is no clear correlative pattern. Note that dissected whelk from areas with a benthic infaunal biomass > 300 g WM m^{-2} did show an aGSI value approximately 100% greater than elsewhere; however, a low sample size (n = 19) limits the confidence in the statistical result (Fig 7a; D*). In contrast, depth (analysed here as a categorical variable), appears to have a negative relationship with both reproductive output (aGSI) and average size (TSL). Average ovary weight (ANOVA; $F_{5,1743} = 16.15$, $p < 0.001$) and average size (ANOVA; $F_{5,8346} = 64.86$, $p < 0.001$) varies significantly between depth categories. Post-hoc Tukey HSD tests show that significant differences are generally observed between groups with increasing depth (Figure 7c and 7d).

<Figure 7>

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

A sample, from within the NORTH survey area in March 2016 (n = 427), showed a multi-modal distribution (Hartigan's dip test for uni-modality; $D_{12.37} = 0.014$, *p*-value = 0.83 [alternative hypothesis accepted, i.e at least bimodal]) with between five and seven modal intervals (cohorts). Using a mixed-population cohort analysis, summary statistics (mean and standard deviation) estimates for individual cohorts may be indicative of the population size-at-age relationship (Fig. 8). The estimates suggest that whelk in this area initially grow approximately 15 mm yr^{-1} with the rate of growth decreasing with age. In the fifth year of growth, whelk reach the MLS (70 mm TSL). Since the sample was collected in March, it is also assumed that individuals have undergone a full annual growth period since initial spawning (age 0).

<Figure 8>

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

4.0 Discussion

The whelk fishery in the Irish Sea (ICES Area VIIa) has recently undergone significant expansion both in terms of landings and effort (MMO, 2017), with landings increasing from 2,900 t yr^{-1} to over 6,700 t yr^{-1} (+227%) between 2011 and 2016, with a similar trend observed globally (FAO, 2017). Our results suggest that, with the exception of one site to the north of the Isle of Man, there is a risk of recruitment overfishing as the average whelk recruits into the fishery (at 45 mm in Wales and 70 mm TSL in the Isle of Man) before they have an opportunity to spawn. It is possible that fishing under the size at maturity may already have resulted in recruitment overfishing in principal fishing grounds in the Irish Sea. This may culminate in long-term stock depletion in a fishery that is increasingly valuable to coastal and island economies in the Irish Sea (DEFA, 2017).

Routine stock assessments are absent throughout the vast majority of the whelk fishery distribution, with the exception of the States of Jersey, which began annual data collection in 1996 using baited-pots (Morel & Bossy, 2004; Shrives et al., 2015) and the inshore waters of Québec, where commercial fishery performance indicators (catch per unit effort; CPUE) are assessed every three years (Brulotte, 2015). There are methodological challenges in using capture data from baited-pots to estimate absolute or relative population densities (Borsetti et al., 2018), considering the unknown effects of highly variable environmental parameters such as tidal strength, season, bait-type and soak-time as well as the inherent sex-specific or size-specific selectivity of whelk pots (McQuinn et al., 1988). An improved sampling method may be to use dredge-based surveys. In a similar study, Borsetti et al. (2018) used a dredge-based survey methodology, whilst acknowleding that gear-specific efficiency studies for dredges may facilitate absolute abundance assessments in the future. However, in the absence of accepted methods to conduct annual stock assessments, the sustainable prosecution of the whelk resources in the Irish Sea is difficult to manage. Fisheries managers in the region now seek to manage whelk fishing with robust evidence (DEFA, 2017; Welsh Government, 2017) and transition towards routine assessments of stock health. The results presented in this paper detail important population parameters, such as size-at-maturity, size-at-age and length~weight relationships ($W=aL^b$), which are essential components of biomass estimates in several stock-assessment techniques. Moreover, the variation within national waters (see table 3 and table 5) may also need to be considered if future stock assessments are attempted at a finer spatial scale, which has been the advice from other studies (Shelmerdine et al., 2007).

The sex-ratio was significantly different to the expected 1:1 ratio, indicating that the catch efficiency of static-gear is higher for females. This is particularly evident during late winter and spring, when females are recovering from egg-laying and are likely to be attracted to baited pots to feed after spawning in order to replenish energy reserves. Similar patterns were observed in data collected elsewhere in the region (Hollyman P. R., 2017a, p. 40). The consistent removal of a higher proportion of females may result in sex overfishing under a sustained level of heavy fishing pressure, which has been shown for other species targeted by static-gear fisheries in the region (Emmerson et al., 2017). In order to protect spawning stock biomass, the sex-dependent selectivity of gear, as well as the underlying biological and environmental drivers, should be carefully considered in a management strategy that may include temporal fishery closures (Hollyman, 2017, p. 294). The results from models presented here highlight that size-at-maturity (L_{50}) and the reproductive cycle of whelks are vital elements of evidence for fisheries managers that wish to initiate appropriate management measures to protect spawning biomass, such as MLS and temporal closures to protect spawning.

