Kent and Essex Inshore Fisheries and Conservation Authority

The size-at-maturity of the common whelk in the Kent and Essex IFCA district

Final Report 2021 – EMFF Funded Study

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Summary

This report provides a summary of the European Marine Fisheries Funded (EMFF) project carried out between 2018 and 2020. The aim of the project was to determine the size-at-maturity of whelks across the Kent and Essex Inshore Fisheries and Conservation Authority (KEIFCA) district, and from this, assess the effectiveness of KEIFCA's minimum landing size of 53 mm shell length at protecting immature breeding stock.

Key outcomes:

- Size-at-maturity for whelk populations was 44.2 mm in Essex and 56 mm in Kent. The combined size-at-maturity for whelks across two sites was 52 mm.
- The large number of samples provides KEIFCA with a robust size-at-maturity estimate that is supported by the earlier findings presented by Dr Phil Hollyman in 2017.
- The KEIFCA MLS of 53 mm protects 66% of immature stock, compared to the national MLS of 45 mm that protects 31% of immature stock.
- Whelks undergo a single, annual reproductive event with their spawning season occurring between September and November.
- The relationship between total shell length and minimum shell width was successfully determined and was not significantly different for whelks between the two sites. Therefore, a riddle with set bar spacings will sort whelks the same from both areas.
- Whelks reach size-at-maturity at between 2.7 to 3 years old.
- The KEIFCA MLS greatly enhances protection of the whelk spawning stock by allowing 26% to 51% of whelks that have not yet reproduced at least once, to be returned. In comparison, the national MLS of 45 mm that protects between 5% to 13%.
- The KEIFCA MLS allows whelks an extra year to grow.

1. Introduction

In 2018, Kent and Essex Inshore Fisheries and Conservation Authority (KEIFCA) began a two-year European Marine Fisheries Fund (EMFF) study in partnership with the local fishing industry. The main aim of which, was to build on the work done by Dr Phil Hollyman, gain further evidence on the size-at-maturity of whelks in the district, determine how riddle sizes and MLSs influence the proportion of catch retained, and the consequences these have for the fishery. The results of this study are presented here alongside Dr Phil Hollyman's work to give a comprehensive overview of our understanding of the district's whelk population.

1.1 Background

The common whelk *(Buccinum undatum*) is a boreal, neogastropod mollusc native to the subtidal waters of the UK and north Atlantic continental shelf (Golikov 1968). Over the past two decades, whelks have rapidly become one of the UK's most economically important fisheries, with landings into the UK, by UK vessels, increasing five-fold from 3,500 tonnes in 1998 (UK sea fisheries annual statistics 1998) to 19,600 tonnes in 2018 (MMO 2018). Over the same period, their value has tripled, from approximately £400 per tonne (UK sea fisheries annual statistics 1998), to £1,200 per tonne (MMO 2018), with the fishery now valued at over £23 million annually (MMO 2017, 2018, 2019).

The species is of considerable importance to vessels of ≤10 metres in length that make up part of the UK's inshore fishing fleet (MMO 2018). Vessels in this smaller size category predominantly work the 0-12 nautical mile inshore zone where whelk populations are found in high abundances between depths of 5 and 100 m (Morel & Bossy 2004; Smith *et al.,* 2013). In 2018, whelks made up nearly a quarter of all shellfish landed by ≤10 metre vessels (MMO 2018), providing an important source of local income to coastal communities.

Currently, the UK whelk fishery is managed under a minimal number of regulations. Whelks are not subject to EU total allowable catch (TAC) as they are a non-quota species (Blue Marine Foundation, 2019) and in England, are currently only managed under a minimum landing size (MLS) of 45 mm (Lawler 2013). In addition, an increase in demand from abroad, near year-round availability of stock, low start-up costs and the decline in alternative fisheries have made it a popular displacement fishery (Haig *et al*., 2015; McIntyre *et al.,* 2014). As a result, the industry has expanded rapidly and raised concerns that whelk populations are at risk of unsustainable exploitation.

1.2 Kent and Essex IFCA

The Kent and Essex Inshore fisheries and Conservation Authority (KEIFCA) are responsible for the management of the commercial whelk fishery within the 0-6 nautical miles of coastal waters in the Kent and Essex district (Fig.1). They have authority under the Marine and Coastal Access Act 2009 (MaCAA) to create and enforce byelaws for the purposes of sustainably managing fisheries resources, and therefore, are well placed to implement regional management of whelk populations.

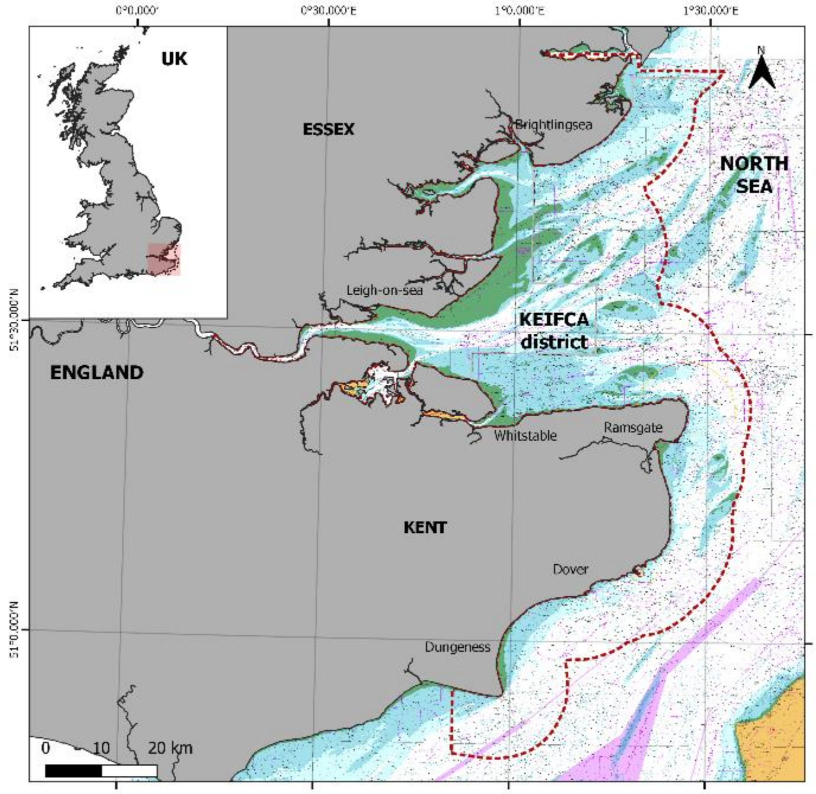

Figure 1. The Kent and Essex Inshore Fisheries and Conservation Authority district. The red hashed line delineates the 6 nautical mile district boundary. Projection WGS 84 / UTM zone 31N EPSG:32631.

The Kent and Essex district has supported a small-scale, seasonal whelk fishery from the early 1900's, with whelks being predominantly sold as bait or to local seaside resorts (Kent and Essex Sea Fisheries Committee 1908). However, between 2009 and 2012, the fishery saw a dramatic increase in effort with landings in the KEIFCA district increasing 25-fold, from 47.8 tonnes to 1186.6 tonnes (MMO 2019) (Fig.2). Much of this increase was seen in the local, non-nomadic fleet, predominantly consisting of vessels in the ≤10 m size category. What was once a supplementary, seasonal fishery, has expanded to support many small-scale fishermen year-round and constitute a significant portion of their income.

Whelks have several life-history characteristics that make them vulnerable to fishing pressure (Shrives *et al.*, 2015). The species are relatively sedentary as adults, do not reach sexual maturity for several years and have limited dispersal potential due to a lack of planktonic larval phase that facilitates migration between populations (Weetman *et al.,* 2006; Shelmerdine *et al*., 2007). In addition, they are known to form discrete sub-populations and demonstrate significant variation in the size-at-maturity even over small spatial scales (Haig *et al*., 2015).

In response to concerns over potential unsustainable exploitation, KEIFCA introduced the Whelk Fishery Permit Byelaw (KEIFCA, 2013) in 2013 requiring all fishermen to obtain a permit to fish for whelks in the district. Whelks are commonly fished by use of static pots that are baited with crab or fish and laid in strings of up to 100 to soak for 24 to 36 hours. The permit scheme attempted to control fishing effort by; a) limiting the total number of pots per holder to a maximum of 300, b) minimise the number of undersized whelks retained by specifying the number and size of pot escape gaps, and c) ensure immature whelks were returned to sea by requiring fishers to pass whelks over a riddle with bar spacings of 22 mm (KEIFCA, 2013). Fishermen commonly grade whelks using a sorting grid (riddle) that is made up of bars spaced at a set width. The spacing between the bars is determined by the length-width ratio of a whelk shell so that undersized whelks fall through, and those at or above the MLS are retained. The 22 mm riddle specified in the byelaw served to retain whelks at or above the national MLS of 45 mm (KEIFCA, 2016).

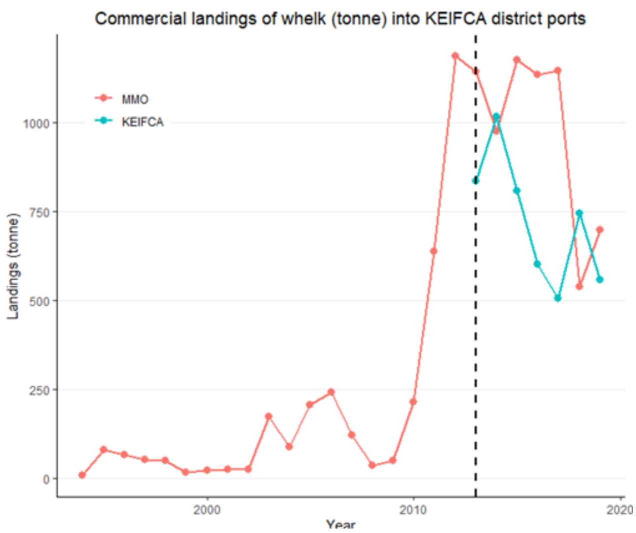

Figure 2. Commercial landings of whelk into KEIFCA district ports from 1994 to 2019. The red line shows the landings statistics taken by the MMO, and the blue line shows the landings statistics collected by KEIFCA since the introduction of the Whelk Fishery Permit Byelaw in 2013. The black hashed line indicates the date the byelaw was introduced.

MLS is an effective tool for protecting immature individuals (Jennings *et al.,* 2001) and is usually set by determining the size at which 50% of the population present mature gonads (L_{50}) (Heude-Berthelin *et al.,* 2011). It is particularly important in the absence of a stock assessment, as is the case with whelks in the KEIFCA district. However, there is substantial evidence to demonstrate that different whelk populations mature at different sizes around the UK, with size-at-maturity ranging from 45 mm to 78 mm in length (Hancock and Urquhart 1959; Lawler, 2014; Haig *et al.,* 2015; McIntyre *et al*., 2015; Emmerson *et al*., 2017). This evidence provides little justification for the nationally applied MLS of 45 mm, that in many areas provides minimal protection to whelk spawning stock. Whelks, therefore, require a regionalised management approach, (Shelmerdine *et al*., 2007; McIntyre *et al*., 2014; Borsetti *et al*.,2018).

In response to concerns that the EU MLS was not protecting the district's whelk spawning stock (Lawler, 2014; Lawler and Vause, 2019; McIntyre *et al.,* 2015), in 2016, KEIFCA raised their riddle spacings to 25 mm, and in 2021, introduced a new MLS of 53 mm, that corresponds with both the size of whelk retained by a 25 mm riddle, and the estimated size-at-maturity (SAM) (Lawler, 2014) of the districts stock. However, still relatively little is known about the baseline life history characteristics of the KEIFCA district whelk population, nor the appropriateness of the local management measures. As commercial demand continues, this information is critical for supporting regionalised management decisions.

