



## Original Article

# Temporal and spatial variation in size at maturity of the common whelk (*Buccinum undatum*)

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There is little common rationale for the 45 to 75 mm total shell length (TSL) minimum landing sizes (MLS) for *Buccinum undatum* among countries in the Northeast Atlantic. Size at maturity and length frequency of *B. undatum* populations vary over small spatial scales; however, the driving mechanism for this is unknown. Size at maturity research for *B. undatum* dates back to the late 1980s; since then, there has been little consensus on laboratory methods or in which season to undertake the research. Here, we assess small-scale spatial variation in size at maturity over a year to identify the seasons that increase error in visual maturity estimates. We compare and contrast results from methods used in the literature to estimate maturity for *B. undatum*. Monthly, *B. undatum* samples were obtained from Welsh fishers between May 2013 and May 2014 from eight sites at four locations ( $n = 5080$ ). All whelks were sexed, weighed, and measured, and up to 60 whelks from each location were assessed for maturity ( $n = 1659$ ). Mature whelks were found in all months, with a peak in reproductive activity through summer and early autumn, followed by the onset of spawning in November. Size at maturity varied between sexes and sites, and ranged from 51 to 76 mm TSL. Whelks caught in shallow waters (0–10 m) matured at a smaller size than those from deeper waters (up to 60 m). Length frequency varied at each site suggesting that a single increase in MLS would impact fishers disproportionately. No methodology trialled was found without inherent errors when used in isolation, though a combination of methods proved ideal. The seasonal variation in maturity estimates suggested that assigning maturity is increasingly difficult outside annual reproductive periods and that prespawning is the ideal time to undertake visual gonad assessments for whelks.

**Keywords:** commercial fishery, gonadosomatic index, minimum landing size, mollusc, morphometric, size at maturity.

## Introduction

The common whelk (*Buccinum undatum*, Linnaeus, 1758) is a neogastropod mollusc, common in the subtidal waters of the North Atlantic shelf waters (de Vooys and van der Meer, 2010). There has been a small artisanal whelk fishery in the United Kingdom since the early 1900s, with annual landings of ca. 4500 t for England and Wales in 1911 (Dakin, 1912). Global trade in seafood and demands for whelks in the Far East led to a dramatic increase in landings through the 1990s (Fahy *et al.*, 2000). More recently, UK landings have climbed from 12 900 t in 2009 to 20 000 t in 2013, with an estimated value of £13.7 million (MMO, 2014). For this reason, whelks are among the most important shellfish fisheries for the United Kingdom (after *Nephrops*, scallop, crab, and lobster). For the most part, entry into the whelk fishery is not restricted and

requires minimal capital investment (traps can be as little as one-third the price of crab/lobster traps; J. A. Haig, pers. obs.). As other fisheries decline or experience restrictions, a displacement of effort into the whelk fishery is expected, resulting in increasing pressure on stocks. There is limited management of whelk fisheries in the North Atlantic, and there are concerns that whelk stocks are currently overfished (Nicholson and Evans, 1997; McIntyre *et al.*, 2015; Shrivies *et al.*, 2015).

Throughout the North Atlantic, the minimum landing size (MLS) for whelk varies considerably (Table 1). It is now well understood that whelk populations vary in their length frequencies, genetic structure, and size at maturity (Table 1) over very small spatial scales (Weetman *et al.*, 2006; Shelmerdine *et al.*, 2007;

**Table 1.** Results from published literature for MLS and size at maturity of *B. undatum* using various methods and sampling months.

Location	L <sub>50</sub> male	L <sub>50</sub> female	Method	Study period	MLS	Reference
England	46.4–76.2	44.8–77.8	Visual	Jan–Mar	45	Hancock and Urquhart (1959); McIntyre et al. (2015)
Ireland	63.2–83.2	–	PL	–	50	Fahy et al. (2000)
Shetland	86	101	–	–	75	Shelmerdine et al. (2007)
France	49	52	Histology	–	45	Heude-Berthelin et al. (2011)
Canada	49–76	60–81	PL/GSI	Apr and May	70	Gendron (1992); Santarelli (1985)
Iceland	45–75	–	PL	May and Sep	45	Gunnarsson and Einarsson (1995)
Sweden	53.5–71.9	51.5–71.5	Microscopy	Oct–Nov	45	Valentinsson et al. (1999)