The length frequency distribution shows significant spatial variation between country and between intra-national fishing grounds. This is also important to policy-makers that need to consider the spatially variable economic impact of a legislative change in MLS. Apart from a correlation between average whelk size and water depth, other important environmental and ecological drivers remain poorly understood for the species such as habitat type, sea bottom temperature and salinity. Benthic infauna biomass, the foundation of the benthic food-web, was hypothesised to influence the mean size of whelk, though no correlative relationship with TSL distribution was observed in the data. It remains possible that benthic infauna biomass correlates with whelk population density, though further investigation is needed to test this hypothesis. The indication that smaller whelk, with lower aGSI values (i.e. lower relative weight of ovaries to total body weight), were caught in deeper waters suggests that there could be habitat partitioning of life history stages driven by biological (food availability and reproductive needs) and environmental (sea-bottom temperature and substrate type) preferences.

Increased temporal monitoring of population structure should reveal how whelks respond to both environmental and anthropogenic factors, such as climate change as well as direct and indirect fishing mortality. The population structure of whelk in the inshore grounds to the east of Douglas exhibit a similar size range (TSL) to that reported by Kideys (1991), suggesting that the levels of fishing experienced in recent years may not have impacted length frequency. This is notwithstanding the increase in fishing effort in other sectors of the industry, which may have either positive or negative, direct or indirect impacts on whelk populations. Within the Isle of Man territorial sea, the principal whelk grounds are subject to heavy fishing pressure from scallop trawling (Shepperson et al., 2014). Bottom-towed, or trawling gear, is known to impact other commercially fished species; for example, egg-bearing female brown crabs are regularly caught as bycatch in the Isle of Man scallop gear (Ondes et al., 2016). Conversely, trawling indirectly influences common whelk populations by providing additional food resources in the form of damaged bivalves, echinoderms, and crustaceans following trawling disturbance (Ramsey et al., 1998). The scavenging opportunities created by benthic disturbance may be a significant energetic input for whelk populations considering the results presented in this study, that benthic infauna biomass shows no clear correlation to whelk population parameters. Understanding this interaction would be a positive step towards ecosystem-based management, a process which would require mapping of commercial effort in order to quantify the cumulative impacts of indirect and direct interactions between fisheries (Murray et al., 2008).

The analysis presented in this paper exhibits progress towards understanding the reproductive cycle of whelk populations in the Irish Sea and, importantly, provides clear rationale for routine assessment of maturity in this region and elsewhere. The methodology discussed, that maturity analysis should be conducted during peak-aGSI, is in agreement with other recent work (Hollyman, 2017, p. 287). McIntyre et al. (2015) attempted to minimize seasonal variability in their analysis of SOM in various English locations by collecting samples during January – May. However, under the assumption that whelk populations in the English Channel and North Sea also spawn in late winter, McIntyre et al. (2015) likely overestimated L_{50} due to low aGSI values in the sampled whelk. Martel et al., (1986b) calculated GSI values with eviscerated weight (total meat weight minus the weight of the testis, digestive gland and seminal vesicle for males, and the total weight minus the weight of the ovary, digestive glans and pallial oviduct for females) used as the denominator, in contrast to this study which used total meat weight. Arguably, eviscerated weight would provide a more accurate GSI as the weight of reproductive organs vary temporally. However, as Welsh data did not include eviscerated weight and in order to conduct a regional comparison in the Irish Sea, the same methodology was adopted for Manx samples. This demonstrates the need for the adoption of a standard assessment protocol to enable comparisons between different studies, in different regions and in different countries. This will become increasingly important to understand the broader scale impacts of increasing fishing pressure as well as climate change and ocean warming. Sea surface temperature data strongly suggests that seasonal onset of maturity, as indicated by an increase in aGSI values within a population (indicating the development and ripening of gonadal organs) being linked to local temperature regimes. Historical sea-surface temperature (SST) data for the Irish Sea region highlights a potential correlative relationship, considering that SST peaks in the Isle of Man during July, August and September (exceeding 13 ºC), whereas peak SST from Welsh waters shows a more prolonged temporal period within which temperature data exceeding 13 ºC, observed from June until November (CEFAS, 2017). However, a greater temporal data-set of aGSI is necessary to understand whether temperature may have a causative effect on aGSI observations. Benthic temperatures would provide a more comprehensive picture, particularly if the water column is highly stratified. The temporal patterns observed show that ovaries are most full during July to September in the Isle of Man, which was also observed by Kideys (1991), and from June to November in Welsh samples.