Here, we present the results of two complementary studies undertaken by KEIFCA. The first conducted in 2017 by Dr Phillip Hollyman and Dr Chris Richardson, used statolith ageing techniques to determine the size-at-age and growth rates of whelks in the district. The second study, conducted over two-years from 2018 to 2019, expanded on the previous study, and built a long-term dataset from which life-history characteristics such as SAM, seasonal variation, population length frequency patterns, reproductive cycle, and morphometric estimates of male maturity could be determined. In addition, the study aimed to determine the relationship between key morphometric parameters such as length and width of individuals which are critical for determining riddle sizes. From this, the appropriateness of current management measures for protecting the district's breeding stock is assessed, with the outputs contributing to the growing volume of work on whelk SAM and discussions on regional whelk management across the UK.

2. Methods

2.1 Field collection

A fisher from Kent and a fisher from Essex each fished five whelk pots once per month for 24 months within their respective areas (fig.3). Each of the five pots was set in a different location attached to commercial fishing strings that typically consist of up to 50 pots. Whelk pots were made of thick plastic with a lead weighted base and drainage holes. The entrance to the pot was covered with mesh netting, and there were no escape holes so that the entire contents of the pots could be retained including undersized individuals. Fishers provided details on the location (latitude and longitude), soak time and date of the pots set. The pots were typically baited with dogfish (*Scyliorhinus cancicula*) and 'soaked' for between 24-48 hours. Samples were placed in separate bags and frozen after landing.

In August 2018, the unavailability of fishers in Essex lead to KEIFCA taking over sampling, and the methodology changing to laying all five pots on a single string in one location per month from then onwards. The location of samples is presented in figure 4. Pots collected by KEIFCA were baited with dog food.

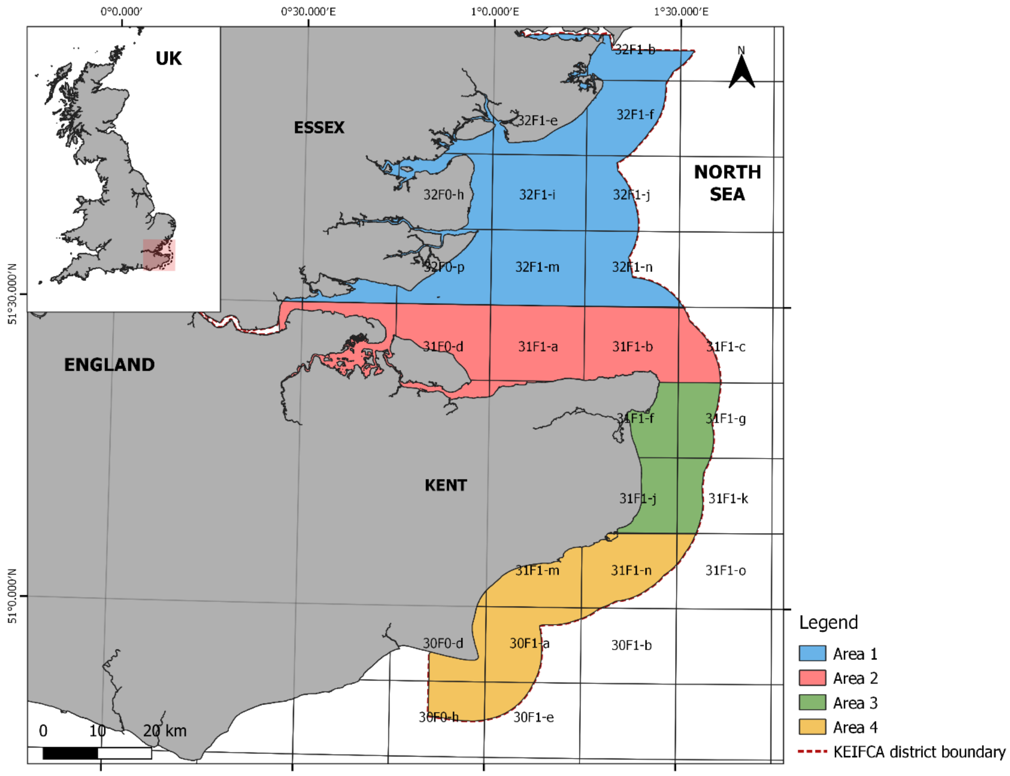

Figure 3. A map of the Kent and Essex Inshore Fisheries and Conservation Authority district where samples of whelk (*Buccinum undatum*) were collected for both studies. The district is split into four main whelk fishing areas delineated by ICES sub-rectangles. In study 1, samples were taken from each of the four areas. In study 2, samples were taken from Area 1 (Essex) and Area 2 (Kent) only. Projection WGS 84 / UTM zone 31N EPSG:32631.

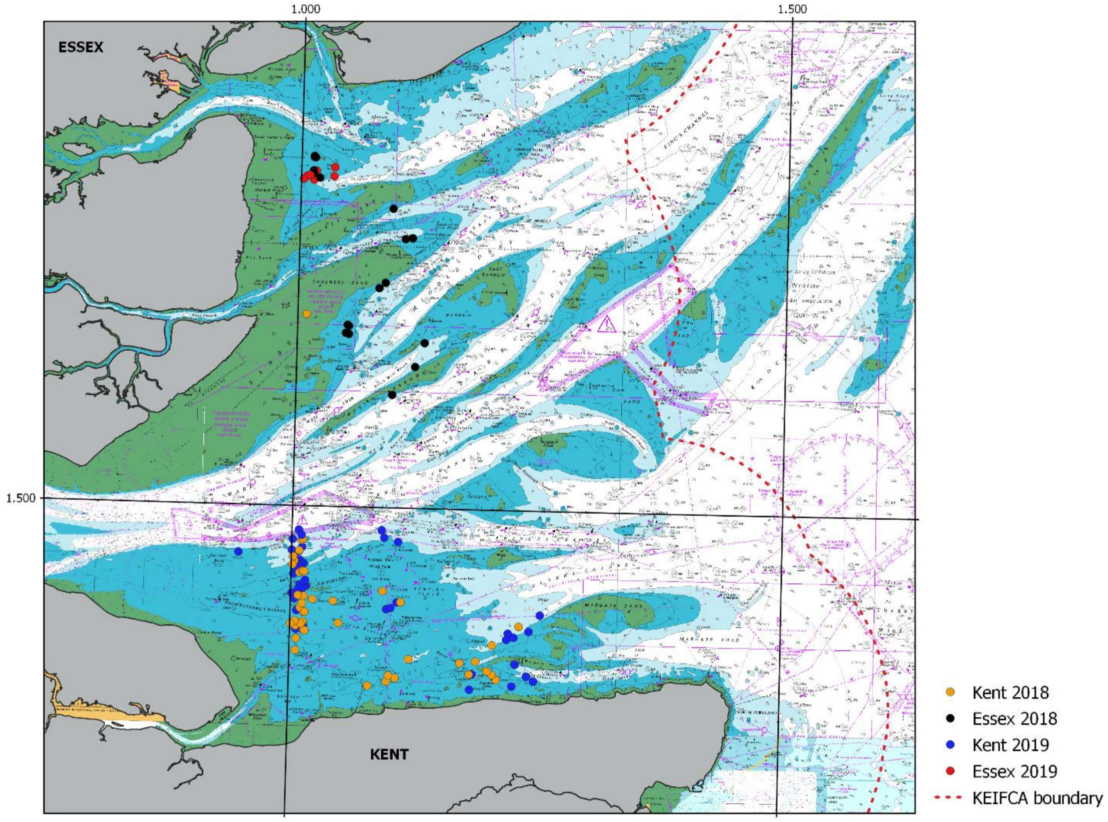

Figure 4. The location of whelk (Buccinum undatum) samples taken by KEIFCA and local fishers as part of the EMFF project. Different colours represent the year samples were taken and their location. Projection WGS 84 / UTM zone 31N EPSG:32631.

2.2 Laboratory analysis

In both studies, samples were defrosted before analysis and individuals were measured (total shell length; 0.1mm, maximum shell width; 0.1mm), and weighed (total wet weight; 0.01g) as detailed in Haig *et al*. (2015). All individuals collected were removed from their shells, sexed, and dissected. For samples collected in 2019, the number dissected was capped at fifty. During dissection, the total wet weight of the body was recorded (0.01g), the gonad/digestive gland was removed and weighed (0.01g) and the degree of differentiation in colour between the dorsal and ventral surfaces was visually inspected to give percent maturity as detailed in Haig *et al.* (2015) and Hollyman, 2017 (Fig.4).

The digestive gland and gonad are encapsulated in the same membrane and so are removed from the body and weighed together (Fig.4). As whelks prepare for reproduction, the difference between the gonad and the digestive gland becomes more apparent. Eggs stored in the female gonads are yellow and can be clearly identified by visual inspection. The proportion of the gonad/digestive gland made up of eggs gives a 'percent maturity' of an individual (Fig.4). Research by Couillard and Brulotte in 2019, validated the use of this visual maturity assessment for whelks by demonstrating its high consistency with all other available methodologies, including histological. Males also demonstrate differentiation of the gonads; however, this is not often as clear as with females. Therefore, in addition to visual maturity inspection, penis length (PL) was measured from the point of attachment to the body to the tip, accounting for natural curvature.

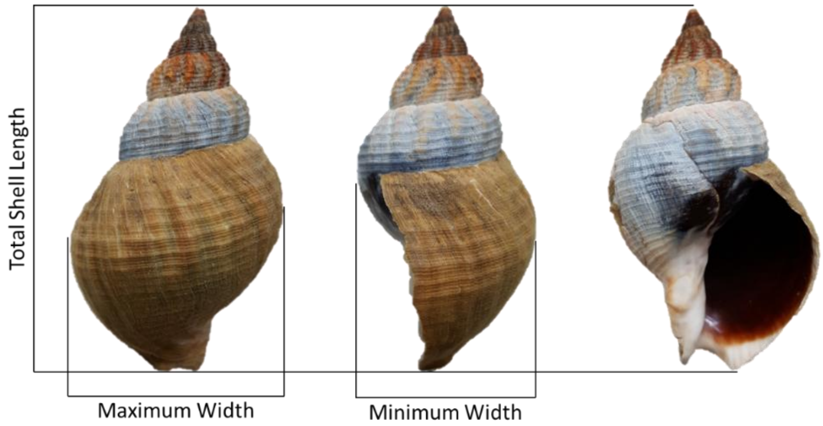

Figure 4. The morphometric measurement of whelk (*Buccinum undatum*) shells. Image copied from: Hollyman (2017)

After processing, the proportion of the gonad/digestive gland to the total wet body weight was calculated to give the gonadosomatic index (GSI):

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

The GSI can be used to indicate the maturity of a whelk outside of the breeding season when there is no discernible gonad/digestive gland differentiation.

Because whelks demonstrate changes in visual maturity throughout the annual breeding cycle, an additional ‘adjusted’ gonadosomatic index (aGSI) was calculated to factor this into assessment. The aGSI was calculated by multiplying the GSI by the percent maturity determined from the visual assessments.

$$aGSI = GSI\ \times\ \%Maturity$$

The aGSI was used to identify the reproductive cycle.