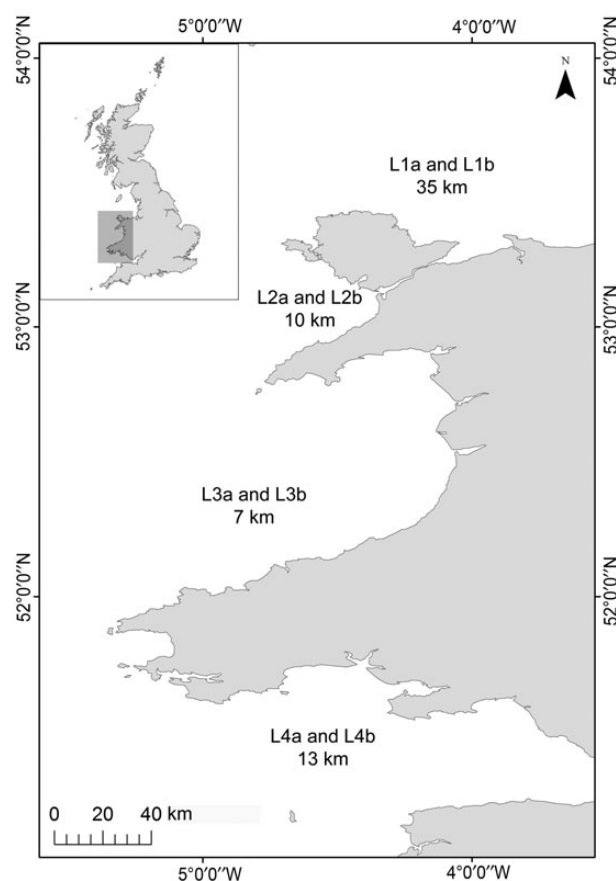
Methods include: Visual, a visual assessment of the differentiation of the digestive whorl; PL, measuring the penis length as an indication of male maturity; Histology, a complete histological assessment of the gonad; GSI, using the weight of the gonad as a gonadosomatic index; Microscopy, microscopic examination for the presence of sperm or oocytes.

Pálsson et al., 2014; McIntyre et al., 2015), providing little rationale for a uniform approach to the application of a single common MLS. It is clear from research undertaken to date that size at maturity for most common whelk populations is greater than the current European Union MLS of 45 mm (Table 1).

As whelks are direct developers, they have limited dispersal potential and display little adult movement (Pálsson et al., 2014) and also display a high degree of spatial variability in life history parameters (Shelmerdine et al., 2007). For this reason, it is not surprising that size at maturity varies over small spatial scales, although there is no current explanation. The phenotypic plasticity displayed by a marine gastropod population can be closely related to mortality and growth rates (Stearns and Koella, 1986), which vary temporally and spatially with fishing pressure (Torroglosa and Giménez, 2010), food and habitat availability (Pardo and Johnson, 2005), parasitic infections (Fredensborg and Poulin, 2006), and environmental parameters such as temperature and salinity (Montory et al., 2014). Size at maturity in England was found to be negatively correlated with depth and temperature (Bell and Walker, 1998; McIntyre et al., 2015), although this pattern did not follow a latitudinal trend to indicate optimum environmental conditions over a broad distributional scale (McIntyre et al. 2015).

At present, a lack of standardized methodology complicates comparisons between size at maturity studies. Morphometric, biometric, visual assessment, and histological methods are used to determine maturity in whelks, and each method could produce a different size at maturity result for the same sample. Ideally, the method introducing the least error is a histological examination of the reproductive structures, although due to the expertise, expense, and time required for histological studies, this is not always a viable option. Whelks display distinct seasonality to breeding periods; therefore, gonads of mature whelks are not obvious throughout the year. Presumably, the ideal time to visually assess gonad maturity is just before the spawning season when the digestive whorl shows full differentiation between the gut and gonad structures. Spawning occurs in the United Kingdom between November and January (Kideys et al., 1993; French, 2011), year-round in Swedish and Danish waters (Valentinsson, 2002), and in autumn in Canadian waters (Martel et al., 1986; Himmelman and Hamel, 1993). In French waters, October was identified as the period when 90% of whelks >59 mm total shell length (TSL) displayed ripe gonads (Heude-Berthelin et al., 2011).

Here, we assess how the spatial scale and time of year affect estimates of size at maturity. We hypothesize that, given the lack of a clear latitudinal gradient in size at maturity, the observed variation is likely in response to local environmental parameters (depth and temperature). We assess a gonadosomatic index (GSI) to confirm

**Figure 1.** Map of Wales, United Kingdom, showing the approximate location of the four sites which were fished for whelk (*B. undatum*) in 2013 and 2014. Precise locations not shown to protect the commercial interests of the fishers involved. The distance (km) between the two sites within each location is situated under each site code.

seasonal patterns in condition and test the usefulness of morphometric estimates of maturity for male whelks. We use available fisheries data to determine whether patterns in maturity correspond to population length frequency patterns to estimate the impact of a potential change in MLS on whelk landings.