Growth was assessed using mixed-modality analysis of length-based data. Identifying growth parameters using direct observations made in laboratory or by investigating statolith ring analysis was outside the scope of this study, although samples have been retained for analysis using the methods developed by Hollyman et al. (2017). Nonetheless, the size-at-age model presented here provides some preliminary detail on growth, which is an important consideration when interpreting L_{50} values, as well as potentially modelling recovery rates of depleted populations and formulating advice for temporal datasets in size-at-maturity. It is recommended that size-at-maturity estimates are repeated over a period of time relevant to the life-history of a species (EU, 2010). In this case, the advice is to perform biennial assessments of size-at-maturity and model the change in the mean average L_{50} of the current and previous assessment (i.e a moving four-year average, a time-period which approximates to age of the average whelk beginning to develop reproductive organs) (ICES, 2008). This method helps alleviate sampling variability, maturity-stage uncertainty and significant changes in fishing practices; however, it may also mask genuine changes in population parameters caused by environmental or anthropogenic factors (ICES, 2008). Acknowledging high spatio-temporal variability is especially pertinent for whelk, considering current fishing pressure on brood stock, restricted movement of populations and changing temperature regimes due to climate change.

When fitting a logistic curve to the maturity data, it does not always follow that output value (L_{50}) should be the recommended MLS. It is important to account for additional information when available, such seasonality and frequency of spawning events (including skipped spawning events as in gadoid species) as well as fecundity-at-size estimates and eggs-per-recruit models (ICES, 2008). In the case of whelk in the Irish Sea, the appropriate time for maturity assessment (i.e. peak-aGSI, when reproductive organs exhibit the clearest distinction between mature and immature) is between June and September. However, our results suggest that egg-laying occurs in late winter, during which time the assessed population is expected to have grown beyond the L_{50} estimate. During that period in the Irish Sea, our data indicates that a whelk may have increased TSL by 5-7 mm. For example, the logistic model applied to the population sampled “North” of the Isle of Man in this study produced an L_{50} estimate of 67 mm TSL. The size-at-age model (shown in figure 8b) estimates an individual is 4.5 years at that size. With an additional 6 months growth until spawning, at age 5, that individual is estimated to be at a size 74 mm TSL. It is therefore vital that growth is understood for this species on a regional basis, as L_{50} values are likely to require a correction factor before being presented as evidence to inform MLS regulations.

5.0 Conclusion

This study provides the most comprehensive scientific evidence to date with which to manage and conserve the common whelk resources within ICES Area VIIa. Additionally, we propose a clear rationale for undertaking routine assessments biennially for size-at-maturity, which are biologically-referenced to the time at which aGSI is at a peak in the population and visual classification of gonads is most accurate. The evidence presented here suggests whelk are subject to fishing mortality before they have the opportunity to lay eggs for the first time with the existing MLS regulations. Although no data is available to indicate that populations are recruitment overfished, current understanding of whelk biology suggests that a precautionary approach should be adopted in order to conserve resources in the light of this additional evidence.

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<Table 1>

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

	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

<Table 2>

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

	Winter		Spring			Summer			Autumn			Winter
Area-code	**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	-	-	-	-	-	-