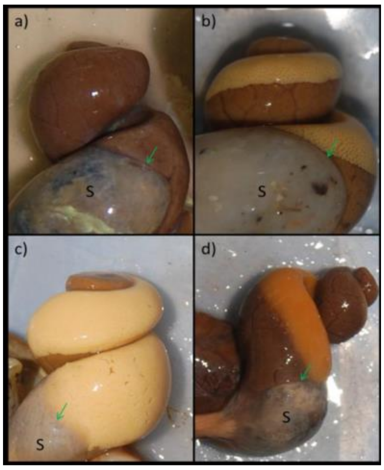

Figure 4. Examples of maturity stages of the common whelk. The images show the differences in the proportion of the digestive gland to gonad in: a) a female whelk with 0% gonad development, b) a female whelk showing 50% development, c) a female whelk showing 100% gonad development and d) a male whelk showing 50% development. The digestive gland and gonad are measured together, the green arrow shows where they are dissected from the body. Source: Hollyman (2017)

2.3 Statistical analysis

All statistical analysis was carried out in R v4.0.2 (R Core Team, 2020). Prior to analysis, shell and weight measurements were visually inspected for normality using QQ-plots. To meet the assumptions of statistical models and achieve normal distribution, transformations were applied to data where necessary. Heteroscedasticity was assessed visually using QQ plots and Levene's test. Outliers were identified using Cook's distance plots, and through visual inspection of the data. Following analysis, residuals were plotted and visually assessed for normality.

2.3.1. Population structure

Inferences on general population structure were made using TSL size-frequency histograms in the 'ggplot2' package in R. Variation in TSL distribution between sexes and locations was investigated using the non-parametric Mann-Whitney *U* test respectively.

2.3.2. Allometric analysis

The 'smatr' (Standardised Major Axis Estimation and Testing Routines) package v3.4-8, developed by Warton *et. al.,* (2018) was used to investigate whether the relationship between whelk body measurements and TSL varied significantly between site and sex respectively. The package fits a linear regression model to log-transformed data and compares both the slope and elevation (movement on y axis) of the resulting regression using pairwise comparisons, similar to ANCOVA analysis.

2.3.3. Sex ratio

To determine if the ratio of males to females caught each month deviated significantly from the expected 1:1 ratio, a binomial test was applied.

2.3.4. Reproductive studies

The seasonal reproductive cycle of mature individuals was determined by visually assessing changes in aGSI in R using the ‘ggplot2’ package. Univariate Kruskal Wallis and post-hoc Dunn’s test was used to determine if seasonal estimates of aGSI were significant.

2.3.5. Size-at-maturity calculations

For calculating the size-at-maturity estimates (TSL_{50}) a logistic regression model was applied following the methodology detailed in Walker (2005). To do this, individuals were assigned a binary maturity factor (immature=0, mature=1) prior to analysis based on their visual maturity (Tab.1). The formula for the logistic regression model is given below:

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

P is the proportion of the population that is mature at any given size (TSL_i), and TSL_{50} and TSL_{95} are the shell lengths at which 50% and 95% of the population are mature respectively.

In R, the logistic regression was carried out by means of a generalised linear model (GLM) with a specified binomial distribution and logit link function. Confidence intervals were calculated by bootstrapping the GLM (1000 runs of the model). The R code used for this analysis was adopted from Harry (2013) and previously used by Haig *et al.* (2015), Hollyman (2017) and Emmerson *et al.* (2017) in similar studies. Data were subset by sex, season, and location, and maturity ogives estimated for each to see how these factors influenced TSL_{50} (the total shell length at which 50% of the population should be mature).

Table 1. Criteria for assigning binary maturity factors to the data from visual maturity measures.

Stage	Description		Binary factor
	Female	**Male**	
Immature	No visual differentiation between the gonad and the digestive gland	No visual differentiation between gonad and digestive gland.	**0**
Mature	>0% to 100% visual differentiation between the gonad and digestive gland.	>0% to 100% visual differentiation between the gonad and digestive gland.	**1**

2.3.6. Estimating maturity in males

The differentiation between the gonads and digestive gland was less distinct in males than females making it difficult to assess visual maturity in males. Penis length (PL) can be used as an alternative measurement of maturity in males in the absence of clear gonad differentiation. To determine the L_{50}

from PL, an iterative search procedure (as described in Haig *et al.,* 2015) was used to model PL against TSL using piecewise linear regression with the following model:

$$TSL = PL \times I(x < c) + x \times I(x > c)$$

The model examines the linear relationship between PL and TSL, and searches for the significant deviation from the linear model, called an inflection point. The inflection point indicates a change in the allometric relationship between shell length and average PL, which can be taken as an estimate of a change in maturity. The inflection point is determined where the total residual mean standard error is the least. In the equation, $\times$ symbolises the main effects and interactions for both variables, and c is the inflection point.

3. Results

A total of 9,508 whelks were collected from the sample locations in north Kent, of which, 7,466 were dissected and assessed for maturity. In Essex, a total of 2,637 whelks were collected, of which 1,845 were dissected and assessed for maturity. All whelks sampled were measured for shell length, minimum width, total weight and sexed.

Sample sizes varied spatially and temporally in both areas due to the nature of collection.

Table 2. The total number of whelks (*Buccinum undatum*) dissected and assessed for maturity each month for all sample locations in both Kent and Essex during the study period. Samples taken in 2019 for dissection were capped at approximately 50 individuals, however, the full catch was measured for shell length, width, total weight and sexed.

	Sample	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Kent 2018	1	60	-	58	99	24	55	45	0	43	345	73	159
	2	78	-	174	-	115	50	91	0	189	30	230	180
	3	80	-	92	196	89	58	49	0	-	127	110	126
	4	205	-	151	128	120	84	29	0	160	-	236	154
	5	166	-	61	152	116	68	40	0	124	114	48	116
	Total	**589**	**-**	**536**	**575**	**464**	**315**	**254**	**0**	**516**	**616**	**697**	**735**
Kent 2019	1	40	50	50	50	50	21	-	-	-	51	50	45
	2	50	44	50	49	50	36	-	-	-	53	51	52
	3	50	46	42	56	50	27	-	-	-	50	51	53
	4	49	47	53	50	58	39	-	-	-	49	49	49
	5	50	50	49	50	51	49	-	-	-	57	52	50
	Total	**239**	**237**	**244**	**255**	**259**	**172**	**-**	**-**	**-**	**260**	**253**	**249**
Essex 2018	1	-	10	26	15	-	-	174	23	153	125	108	90
	2	-	14	44	21	-	-	226	-	-	-	-	-
	3	-	138	42	38	-	-	72	-	-	-	-	-
	4	-	51	28	65	-	-	26	-	-	-	-	-
	5	-	78	25	-	-	-	-	-	-	-	-	-
	Total	**-**	**291**	**165**	**139**	**-**	**-**	**498**	**23**	**153**	**125**	**108**	**90**
Essex 2019	1	-	-	-	-	13	36	51	51	-	51	51	-
	2	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-
	5	-	-	-	-	-	-	-	-	-	-	-	-
	Total	**-**	**-**	**-**	**-**	**13**	**36**	**51**	**51**	**-**	**51**	**51**	**-**

3.1 Population structure

The size frequency distribution of whelks sampled varied between sex, location (Fig.5), and season (Fig.6). The size distribution of whelk sampled in Kent (Area 2) was significantly different from those in Essex (Area 1) (Mann-Whitney *U* Test: $p<0.001$), with the mean TSL being 6.5mm larger in Kent

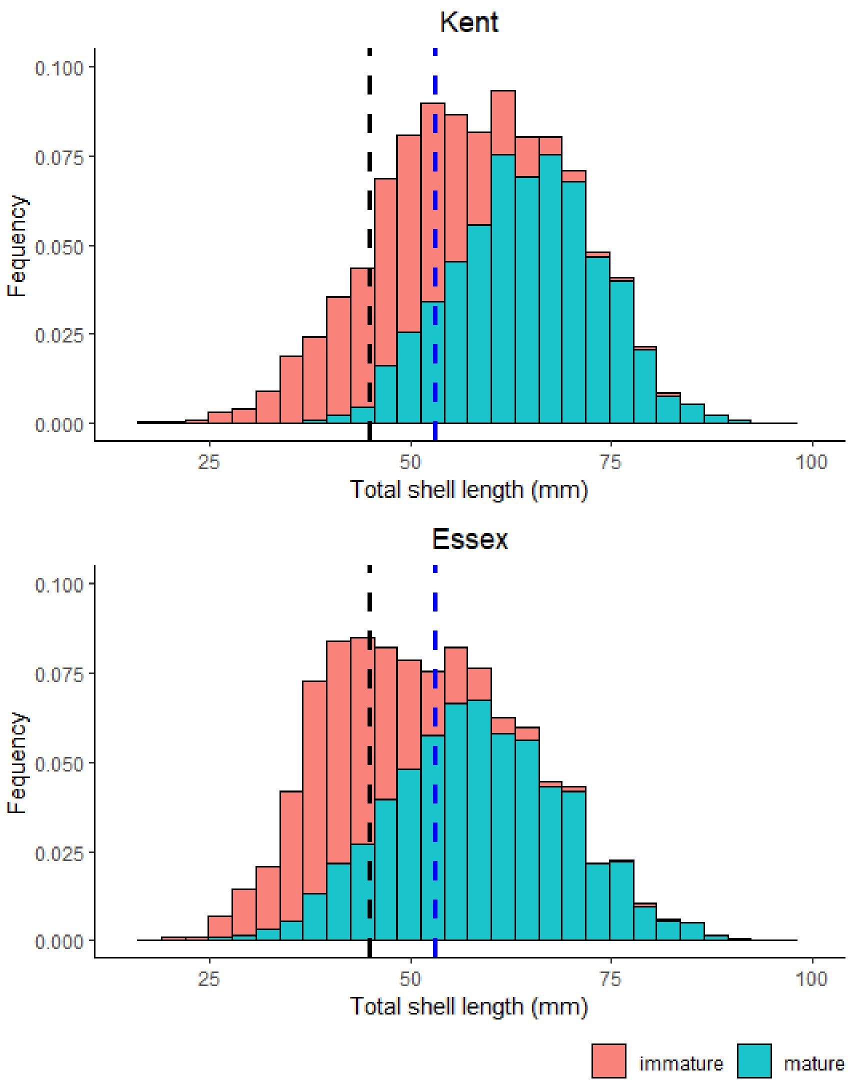

Figure 5. Length frequency histograms of the total shell length (TSL: mm) for *Buccinum undatum* sampled from Kent (a), and Essex (b). The hashed black line represents the EU MLS of 45 mm, and the blue hashed line represents the KEIFCA MLS of 53 mm. Red bars indicate the proportion of immature individuals and the blue bars indicate the proportion mature.

(58.4±11.5 mm) than for Essex (51.9±11.3 mm). The aggregated size distribution for both sites is demonstrated in Fig.5. Assuming that the size distributions are reflective of a yearly catch, approximately 87% of whelks caught in Kent (Fig. 5a), and 68% of whelks caught in Essex (Fig. 5b) could be legally retained under the EU MLS. In comparison, under the new KEIFCA MLS, 67% of whelks could be retained in Kent and 45% in Essex.

The length distribution of male and female whelks was significantly different from each other for both Kent (Mann-Whitney *U* Test: $p<0.005$) and Essex (Mann-Whitney *U* Test: $p<0.005$), with the mean length of males being slightly larger than females. The mean TSL in Essex was 52.9±11.3 mm for males and 51.3±11.2 mm females, and in Kent, the mean TSL was 58.9±11.6 mm for males and 58.0±11.5 for females.

Length distribution of sampled whelks also varied between seasons, with both Kent and Essex demonstrating similar seasonal trends (Fig.6). A bimodal pattern was witnessed in autumn and winter, and a skewed distribution towards larger whelks was observed in the spring and summer. The proportion of the catch retained under the nation MLS of 45 mm, KEIFCA MLS of 53 mm, and the respective L_{50} estimates for Kent and Essex samples is detailed in table 3.