## Methods

Four fishers in Wales were each asked to fish two whelk traps (pots) and land the total contents of those two pots from one day's catch

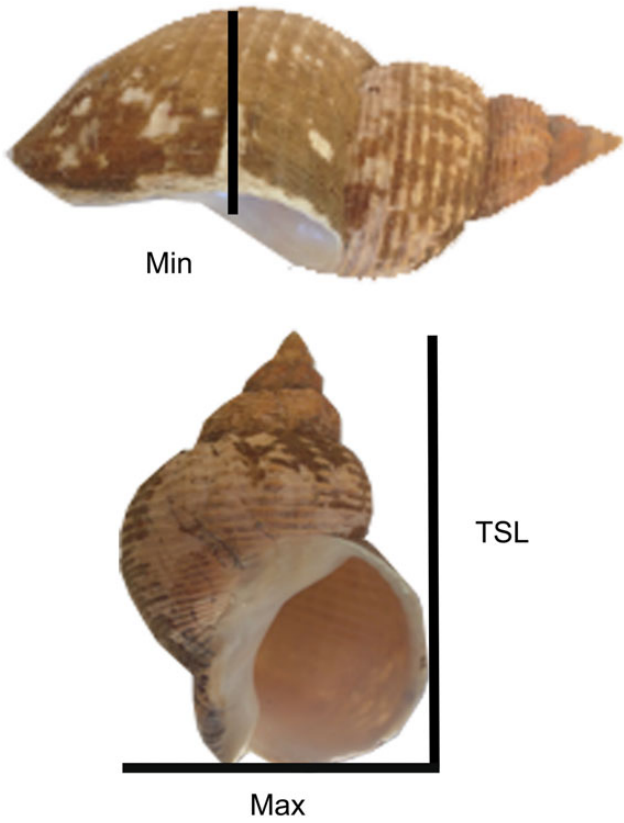
(with a preference for catches experiencing a typical soak time of 24–48 h) each month. Fishers attached each pot separately to a different string of pots (of 15–50) and fished them using available bait throughout the year [which was typically a combination of dogfish (*Scyliorhinus canicula*) and crab]. Fishers were asked to record the coordinates of the fished pots and land the total contents each month for 13 months (Figure 1). The supplied pots were 36-l “Fish-tec” or “stand-up” pots (Figure 2) weighted with lead (diameter 320 mm and height 350 mm), with drainage holes in the base of the pot (30 mm in diameter). The Fish-tec pots were chosen due to their reported ability to fish in any tide and along with any other gear (advice given by active whelk fishers). For this reason, they were chosen as the most appropriate for the four locations in Wales. Some gaps occurred in the fishery-dependent data due to inclement weather, boat repairs, or because fishers changed fishing gear to target another species. Fishers operated in one of the four distinct locations in Wales. Upon viewing the coordinates from science pot returns, it was possible to assign two distinct sites (or fishing patches) within each of those four locations. Each site was fished regularly throughout the year; after discussing with the fishers, it was clear that each of the whelk “patches” was targeted during the fishing year. To maintain the fishers’ commercial confidentiality, the exact locations and sites are not reported.

Whelks were stored frozen and defrosted before dissections. All whelks were weighed wet, and minimum shell width, maximum

shell width, and TSL were recorded (Figure 3). A total of 30 randomly chosen whelks were selected from each pot sample (60 whelks per monthly sample per location) from each month and each location for visual maturity assessment. Each whelk was carefully removed from the shell, and the whole body was weighed (in grammes to two decimal places). Sex was determined by the presence/absence of a penis. The whorls were inspected for differentiation between digestive and gonad structures, and one of the three maturity stages was assigned depending on the development of the gonad (Table 2). The digestive whorl was then dissected away to obtain its wet weight. Whelks were considered mature if any differentiation was observed (Figure 2). Whorl wet weight was divided by total eviscerated body wet weight and multiplied by 100 to provide a GSI for each whelk. Previously, GSI was calculated as gonad weight/total weight less digestive whorl weight (Martel *et al.*, 1986; Gendron, 1992). This method was not possible here as dissecting away the



**Figure 2.** The “Fish-tec” or “scientific stand-up” whelk pot was attached and fished alongside the fisher’s pots; in this figure, it is fished alongside “lay-down” whelk pots. Inset: An adult female whelk (*B. undatum*) extracted from the shell showing the differentiated digestive whorl (containing yellow eggs).