<Table 3>

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

	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

<Table 4>

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

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

<Table 5>

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

	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*

Fig 1

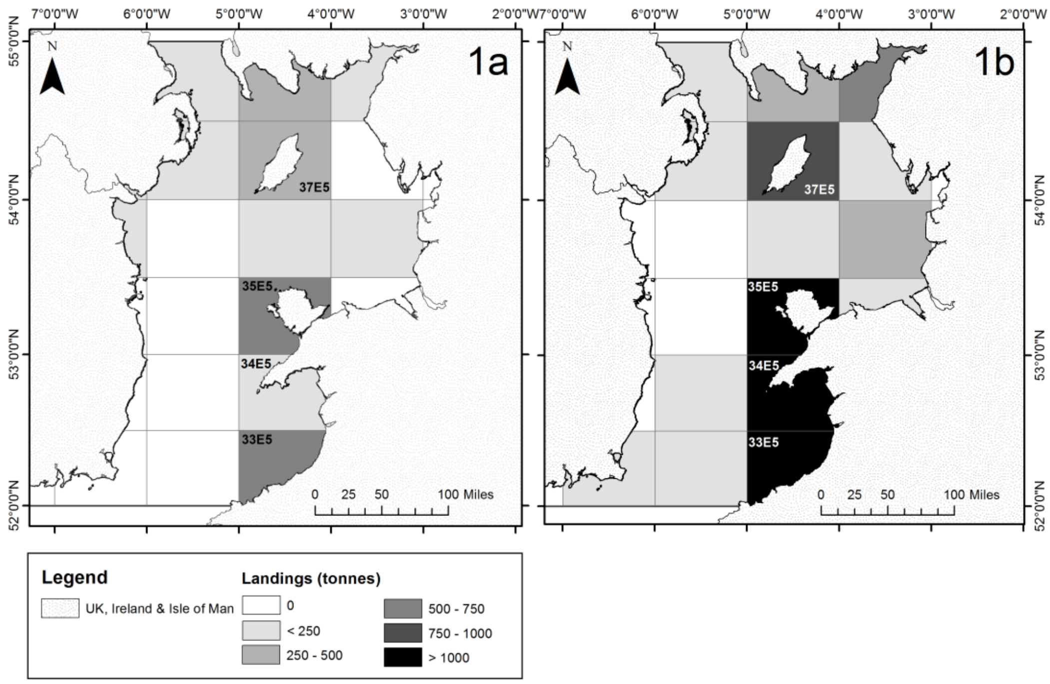

1a
1b
7°0'0"W
6°0'0"W
5°0'0"W
4°0'0"W
3°0'0"W
2°0'0"W
55°0'0"N
54°0'0"N
53°0'0"N
52°0'0"N
N
37E5
35E5
34E5
33E5
0 25 50 100 Miles
Legend
UK, Ireland & Isle of Man
Landings (tonnes)
0
< 250
250 - 500
500 - 750
750 - 1000
> 1000

Fig 2

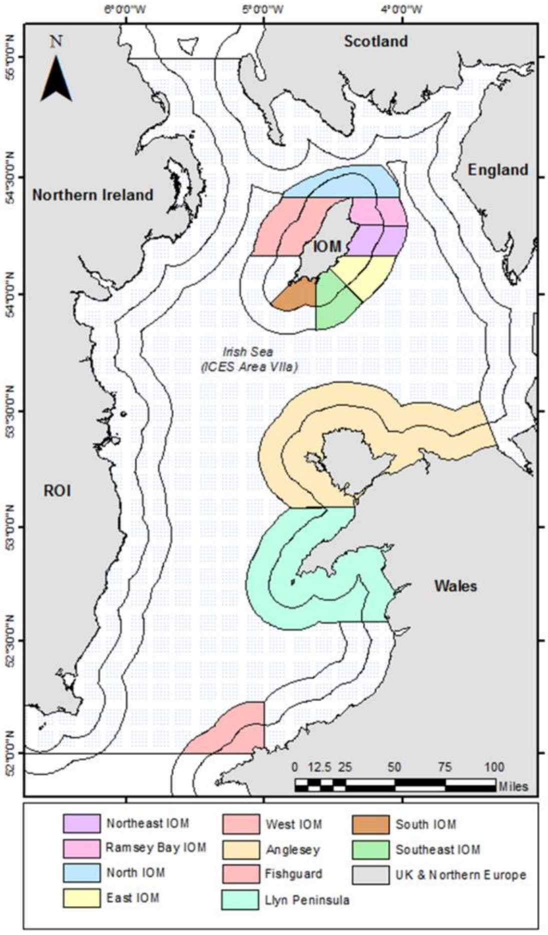

6°0'0"W
5°0'0"W
4°0'0"W
55°0'0"N
54°30'0"N
54°0'0"N
53°30'0"N
53°0'0"N
52°30'0"N
52°0'0"N
N
Scotland
England
Northern Ireland
IOM
Irish Sea
(ICES Area VIIa)
ROI
Wales
0 12.5 25 50 75 100
Miles
Northeast IOM
Ramsey Bay IOM
North IOM
East IOM
West IOM
Anglesey
Fishguard
Llyn Peninsula
South IOM
Southeast IOM
UK & Northern Europe