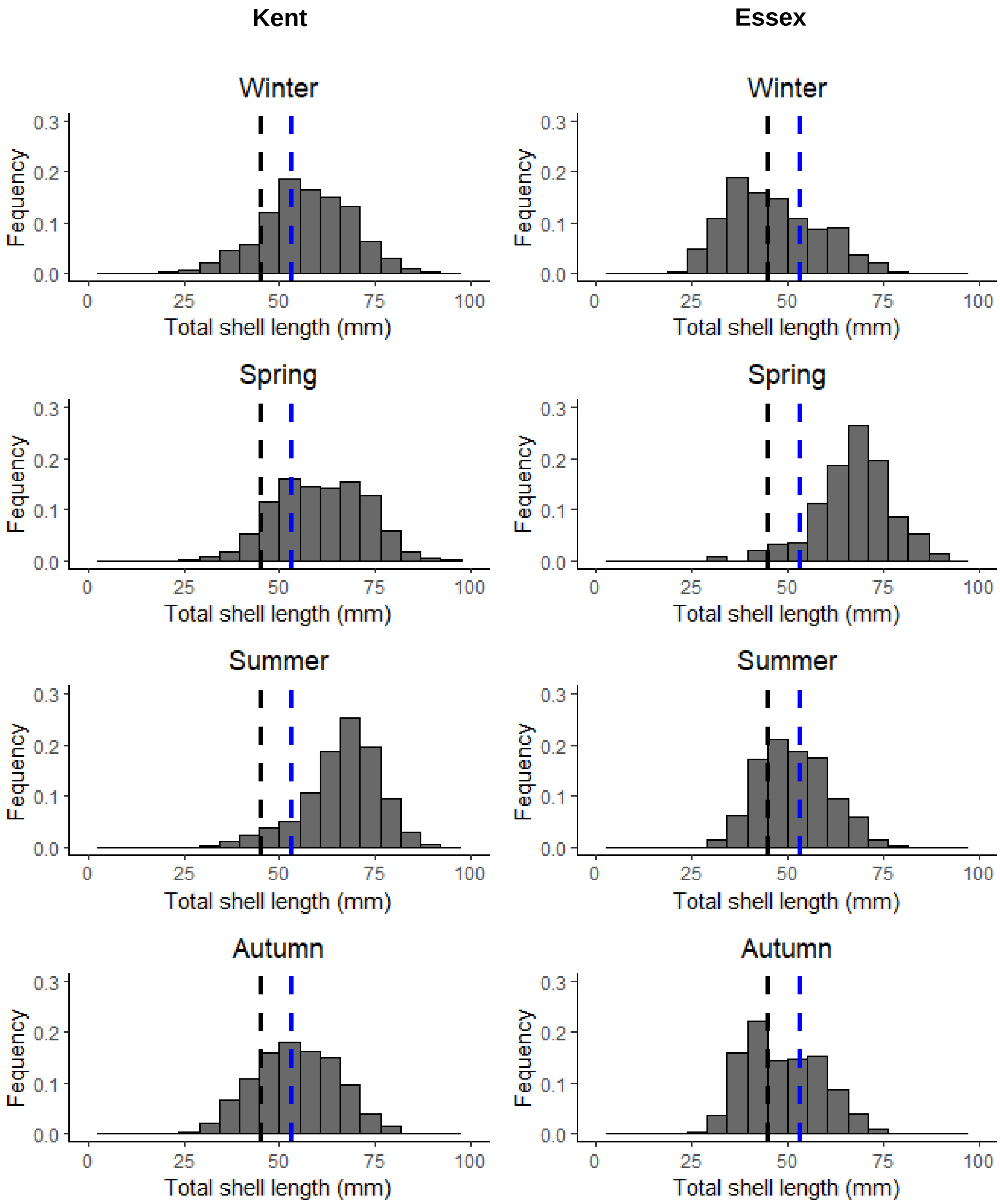

Figure 6. The seasonal size-frequency (TSL) distribution of *B.undatum* for area 1 and area 2 respectively. The black hashed line indicates the national MLS of 45 mm, and the blue hashed line indicates the KEIFCA MLS of 53 mm. Any individuals to the right of these lines will be retained under the respective MLS.

Table 3. The proportion of the catch above the national and KEIFCA MLS's and L50 estimates for Kent and Essex respectively.

Season	Kent			Essex		
	>45 mm	**>53 mm**	**≥L_{50} (56 mm)**	**>45 mm**	**>53 mm**	**≥L_{50} (44.2 mm)**
Winter	86%	63%	53%	49%	30%	50%
Spring	92%	74%	64%	97%	92%	98%
Summer	96%	91%	87%	74%	45%	77%
Autumn	79%	54%	44%	58%	34%	60%

3.2 Allometric analysis

3.2.1 Total weight and TSL

To identify the relationship between TSL and total weight, a growth curve was calculated using the equation $W = aTSL^b$. Linear regression on log transformed data revealed a significant relationship between total weight and TSL (R^2= 0.958, p<0.001). The equation of the growth curve was determined to be $W = 0.000246\, TSL^{2.853}$ (Fig. 7a).

The relationship between total weight and TSL was not significantly different between sample locations (slope: p>0.1), but elevation of the linear regression was significantly different (elevation: p<0.001). This indicated that a whelk from Essex is heavier than a whelk from Kent of the same length. However, due to the volume of data, it is possible that this result was detected though it is not biologically meaningful. Therefore, further visual analysis of the regression and ANOVA was applied to further validate the test result. ANOVA results determined the relationship between total weight and TSL was not significantly different between Kent and Essex. Visual inspection of the data showed regression lines to be in proximity, particularly in the area where points were most dense. It was, therefore concluded that the relationship between TSL and wet weight did not have a significant interaction with location.

3.2.2 Foot weight and TSL

The edible portion of a whelk is the foot; therefore, calculating the proportion of weight made up of the foot can be used as a measurement of yield. The relationship between foot weight and TSL was calculated by applying the same growth curve equation as above. Linear regression on log transformed data revealed a significant relationship between foot weight and TSL (R^2=0.892, p<0.001). The equation of the growth curve was $W = 0.0000117\ TSL^{3.291}$.

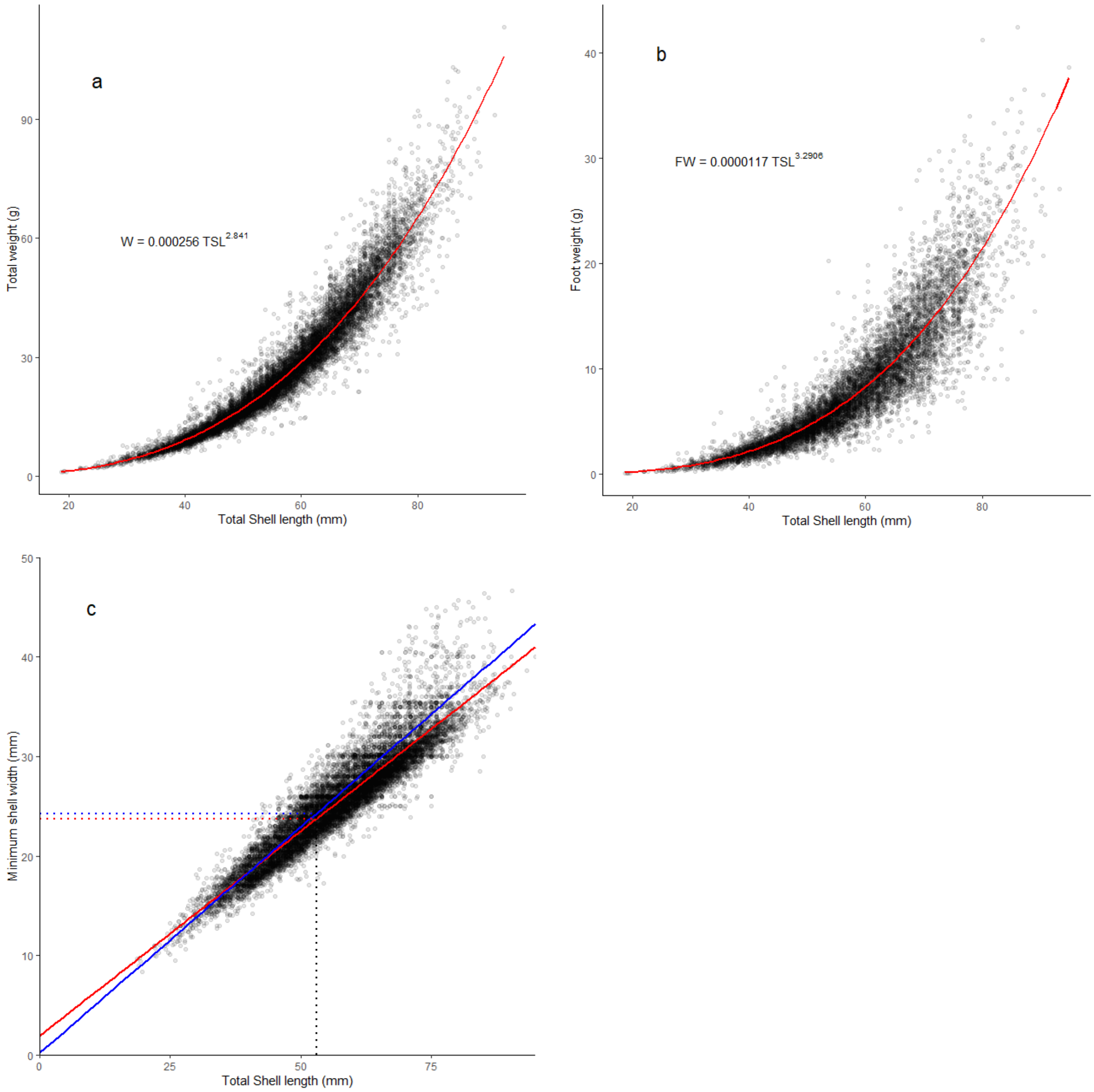

Figure 7. a) The TSL (mm) by total weight (g) relationship for whelk in Kent and Essex combined. b) The TSL (mm) by foot weight (g) relationship for whelk in Kent and Essex combined. c) The TSL (mm) by minimum width (mm) for whelk in Kent and Essex, line of best fit shown for Kent (blue) and Essex (red) respectively.

Table 3. Average (mean) weight and shell measurements for whelks caught in Kent and Essex sample sites respectively.

	Shell length (mm)	**Shell width (mm)**	**Total weight (g)**	**Body weight (g)**	**Foot weight (g)**

Kent	Female	58.0±11.5	26.0±5.1	29.3±15.6	15.9±10.1	7.8±5.0
	Male	58.9±11.6	26.0±5.2	30.1±16.6	16.8±10.9	9.7±6.7
Essex	Female	51.3±11.3	23.6±5.6	21.3±13.4	11.7±8.6	6.0±4.3
	Male	53.1±11.5	24.4±6.2	23.7±15.9	13.7±9.9	8.1±5.8

Linear regression on raw data revealed a significant relationship between TSL and shell width (Kent: R^2=0.855, p<0.001; Essex: R^2=0.844, p<0.001). The linear relationship was used to produce the following equations for determining minimum shell width from TSL:

$$\text{Essex Min shell width} = (0.454 \times \text{TSL}) + 0.224$$
$$\text{Kent Min shell width} = (0.411 \times \text{TSL}) + 1.937$$

The equations can be used for estimating appropriate spacings of riddle bars. For example, sorting bars would need to be ~24 mm apart to retain whelks of KEIFCA MLS of 53 mm TSL (Fig 6c).

Smatr analysis on log transformed data showed the relationship between length and width was statistically different between sexes (slope: p<0.001; elevation: p<0.001) and locations (slope: p<0.001; elevation: p<0.001). Visual inspection of the graphs, however, did not show any clear differentiation between the regressions of each group. It is, therefore, likely that the volume of data has resulted in a significant result being detected, however, it is so small that it is unlikely to be biologically meaningful.