**Figure 3.** The morphometric measurement of *B. undatum* shells showing minimum width (top, Min), maximum width (Max), and TSL (bottom). This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

**Table 2.** Maturity stage assessment of the whelk *B. undatum* using basic visual methods.

Stage	Description
Immature	No differentiation in digestive whorl
Developing	Differentiation in the digestive whorl, possibly a visible vas deferens in males
Mature	Differentiation in the digestive whorl obvious, visible vas deferens in males



gonad portion of the digestive whorl was an incredibly time-consuming operation, and the liquid nature of the whorl after dissection made measuring gonad and digestive parts of the whorl separately highly susceptible to error. Histology was not possible due to the expense and time constraints on the project.

All statistical analyses were run in R (R Core Team, 2014). Maturity data were converted to binary form (immature = 0 and mature = 1). Population estimates for size at maturity were estimated using a logistic regression model (Roa *et al.*, 1999) reformulated by Walker (2005) to produce:

$$P(l) = (1 + \exp^{-\ln(19)[(l-\beta_1)/(\beta_2-\beta_1)]})^{-1}, \quad (1)$$

where  $P(l)$  is the proportion of the population mature at TSL, and  $\beta_1$  and  $\beta_2$  are curve parameters corresponding to  $L_{50}$  and  $L_{95}$ , respectively. Parameters were estimated using a generalized linear model with a logit link function and a binomial error structure.

Confidence intervals were added by bootstrapping the generalized linear model (10 000 runs). The significance of the fitted models was tested by comparing the deviance explained relative to the null model using Chi-squared tests. The base R code was constructed by Harry (2013) and is available online. Data were subset by sex, season, and location to detect patterns for each.

To determine if male penis length is an effective indicator of male maturity, an iterative search procedure was used with the following linear model:

$$\text{TSL} = \text{PL} \times I(x < c) + x \times I(x > c), \quad (2)$$

where  $\times$  is main effects and interactions for both variables, TSL is the total shell length, and PL is the penis length. Two sets of parameters are modelled depending on the  $x$  value (i.e.  $I(x < c)$  is 1 if  $x$  is less than the breakpoint and 0 if it is above), and  $c$  is the breakpoint at which the lowest residual mean standard error value was obtained for each iteration (Crawley, 2007).

**Table 3.** The total number of whelks (*B. undatum*) caught with the two scientific pots in each month for each location fished in Wales.

	2013									2014						
	Spring				Summer			Autumn			Winter			Spring		
Location	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
L1	–	–	–	91	–	87	–	68	152	212	–	–	57	–	–	112
L2	–	–	–	66	140	158	183	–	75	64	–	–	–	–	69	332
L3	–	–	–	257	365	182	168	–	53	128	38	–	88	27	–	–
L4	132	220	–	54	156	129	–	155	173	372	139	261	–	–	–	112

L1, north Wales; L2, north mid-Wales; L3, south mid-Wales; L4, south Wales.