Fig 3

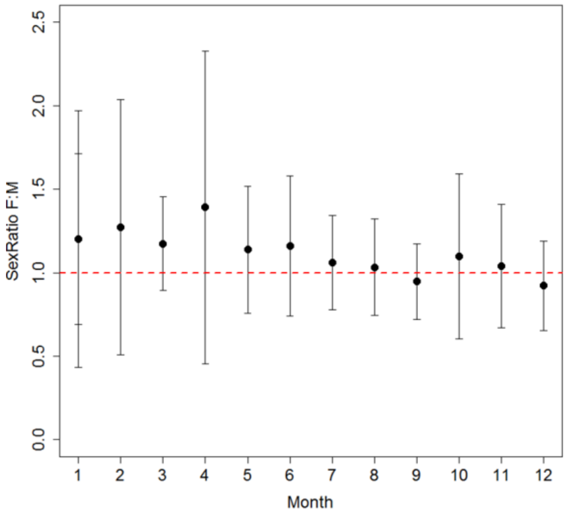


Fig 4

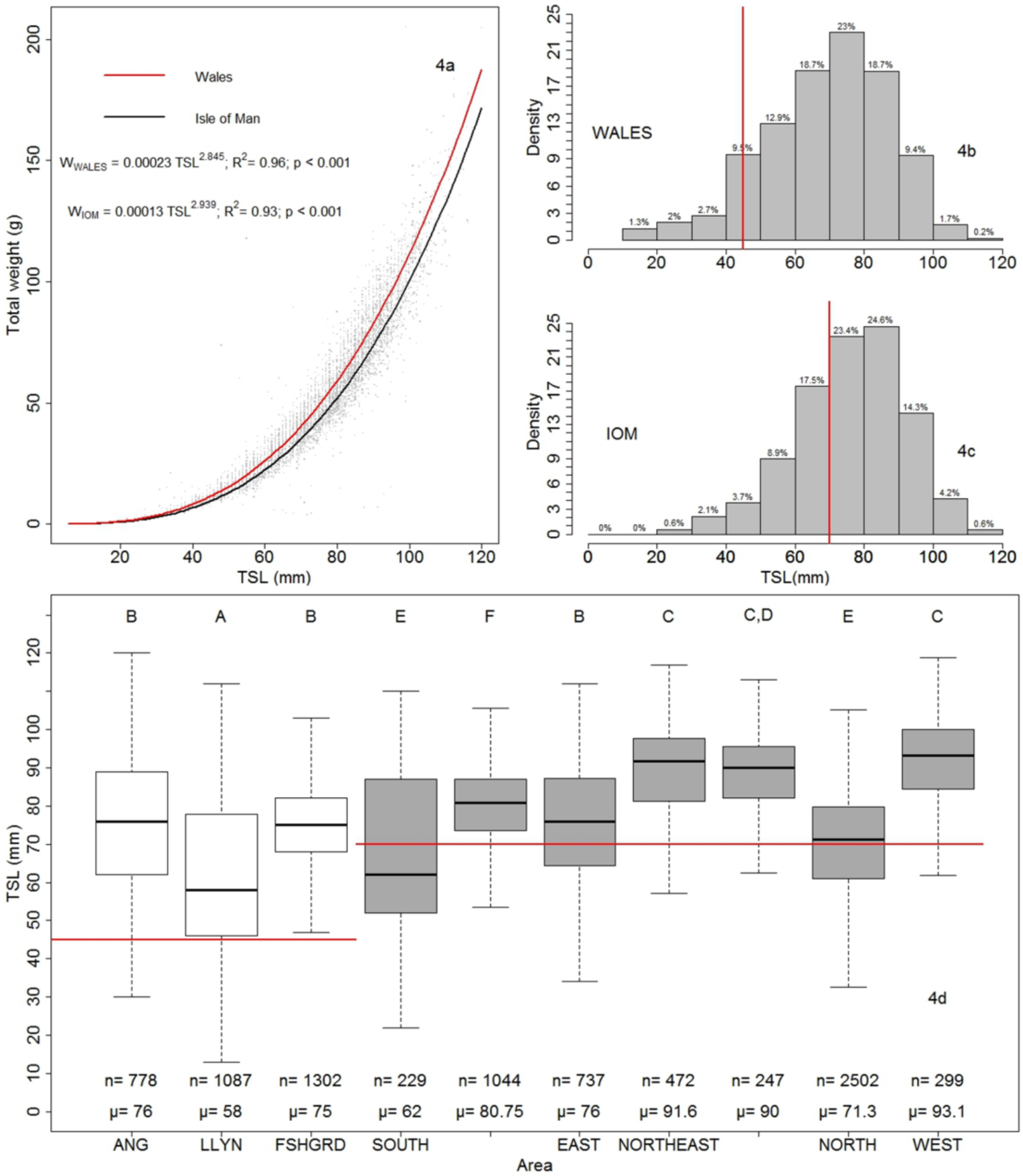

4a
Wales
Isle of Man
W_{WALES} = 0.00023 $TSL^{2.845}$; R^2= 0.96; p < 0.001
W_{IOM} = 0.00013 $TSL^{2.939}$; R^2= 0.93; p < 0.001
Total weight (g)
TSL (mm)
WALES
4b
Density
IOM
4c
TSL(mm)
4d
TSL (mm)
B A B E F B C C,D E C