3.3. Sex ratio

The mean average sex ratio of females to males was 1.49:1 (±0.31) for Kent, and 1.69:1 (±0.54) for Essex. Both were significantly different from the expected 1:1 ratio (Binomial Test: p<0.001). The sex ratio varied temporally throughout the year (fig.6), though females were seen in lower numbers from October to January.

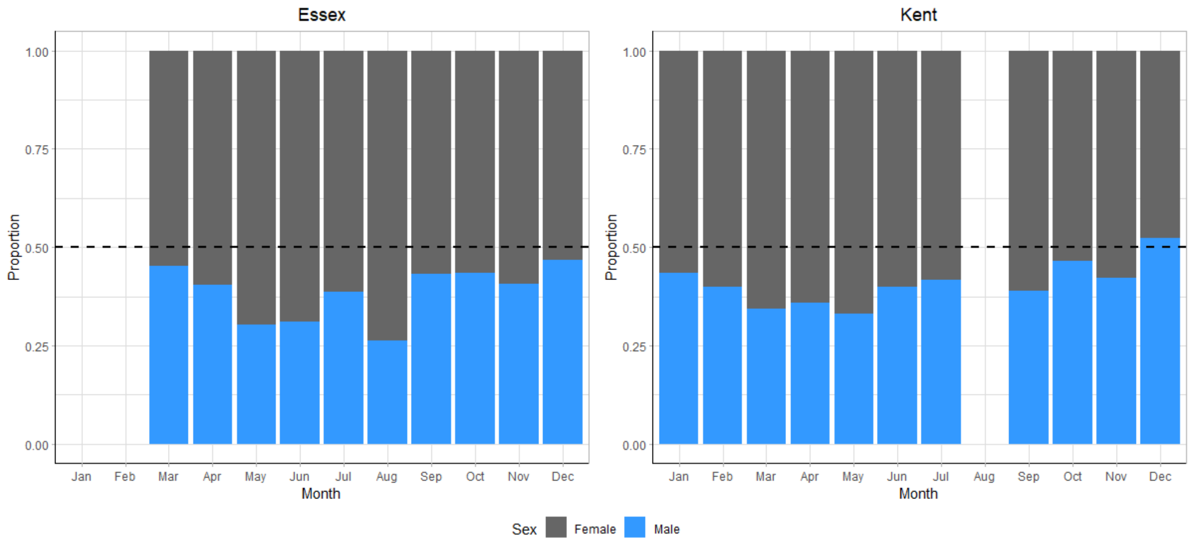

Figure 6. The pooled two-year monthly sex ratio of females (grey) to males (blue) sampled in Kent and Essex. The horizontal dashed line indicates the 1:1 ratio.

3.4. Reproductive cycle

The timing of the whelk's reproductive cycle is reflected in the monthly variation in the aGSI of mature individuals (fig.7a & 7b). Visual inspection reveals females show a distinct increase in the aGSI beginning in the spring (March to April) and reach peak maturity around June. The peak lasts from June to October, before dropping off in December. A similar, though less pronounced pattern is reflected in males, with aGSI peaking around September to October. These patterns mirror the seasonal patterns found in other whelk populations across the UK (Emmerson et al., 2017; Haig et al., 2015; Hollyman 2017).

The seasonality of aGSI was investigated for both males and females (fig.7c & 7d) by grouping the 18 monthly samples from each site into 3-month seasons (December, January, February = winter; March, April, May = spring; Jun, July, August = summer; September, October, November = Autumn). Statistical analysis revealed that the mean estimated aGSI varied significantly according to season (Kruskal Wallis: $p<0.001$), with significant differences in aGSI occurring between all seasons (Dunn's Kruskal-Wallis post-hoc test, $p_{adj}<0.001$ between all seasons). Winter had the lowest mean average aGSI, followed by spring and summer, with the highest average aGSI peaking in autumn. The seasonal cycle of gonad maturity is demonstrated visually in figure 7c&d.

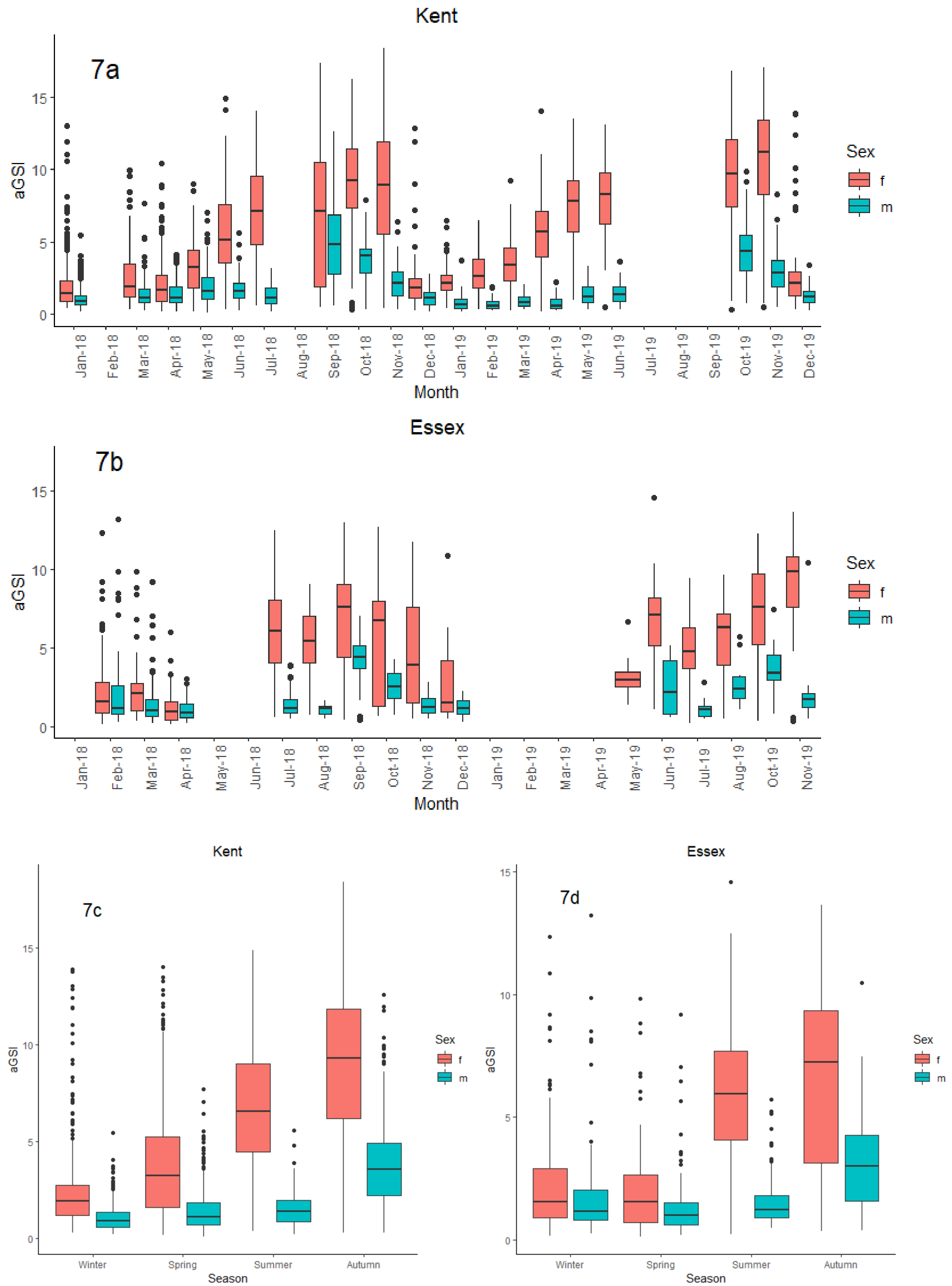

Figure 7. Boxplots showing seasonal variation in adjusted gonadosomatic index (aGSI) for mature male (blue) and mature female (pink) whelk (*Buccinum undatum*) from; 7a) whelk populations sampled in north Kent waters over the two-year

sample period; 7b) whelk populations sampled in Essex waters over the two-year sample period; 7c) the seasonal aGSI for Kent (pooled yearly data), and; 7d) the seasonal aGSI for Essex (pooled yearly data). Boxplots show the median (horizontal black lines), inter-quartile range (coloured boxes), max and minimum values (vertical whisker lines) and outliers (black dots).

Considering that the season in which a sample is taken has a significant effect on maturity, it seems appropriate that estimates of size-at-maturity (L_{50}) should be modelled using samples obtained in the summer and autumn months. At this time, the differentiation between the gonad and digestive gland is most visible when ovaries and testes mature, and the likelihood of a false maturity classification is minimised.

3.5. Size-at-maturity

To determine the TSL at which a whelk was 50% mature (TSL_{50}), a generalised linear model (GLM) with binomial distribution was applied to the summer and autumn aggregated two-year dataset, for females, males, and combined sex for each site, respectively. For each model, TSL was a significant explanatory variable for maturity with a high level of confidence ($p<0.001$ for all six models). The resulting ogives are presented in figure 8, and results for TSL_{50} and TSL_{95} are presented in table 3.

The smallest observed mature individuals were 26 mm in Essex and 31.7 mm in Kent. The largest observed immature individuals were 80.7 mm in Essex and 86 mm in Kent.

Table 3. The estimated L_{50} and L_{95} values (mm) for female, male and combined genders of *Buccinum undatum* collected from sample sites in north Kent and Essex. The upper and lower 95% confidence intervals are given, along with the significance of the generalised linear model (GLM).

Site	Gender	L_{50}	Lower CI	Upper CI	L_{95}	Lower CI	Upper CI	Sig.	n
Kent	Female	55.6	55.0	56.1	67.5	66.4	68.7	p<0.001	1833
	Male	56.7	56.0	57.5	71.9	70.0	74.0	p<0.001	1248
	Combined	56	55.5	56.5	69.3	68.2	70.4	p<0.001	3081
Essex	Female	43.7	42.8	44.5	54.4	52.8	55.9	p<0.001	701
	Male	45.1	43.9	46.3	59.3	56.6	61.9	p<0.001	446
	Combined	44.2	43.5	44.9	56.4	54.9	57.9	p<0.001	1147