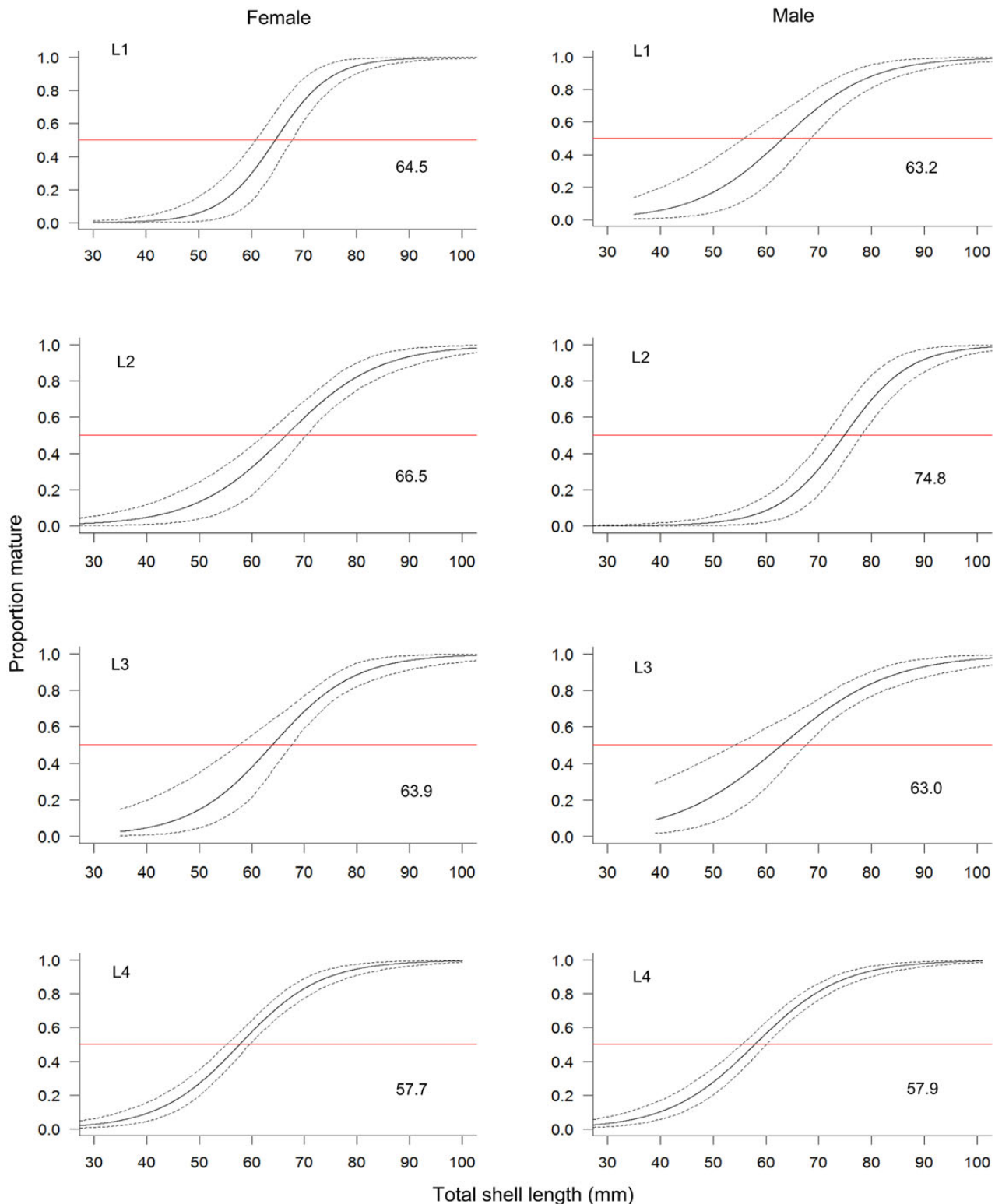
**Table 4.** Summary statistics and size at maturity ( $L_{50}$ ) for each sex, location, and season for the common whelk (*B. undatum*) populations collected from Welsh waters in 2013–2014.

Data	Subsample	Total number caught	Sampled for maturity	Min TSL	Mean TSL	Max TSL	Lower CI	$L_{50}$	Upper CI
Females	Summer	834	210	22	68.1	110	56.4	60.4	63.8
	Autumn	745	230	25	63.9	102	63.1	66.2	69.4
	Winter	361	207	25	63.5	106	54.5	57.5	60.2
	Spring	746	205	13	64.3	113	52.6	57.8	61.9
	L1	441	178	30	75.1	111	60.8	64.5	67.8
	L2	571	160	13	59.2	107	62.0	66.5	70.2
	L3	708	173	35	74.2	113	57.7	63.9	67.5
	L4	966	341	15	57.9	100	55.5	57.7	59.6
Males	Summer	734	211	12	69.8	111	57.1	61.7	65.3
	Autumn	707	257	27	65.7	104	59.9	63.0	66.0
	Winter	353	182	29	62.4	120	55.9	59.8	63.2
	Spring	600	157	13	65.4	118	57.2	63.1	67.9
	L1	338	130	35	74.8	120	55.7	63.2	68.6
	L2	512	137	13	61.9	112	71.3	74.8	78.3
	L3	598	174	39	74.5	111	54.5	63.0	67.8
	L4	946	366	12	60.7	101	55.5	57.9	60.0
Site	L1a	368	178	38	79	120	47.8	59.2	65.1
	L1b	87	40	34	79.1	110	–	–	–
	L2a	322	83	22	60	104	70.9	76	82.5
	L2b	765	214	13	61	112	64.2	68.3	71.6
	L3a	141	80	42	81	106	55.5	69.7	75.2
	L3a	1165	267	35	74	113	57.6	62.6	65.8
	L4a	513	222	12	72	101	62.9	65.4	68.1
	L4b	1387	475	15	54	88	55	56.7	58.4

TSL, total shell length;  $L_{50}$ , the TSL where 50% of the sampled population was found to be mature; Lower and upper CI, bootstrap for 95% confidence intervals (runs = 10 000).

To investigate broadscale patterns in  $L_{50}$ , data were collated from other published studies for comparison with the findings in the present study (Table 1). For each study, latitude, longitude, water depth (if available), and mean summer and winter sea surface

temperatures (SSTs) were compiled. Where SST was not stated, it was accessed from [Hanna \*et al.\* \(2006\)](#) for Iceland, [NEODAAS \(2015\)](#) for Wales, and [ICES \(2015\)](#) and [Cefas \(2015\)](#) for other published literature.