n= 778 n= 1087 n= 1302 n= 229 n= 1044 n= 737 n= 472 n= 247 n= 2502 n= 299
μ= 76 μ= 58 μ= 75 μ= 62 μ= 80.75 μ= 76 μ= 91.6 μ= 90 μ= 71.3 μ= 93.1
ANG LLYN FSHGRD SOUTH EAST NORTHEAST NORTH WEST
Area

Fig 5

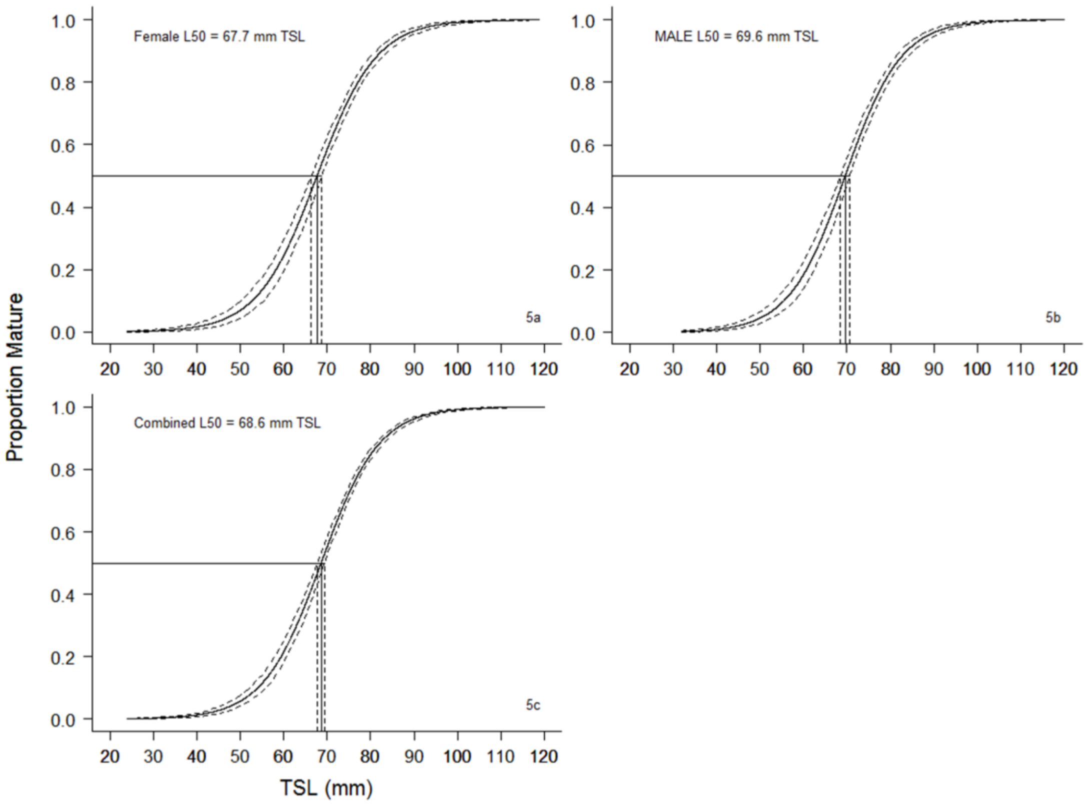

Female L50 = 67.7 mm TSL
5a
MALE L50 = 69.6 mm TSL
5b
Combined L50 = 68.6 mm TSL
5c
Proportion Mature
TSL (mm)