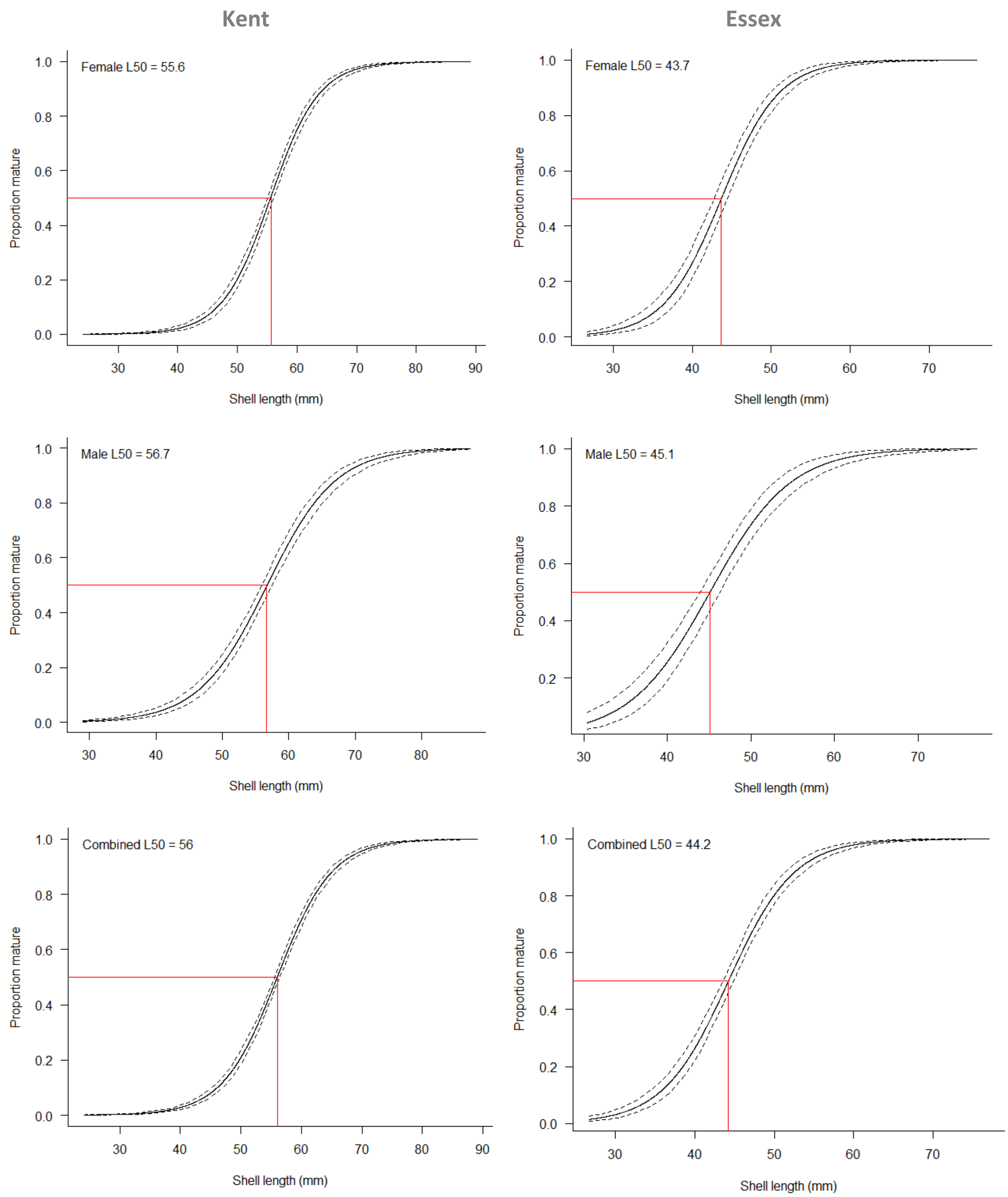

Figure 8. Maturity ogives for female, males and combined genders of *Buccinum undatum* populations from north Kent and Essex sample sites. The red lines indicate the shell length at which 50% of the population is likely to be mature (L_{50}), this value is also shown in the inset for each plot. The dotted lines represent the upper and lower confidence intervals for the respective GLM.

3.6. Estimating maturity in males using penis length

During dissection, visual assessments of maturity were often more distinct in females in comparison to males, leading to concern that there may be a higher likelihood of their being classed 'mature'.

Therefore, the use of penis length (PL) as an alternative measure of maturity in males was investigated using an iterative search procedure similar to studies conducted by Haig et al., in 2015.

Firstly, logistic regression with binomial distribution was applied to the summer and autumn aggregated two-year dataset for Essex and Kent samples respectively (similar to before just replacing the length with PL). Regression analysis estimated that the penis size-at-maturity (P_{50}) in males was 21.3 mm in Kent and 14 mm in Essex. The use of an iterative search procedure identified an inflection point in the PL:TSL relationship at 56.7 mm TSL for Kent (Fig.9a), and 47.4 mm TSL for Essex (Fig.9b). The inflection point indicates a change in the allometric relationship between shell length and average PL, which can be taken as an estimate of a change in maturity. The results here match closely with the TSL_{50} results calculated by gonad maturity.

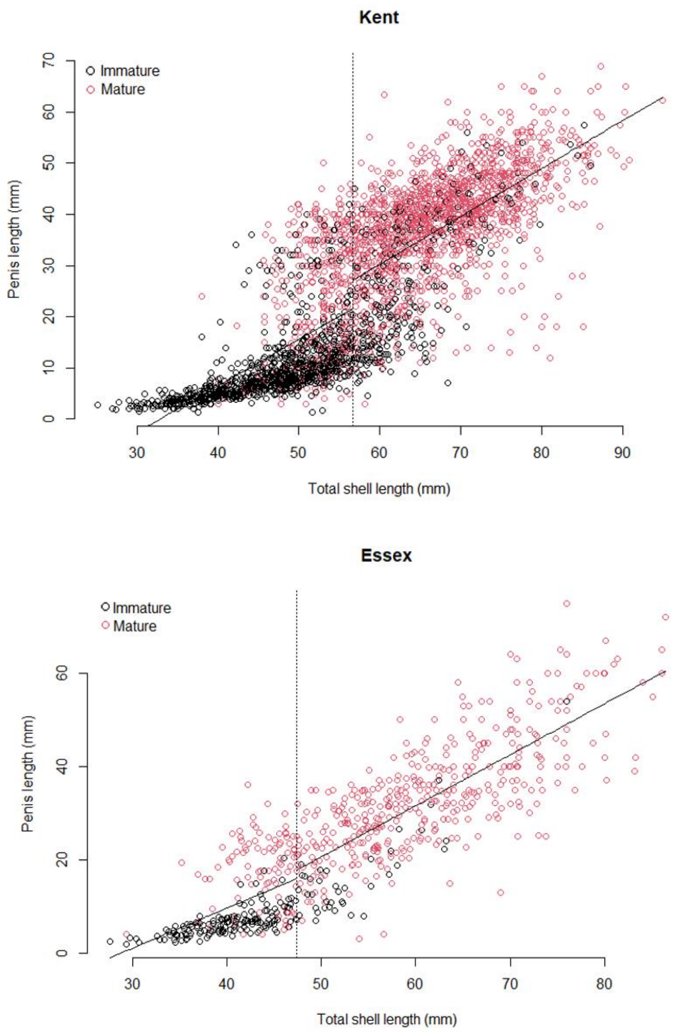

Figure 9. Inflection point indicating allometric growth based on morphometric variance between iterative tests on linear models of penis length and TSL for the whelk *B. undatum* in Kent (a) and Essex 2 (b). The dotted vertical line is the value with the lowest mean standard error. Red circles identify mature individuals, while black identify immature individuals determined from visual examination of the gonad

3.7. Size-at-age analysis and growth curves (Phil Hollyman analysis)

Statolith aging techniques were used in the previous study carried out by Dr Phil Hollyman to determine growth curves for sample populations from each of the four areas of the district. The pattern of growth differed between locations with whelks from area 2 growing quicker than area 1, 3 and 4 (Fig. 10), reaching the national MLS of 45 mm and KEIFCA MLS of 53 mm a year earlier than the others.

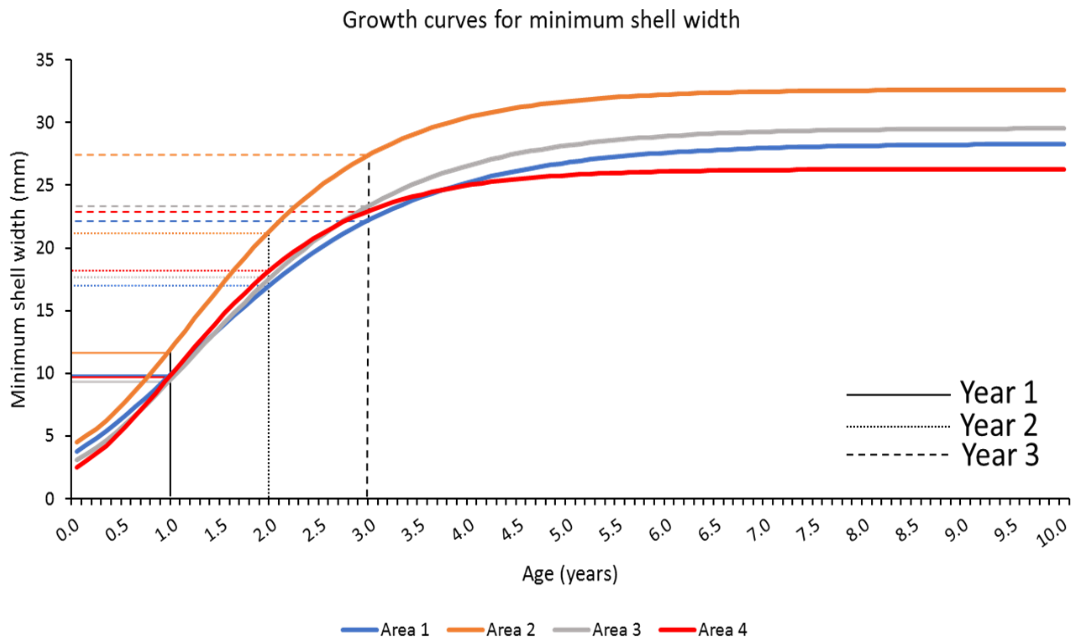

Figure 10. Growth curves for each of the four areas. Age (years) is plotted against minimum shell width (mm). The vertical and horizontal lines highlight the sizes whelks reach at year,1, 2 and 3 respectively. * Phil Hollyman and Chris Richardson report

Individuals demonstrated a clear increase in maturity between year 2 and 3, as the proportion of the population mature increased from 10-20% in year 2, to 50 to 72% in year 3. Table 5 presents the percentage of the population that will be mature in each year class.

Table 5. A summary table of whelk sizes (Shell length mm) for years 1, 2, 3 and 4. The % maturity of each area at each year is also included in the table

	Year 1		**Year 2**		**Year 3**		**Year 4**	
	Shell length (mm)	% mature	Shell length (mm)	% mature	Shell length (mm)	% mature	Shell length (mm)	% mature
Area 1	20.6	3.0	36.6	20.0	48.1	62.0	54.7	80.8
Area 2	23.1	0.0	45.2	17.0	59.2	72.0	66.1	85.8
Area 3	20.2	2.0	38.3	10.0	51.0	55.0	58.1	76.0
Area 4	21.5	0.0	40.1	13.0	50.4	50.0	54.9	64.8

From this we can see that it takes whelks approximately 2 years to reach the national MLS of 45 mm and 2.7 to 3 years to reach SAM and the KEIFCA MLS of 53 mm (tab.4).

Table 4. The time taken (in years) to reach key sizes and life stages for each of the four areas.* Phil Hollyman and Chris Richardson report

	Area 1	Area 2	Area 3	Area 4
Time taken to reach 45 mm	2.7	2	2.5	2.4
Time taken to reach riddle size of 25mm	3.9	2.5	3.4	4
Time taken to reach L_{50}	2.7	2.7	3	3

3.8. Likelihood of reproduction

Using growth calculations and SAM estimates, it is possible to determine the likelihood of a whelk having reproduced at least once at a given size. Figure 11 demonstrates the proportion of the population for each of the four sample areas that will have reproduced at least once (blue) compared to the proportion classed as mature (green). The percentage of the catch classed as mature compared to having reproduced at least once is presented in table 6.

Table 6. The percentage of the sample population classed as mature vs the percentage classed as having reproduced at least once**.**

	% classed mature	% reproduced at least once
Area 1	79.5%	24.7%
Area 2	51.2%	25.1%
Area 3	39.4%	11.9%
Area 4	46.3%	20.3%

The percentage of the catch that has not reproduced at least once that is protected by the national MLS of 45 mm and the KEIFCA MLS of 53 mm respectively is presented in table 7. The KEIFCA MLS of 53 mm protects considerably more whelks that have not yet reproduced, providing greater protection to the districts spawning stock.

Table 7. The percentage of individuals that have not reproduced that are protected under the national MLS of 45 mm and the KEIFCA MLS of 53 mm respectively.