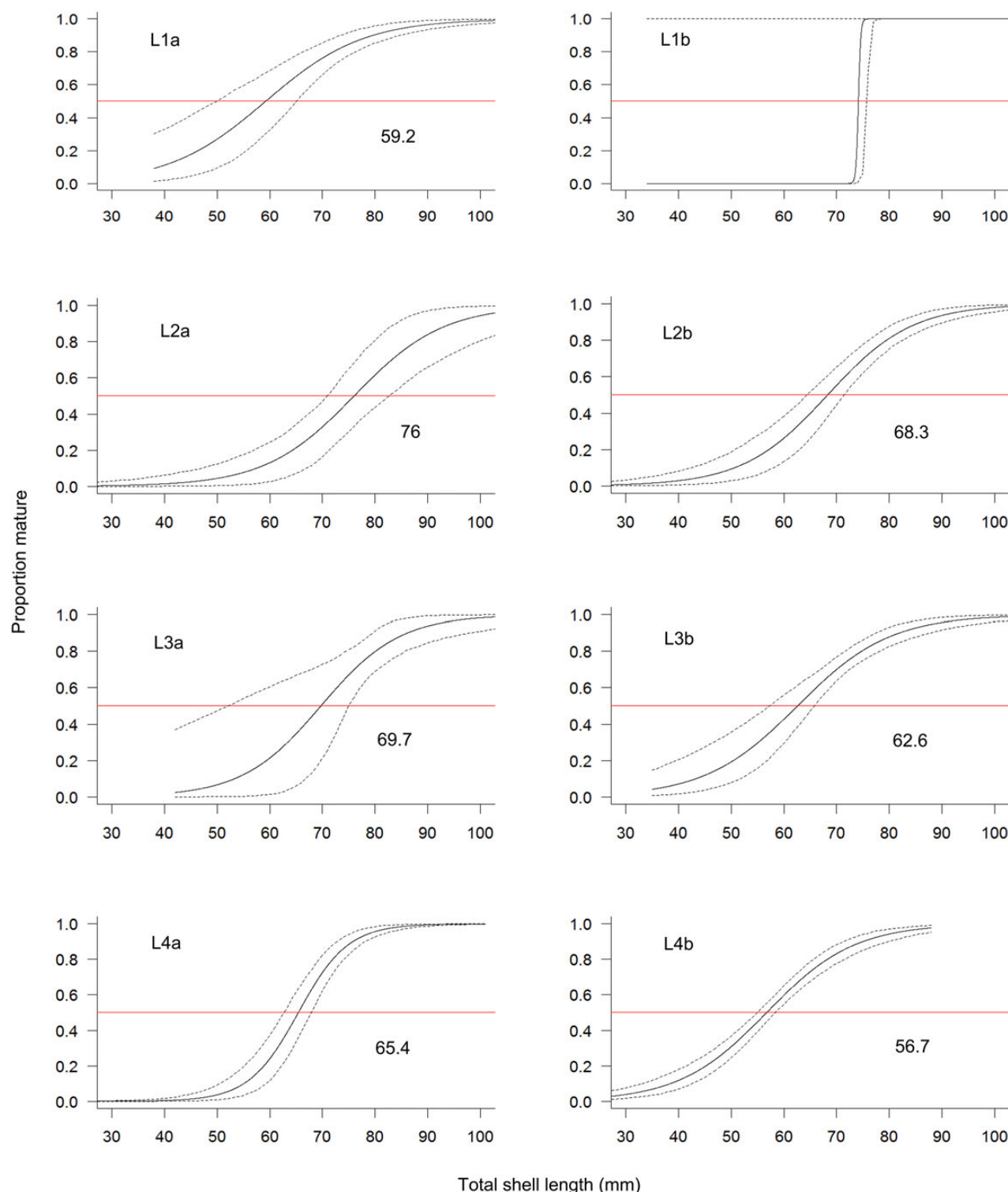
**Figure 4.** Maturity ogive of model fit for female and male whelk (*B. undatum*) from Wales. L1, north; L2, north mid-Wales; L3, south mid-Wales; L4, south Wales. The proportion where 50% of sampled whelks were found mature is marked by the horizontal line and displayed in the bottom right corner of each figure. This figure is available in black and white in print and in colour at [ICES Journal of Marine Science](#) online.

## Results

A total of 5080 whelks were caught and measured over the duration of the project, 1659 of which were dissected and maturity successfully determined. The main body of research commenced in May 2013,

although some earlier samples were obtained for south Wales (Table 3).