Fig 6

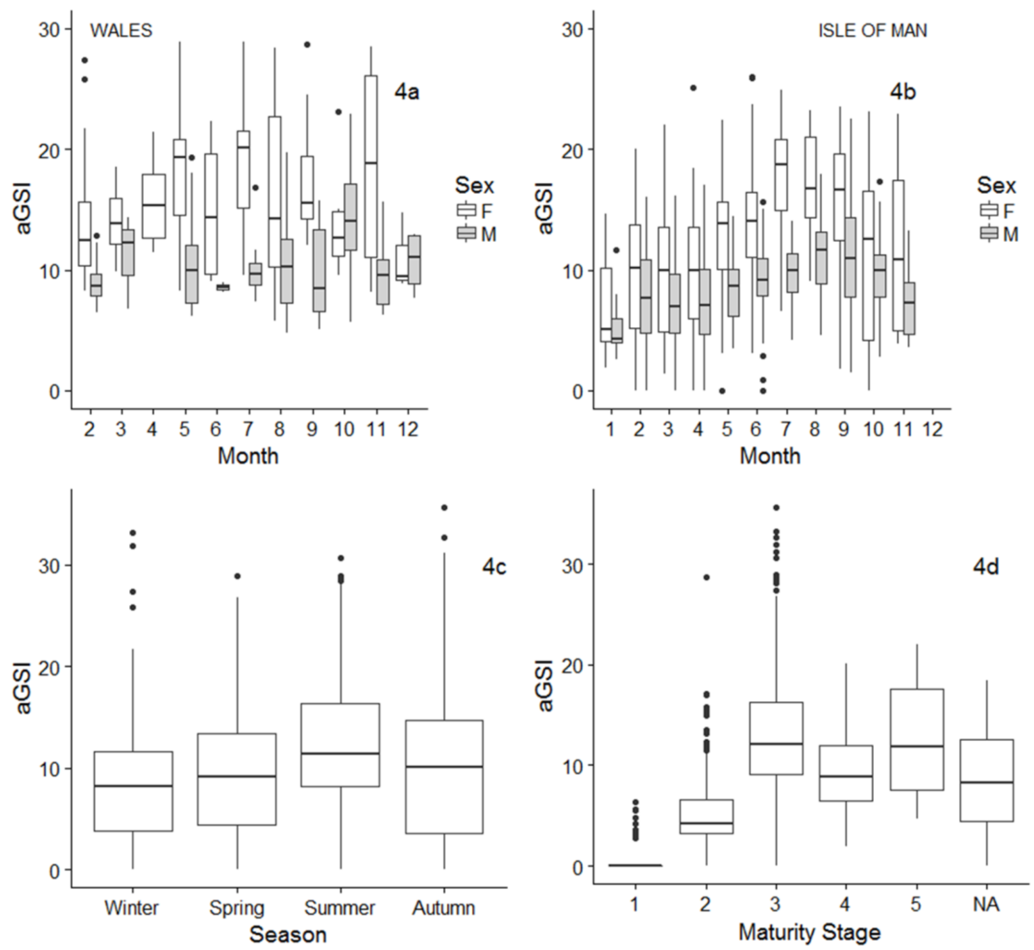

WALES
4a
aGSI
Month
Sex
F
M
ISLE OF MAN
4b
aGSI
Month
Sex
F
M
4c
aGSI
Winter
Spring
Summer
Autumn
Season
4d
aGSI
1
2
3
4
5
NA
Maturity Stage