	% of non-reproduced population protected under 45 mm	% of non-reproduced population protected under 53 mm
Area 1	13%	51%
Area 2	5%	26%
Area 3	26%	80%
Area 4	42%	76%

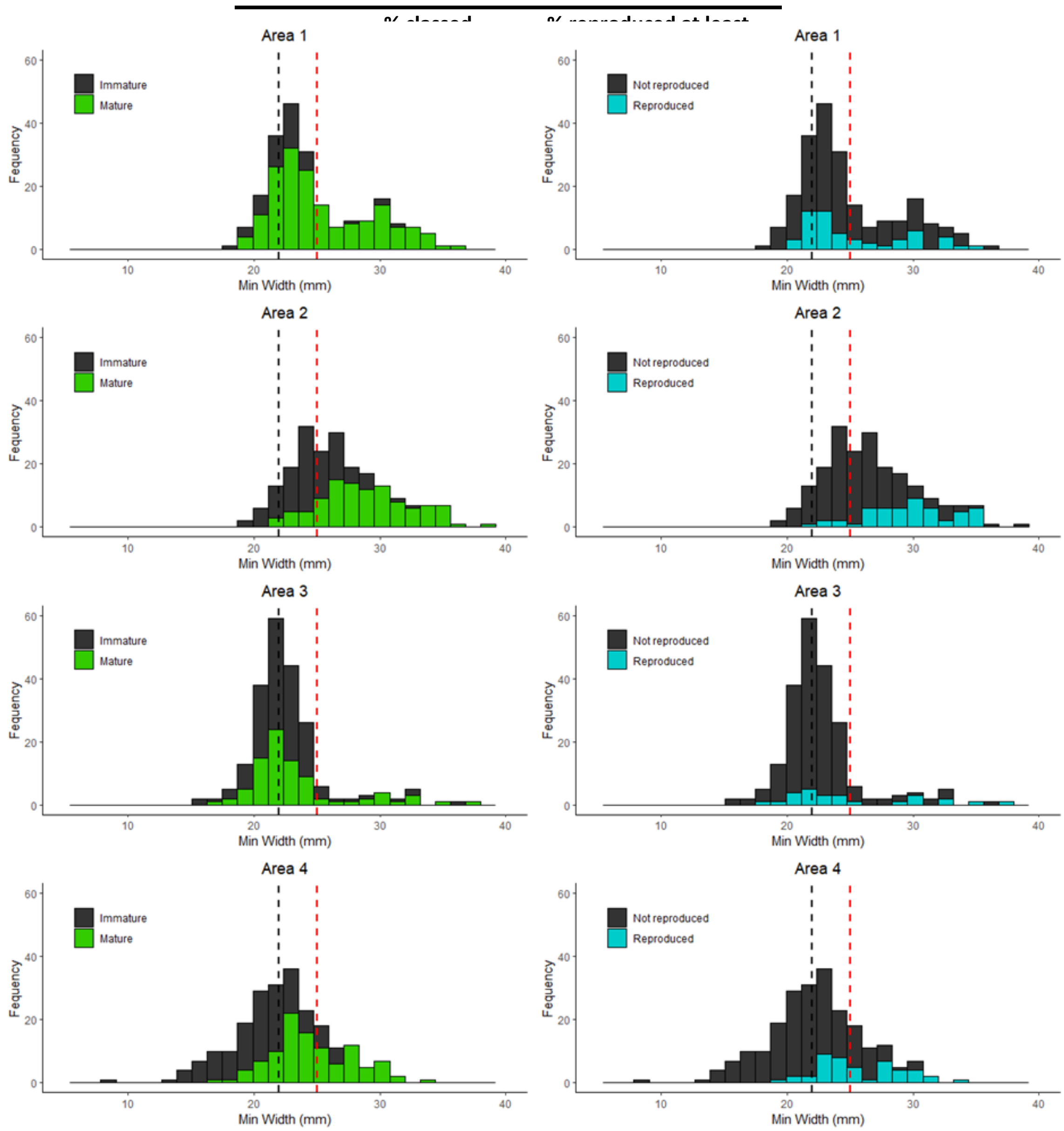

Figure 11. The proportion of mature individuals (green) vs the number of reproduced individuals (blue) from each of the four areas across the district. The hashed black line indicates the national MLS of 45 mm, and the red hashed line indicates the KEIFCA MLS of 53 mm.

4. Discussion

4.1 Size at maturity

The two studies presented here successfully determined the size-at-maturity for a single population of whelks from each the Essex (area 1) and Kent (area 2) fishing areas within the KEIFCA district. The two sites were chosen because they are situated on either side of the Thames Estuary, and in previous research had been found to display different SAM estimates. SAM varied significantly between the two neighbouring populations of area 1 (L_{50} 44.2 mm) and area 2 (L_{50} 56.1 mm).

This two-year comparison of area 1 and 2 accounting for spatio-temporal variation confirmed the initial findings presented in Dr Phil Hollyman's report and alleviated the possibility that previous results were due to limited sampling. This high degree of variability in size-at-maturity is consistent with previously published studies from across the UK (Haig *et a*l., 2015; McIntyre *et al*., 2015; Hollyman 2017; Emmerson *et al*., 2017).

The size-at-maturity results show that the national MLS of 45 mm is not sufficient to protect whelk breeding stock across the district because a substantial proportion of the catch has not yet reached sexual maturity. The outcomes of study 1 and 2 support KEIFCA's MLS of 53 mm, which allows a greater portion of the stock to reach sexual maturity before becoming a harvestable size. However, the KEIFCA MLS of 53 mm falls 3 mm short of the combined L_{50} estimate for whelks in area 2. This large difference in size-at-maturity highlights a common difficulty in managing whelk fisheries even over small spatial scales. Sample sites from area 1 and area 2 are approximately 43 miles apart, but sample populations display ~12 mm difference in size-at-maturity. The application of different management measures on such a small spatial scale is impractical for enforcement purposes and, therefore, stock is managed as a single unit across the KEIFCA district. However, the increase in MLS still provides considerably enhanced protection for the immature whelk stock in area 2, increasing the proportion of immature whelks protected from 31 to 66%. In addition, the KEIFCA byelaw specifies a riddle spacing of 25 mm which corresponds with a whelk of 56.2 mm, and therefore, should provide sufficient protection to area 2's immature stock.

4.2 Size-at-age and growth

The size-at-age analysis in this study also demonstrates that setting an MLS at the L_{50} estimate alone may not provide sufficient protection to whelk breeding stocks. Frequency of spawning events, age-at-maturity, and the likelihood of individuals having reproduced at least once before their removal, are also important life-history factors to consider. Monthly gonad maturity analysis over two years has demonstrated that whelks undergo an annual breeding cycle, with spawning taking place once a year between September and November. In addition, growth curves calculated from statolith analysis in study 1 for each of the four fishing areas demonstrated that it takes between 2.7 to 3 years for a whelk to reach size-at-maturity. Therefore, if a three-year-old whelk is caught before the breeding season, though it may be at sizeable maturity, it will be removed from the population before it is likely to have bred at least once. This is because in the previous year, at two-years-old, a whelk is only between 10 and 20% likely to be mature at the time of spawning (tab.4). For whelks in the KEIFCA district, 68 to 81% of mature whelks will not have reproduced at least once by three years of age. However, by allowing an additional year, whelks grow a further 4 to 7 mm in length, increasing the likelihood of having reproduced (in the previous year's spawning event) into the 50 to 72% range.

When considering size-at-maturity estimates alone, it may seem that an increase in MLS from 45 mm to 53 mm 'over protects' whelk stocks in areas 1, 3 and 4. However, when accounting for size-at-age calculations, the KEIFCA MLS of 53 mm grants an additional year for growth and significantly increases the likelihood of individuals contributing to the recruitment cycle before being removed from the population. The KEIFCA MLS protects between 26 and 80% of individuals that have not yet reproduced, in comparison to the national MLS that protects between 5 and 42%. However, to protect whelk stocks in area 2 and ensure that 50% of the population has had the opportunity to spawn, further protective measures are required. Currently, size-at-maturity studies dominate much of the research and regulatory studies conducted for whelk fisheries across the UK (Haig *et al*., 2015; Emmerson *et al*., 2017; Lawler, 2014). The results of this report highlight the importance of considering size-at-age and breeding cycles in calculating an appropriate MLS and modelling the recovery rates of depleted stock (Hollyman *et al*., 2018).

For many marine species, there is a positive relationship between the size and age of female individuals and the quality and quantity of their progeny (Marshall *et al.,* 1998; Vallin and Nissling 2000). In 2002, research conducted by Valentinnson demonstrated that larger, older, female whelks produced a greater number of eggs than younger females, though the quality of egg was not significantly different. Older, larger females likely account for a disproportionately large share of the potential recruitment in populations of *B. undatum* (Valentinsson, 2002). Observations during dissection in study 2, indicated that larger females were more likely to reach a higher visual maturity at the time of spawning than their smaller counterparts. SAM calculations consider all whelks that display gonadal maturity as equally mature and do not consider fecundity-at-size. Spawning stock biomass, is likely to be a better measure of spawning stock than the number of mature individuals in a population (Valentinsson, 2002). For exploited species, knowledge of maternal effects can be useful, but is not often considered in whelk stock management (Vallentinson, 2002).

The reason for the differences in SAM and mean average size between the four study areas is unclear and could not be determined within the scope of this study. Latitudinal trends (Hollyman 2018, McIntyre *et al*., 2015), bathymetry (Haig *et al*., 2015), food availability (Gendron, 1992; Fahy et al., 2006) and sea-bottom temperature (Emmerson *et al.,* 2019) have previously been found to correlate with trends in asymptotic size and offer a potential explanation for localised variation in the SAM and variable growth rates. In 2019 Emmerson *et al*., identified a significant negative linear relationship between sea-bottom temperature (in degree days) and the average size of whelk on a regional scale. Emmerson *et al's*., results indicated that warmer sea-bottom temperatures accelerate the growth rate of individuals at early life-stages but limits the maximum potential size as growth rate slows for whelks at a younger age. SAM has also been shown to be positively correlated with depth indicating whelks either move to deeper, cooler water as they increase in size, or that the conditions for a larger body size provided for in deeper water. Early investigations into the average sea-bottom temperatures using Copernicus Marine Environmental Monitoring Service (CMEMS) (http://copernicus.eu) indicates that area 1 and 2 in this study have experienced similar temperatures (Kent: 1469.7, Essex: 1456.9 degree days) over the past 5 years. The two sample sites also display similar depth profiles with a range of 3 - 10 m. A possible explanation for the difference in SAM may, therefore, lie in the local hydrographic conditions or habitat type.

When considered against a wider geographical range, whelks in area 1 show considerably lower SAM than surrounding populations. Fishing grounds of area 1 and 2 fall on either side of the Thames Estuary respectively and are subject to differing hydrographic conditions, habitat type, food availability and fishing pressures which may also offer some explanation to the differing SAM and mean average sizes.

Figure 12. Size-at-maturity estimates for whelks in the inshore (0-6 nm) of south-east England. Projection WGS 84 / UTM zone 31N EPSG:32631 .

4.3 Maturity and reproductive cycle

Whelks demonstrate a clear annual reproductive cycle of in the KEIFCA district (Fig. 13). The seasonal onset of maturity, as indicated by the ripening of the gonads and increase in aGSI values, begins in the early summer (May) and drops off mid to late autumn (October) indicative of a spawning season. Due to the seasonal nature of reproduction, the ideal season for maturity calculations based on visual assessment is the summer and autumn when most individuals display maximum gonad differentiation. At any other point in the year, mature whelks are less likely to be assigned mature which would lead to a lower SAM estimate. The similar SAM estimates of study 2 compared with study 1 also show that future assessments do not need to undertake such extensive sampling in order to obtain reliable SAM estimates. A representative sample (~250 individuals) taken annually between July and September from each of the four areas would be enough to monitor long-term changes in SAM that could be indicative of recruitment over-fishing.