Maximum likelihood estimates of the size at which 50% of whelks were mature ( $L_{50}$ ), estimated by the generalized linear



**Figure 5.** Maturity ogive of model fit for female and male whelk (*B. undatum*) from sites within each Welsh location. Two locations were sampled from each location L1a and b, north Wales; L2a and b, north mid-Wales; L3a and b, south mid-Wales; L4a and b, south Wales. The number in the bottom right of each figure is the TSL (mm) at which 50% of sampled whelks were found mature ( $L_{50}$ ). This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

models with binomial distribution, had a considerable range of 51–76 mm TSL (Table 4 and Figure 4). The slope gradient for the maturity ogives was gradual for all data subsets, highlighting that size at maturity occurred over a wide range of sizes even within a small subset of a population (i.e. at site level). Sufficient data were available to determine size at maturity for all sites except L1b, which had insufficient data to fit the model with confidence. At the site level, low replication meant that males and females were pooled; thus,  $L_{50}$  estimates displayed wider confidence intervals to account for variation between sexes. Regardless of this source of error, all site-level ogives were highly significant when tested against the null model (Figure 5).

Using bathymetry chart layers in ArcGIS (ESRI, 2012), we mapped the location from each pot haul and assigned each whelk to a 10-m depth bin, resulting in five mean depth categories (5, 15, 25, 35, 45, and 55 m). *Buccinum undatum* had increasing  $L_{50}$  values with water depth ( $F_{5,1001} = 89.2$ ,  $p < 0.001$ , Figure 6), and there was a significant interaction between sex and depth (ANCOVA,  $F_{5,1001} = 8.3$ ,  $p < 0.001$ ).

The method used to calculate the GSI included both stomach and gonad weights; thus, it was not possible to delineate between the two without additional observations. Thus, a decrease in GSI could only be attributed to cessation of feeding or spawning with the addition of visual differentiation data. Seasonal patterns were observed regardless. The GSI was higher for females than for males (ANCOVA,  $F_{1,1557} = 180.77$ ,  $p < 0.001$ ) in all seasons ( $F_{3,1557} = 48.82$ ,  $p < 0.001$ ) and was different among locations ( $F_{3,1557} = 23.66$ ,  $p < 0.001$ ). An interaction was found between the season and the location ( $F_{8,1535} = 4.12$ ,  $p < 0.001$ ). Autumn and spring were significantly different from winter and summer for both

sexes (Tukey HSD,  $p_{\text{adj}} \leq 0.001$ ). In both sexes, this resulted in an increase in the GSI in autumn and spring, indicative of an increase in either feeding or reproductive activity. When assessing monthly patterns, GSI was found to be highest in October, but only for locations L1 and L3 (Tukey HSD,  $p < 0.05$ , Figure 7). At L4, the GSI varied among most months, although it was significantly higher in both May and September ( $p_{\text{adj}} \leq 0.05$ ). To determine if peaks in GSI were due to feeding or gonad development, we compared per cent mature among months.

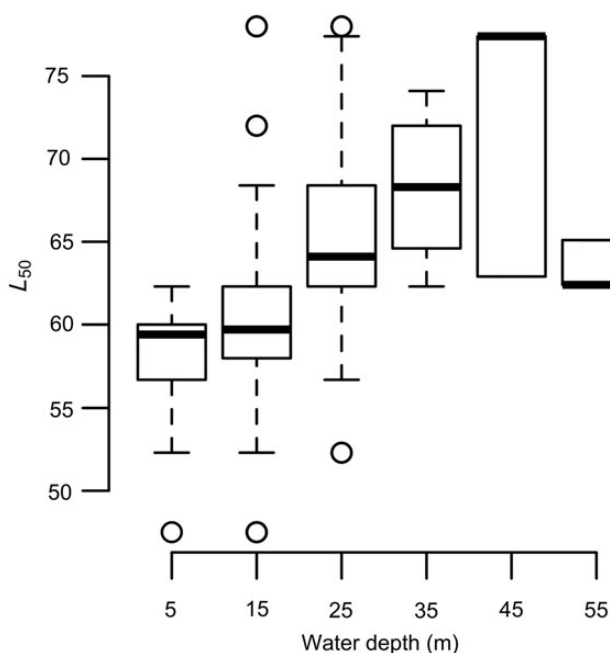
Mature whelks were found in all months throughout the sampling period (Figure 8), with a noticeable increase in the proportion of whelks without visible gonads (although they were of mature size classes) in samples from October and November, indicating possible spawning time (Figure 7). An analysis of covariance found that the pattern in the proportion of mature whelks did not vary between sexes, although it did vary with season ( $F_{3,1519} = 10.13$ ,  $p \leq 0.001$ ) and site ( $F_{7,1519} = 23.82$ ,  $p < 0.001$ ), with an interaction between sex and season ( $F_{3,1519} = 3.44$ ,  $p = 0.01$ ) and season and site ( $F_{9,1519} = 4.68$ ,  $p < 0.001$ ). Tukey *post hoc* testing identified a peak in the proportion of mature whelks in autumn compared with spring or summer ( $p_{\text{adj}} \leq 0.001$ ).