Fig 7

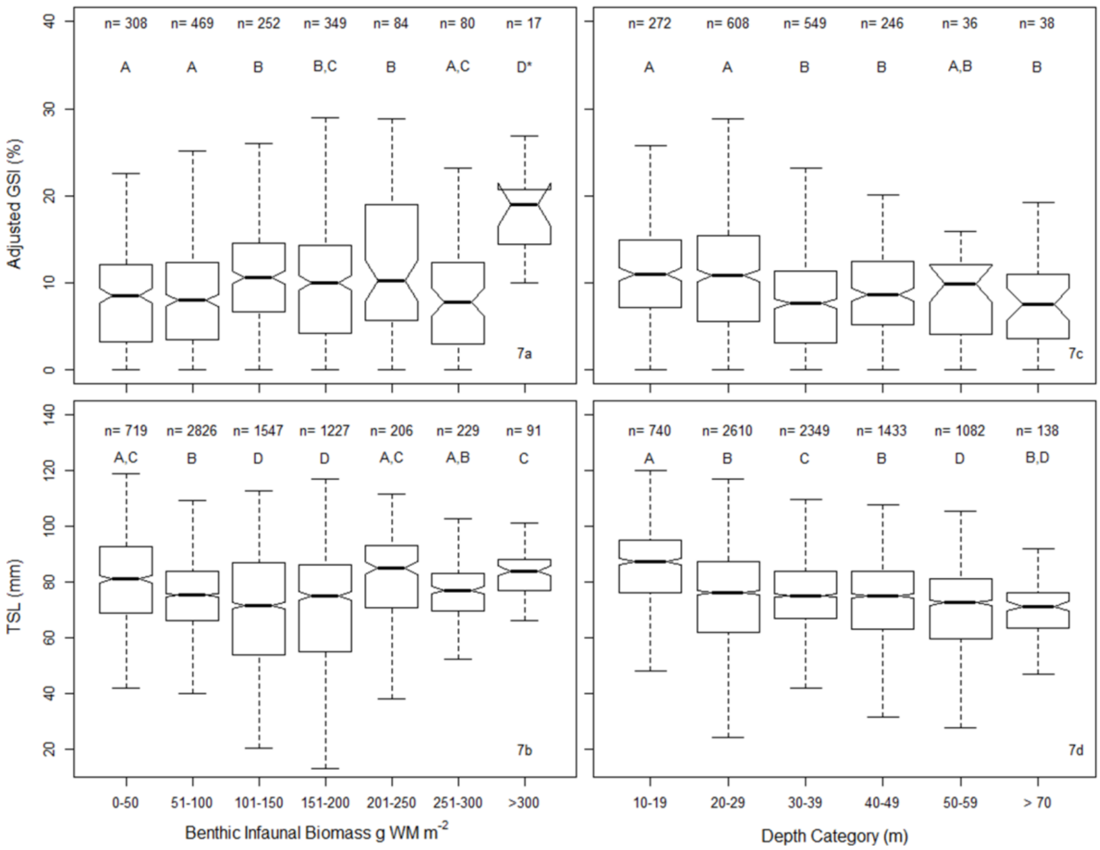
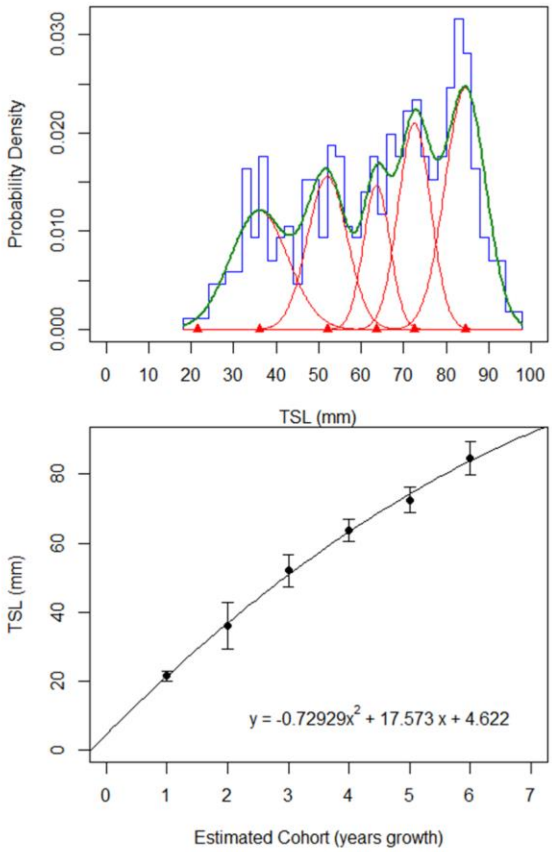

Adjusted GSI (%)
TSL (mm)
n= 308 n= 469 n= 252 n= 349 n= 84 n= 80 n= 17
A A B B,C B A,C D*
7a
n= 272 n= 608 n= 549 n= 246 n= 36 n= 38
A A B B A,B B
7c
n= 719 n= 2826 n= 1547 n= 1227 n= 206 n= 229 n= 91
A,C B D D A,C A,B C
7b
n= 740 n= 2610 n= 2349 n= 1433 n= 1082 n= 138
A B C B D B,D
7d
0-50 51-100 101-150 151-200 201-250 251-300 >300
Benthic Infaunal Biomass g WM m-2
10-19 20-29 30-39 40-49 50-59 > 70
Depth Category (m)

Fig 8


Probability Density
0.000
0.010
0.020
0.030
0 10 20 30 40 50 60 70 80 90 100
TSL (mm)
TSL (mm)
0
20
40
60
80
y = -0.72929x^2 + 17.573 x + 4.622
0 1 2 3 4 5 6 7
Estimated Cohort (years growth)