During analysis visual maturity in males was more difficult to discern than females, with many large individuals (>50 mm TSL) exhibiting no differentiation in the digestive whorl and, therefore, being classed as immature. At larger sizes, whelks have been thought to skip reproductive years (Matel et al., 1986; Gendron 1992), similar to some gadoid species (reference) and offering some explanation as to why apparently mature individuals may not display obvious gonad differentiation. An investigation into the use of PL as an indication of maturity was therefore conducted to help future study and validate the L_{50} calculations of male whelks. This was done by identifying a change in the allometric relationship between shell length and average PL, called the inflection point, which can be taken as an estimate of a change in maturity. The iterative process identified an inflection point similar to the L_{50} value (area 1: morphometric inflection = 47.4, area 2: morphometric inflection 56.7), helping to both validate the initial L_{50} estimates, and validate the use of PL as an effective measure of maturity in the absence of visual gonad differentiation.

4.4 Allometric analysis

Despite whelks demonstrating significant differences in average size and size-at-maturity from area 1 and 2, allometric analysis revealed that the sample populations did not have significantly different relationships between TSL and other body measurements. Whelks from area 1 and 2 put on a similar amount of weight per mm of TSL. The relationship between foot weight and TSL was also the same. As the foot is the edible portion of the whelk and therefore a measurement of yield, it can be concluded that whelks from both areas have similar yield per mm TSL. Whelks from both areas also had a similar relationship between shell width and TSL. The relationship between shell width and TSL is critical to determining whether riddle sizing will have a uniform effect on whelk stock across the district as riddles sort whelks by width. In addition, it demonstrates that the specified riddle size of 25 mm in the KEIFCA byelaw correlates with a ~54 mm length whelk in any of the four study areas,

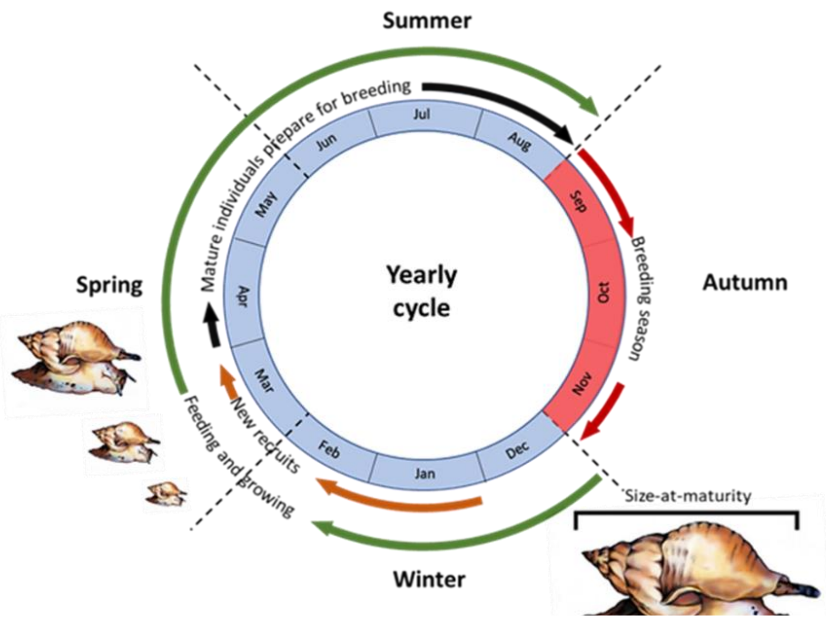

Figure 13. The annual whelk reproductive cycle in the KEIFCA district.

catching closely with the KEIFCA MLS of 53 mm and providing an effective means of sorting whelks across the district.

4.5 Catch composition and implications of raising the MLS

The length frequency distribution and mean average size of whelks differed significantly between area 1 and 2. The application of a 53 mm MLS therefore means that fishers from area 1 may be disproportionately affected because a larger proportion of mature individuals are ineligible for retaining. However, fishing effort and annual landings are far greater in area 2 than area 1, with catch return data showing that 716 tonnes of whelk were caught and landed in area 2 between 2018 and 2019, in comparison to 76 tonnes from area 1 over the same period (Fig 14.; KEIFCA, catch returns 2021). Fishing grounds in area 2 are some of the most productive in the district, have supported a whelk fishery for over a century, and account for a large portion of the local fishermen's income. It could be argued that management measures and MLS's should be weighted in favour of protecting more heavily fished stock, that support a greater number of fishers, in order to sustain a viable fishery for a larger portion of the fleet.

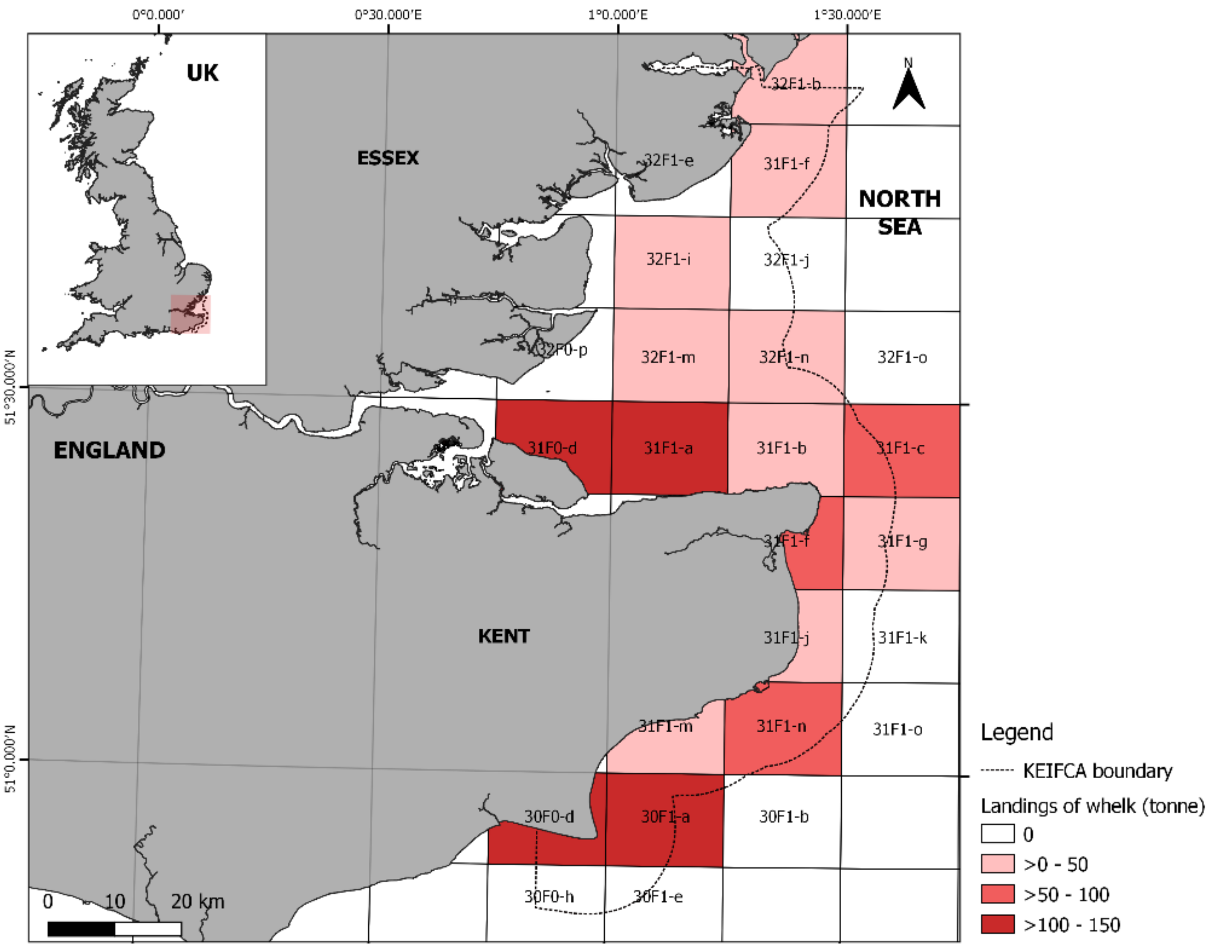

Figure 14. The spatial distribution of whelk (Buccinum undatum) landings between 2018 and 2019 by inshore >10m boats in the KEIFCA district by ICES sub-rectangle. Projection WGS 84 / UTM zone 31N EPSG:32631 .

Seasonal fluctuations in length frequency were also observed, with catch in summer and spring months consisting of a greater proportion of larger individuals above the MLS. In addition, the sex ratio of catch was significantly different from the expected 1:1 ratio, with females contributing a greater portion of the catch. It is, therefore, possible that during the spring and summer months, fishers are disproportionately removing larger female individuals from the population, and potentially altering the population structure and recruitment potential.

4.6 Future Management

Regulatory bodies such as KEIFCA must achieve a balance between the practicality of management, life-history parameters of the population, fishing intensity, and the local fleet dynamics, when determining management measures that aim to ensure the sustainability of a fishery. Despite the increasing volume of research being undertaken, the *B.undatum* fishery is still considered data poor and stock assessments are not available for much of the UK. The results presented here demonstrate the importance of understanding the life-history of whelks in determining effective management and setting an MLS, however, there are several equally important factors that require consideration.

The lack of a baseline stock assessment means it is difficult to determine whether the current levels of fishing are high enough to cause long-term depletion of stock or a reduction in SAM due to recruitment overfishing. It is, therefore, critical that data on the fleets catch per unit effort (CPUE) is obtained, and a stock assessment carried out. Using MLS as the sole tool for management would require a considerable increase across many parts of the UK. Such a measure is often unpopular with fishermen given the immediate drop in yield and increased effort they may incur. Limiting effort by introduction of a permitting scheme, pot limits and specifying riddle sizing, as stipulated in the KEIFCA Flexible Whelk Permit Byelaw are simple to enforce and have contributed to the effective management in the district. Analysis of landings data in the district shows it has remained relatively consistent over the past 5 years (KEIFCA landings data), indicative of a stable stock, though this conclusion is tentative in the absence of CPUE metrics.

Closed seasons have also been used in other shellfish fisheries as a measure of catch limitation and protection of breeding stock. Knowledge of the whelk spawning season and growth rates as presented here could also be used to determine the timing of a closed season that protects first year spawning stock and increases the number of individuals reproducing at least once before removal.

Many of the under 10m fishers in the KEIFCA district target a variety of commercial species in addition to whelk, the relative contribution of these to their landings and income fluctuate dependent on the season, availability and price. Future analysis of CPUE data could look to identify the influence of socio-economic and alternative species availability on whelk fishing effort in the district. By establishing a holistic view of both the industry dynamics, baseline stock levels and life-history characteristics of the species, KEIFCA could ensure they develop effective management to secure the long-term viability of a key stock in their district.

5. Conclusion

This study provides the most comprehensive scientific evidence to data on the life-history characteristics of common whelk in the KEIFCA district. The current 53 mm MLS proves to have greatly increased the number of immature individuals protected and allows a significantly larger proportion of the population to reproduce at least once before they are removed from the population. However, the KEIFCA MLS is still potentially too low to protect the spawning stock for area 2 based on L_{50} and size-at-age estimates.

Continued monitoring of the stocks SAM is recommended to be able to detect the presence of recruitment overfishing and the effectiveness of the 53 mm MLS. Further work should look to establish a baseline stock assessment, and CPUE to provide a comprehensive view of the key factors influencing the fishery.

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