GSI was significantly different between maturity stages (ANOVA,  $F_{1,772} = 24.14$ ,  $p < 0.001$ ) and was highest for mature females (Tukey HSD,  $p_{\text{adj}} < 0.001$ ). Developing female GSI was not significantly different from immature females ( $p_{\text{adj}} = 0.34$ ), indicating that GSI would only identify fully developed females and thus overestimate size at maturity if used in isolation.

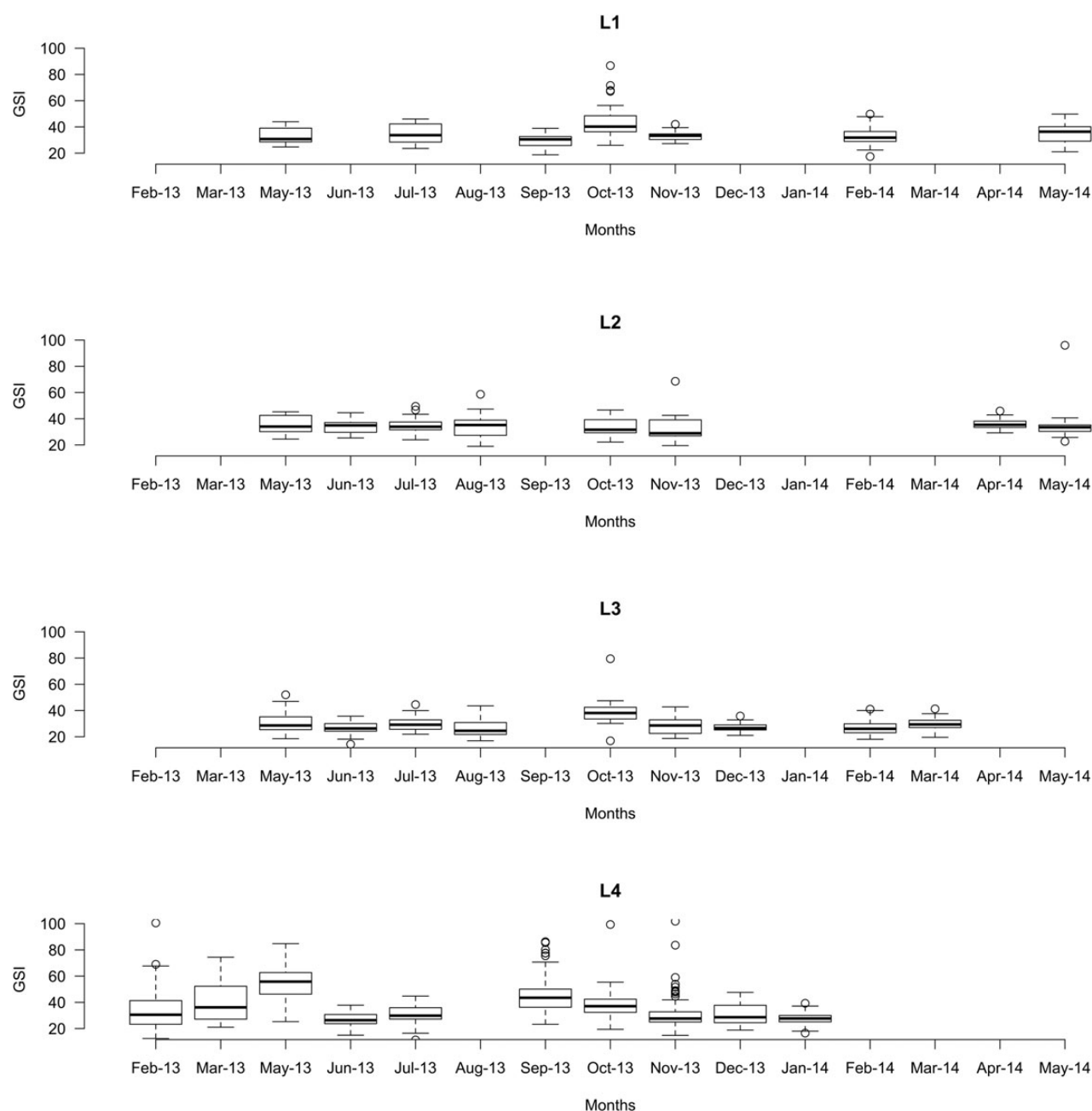
Male whelk maturity was also assessed using a morphometric index of penis length to TSL, where whelks with a penis length  $> 50\%$  of the TSL ( $PL_{50}$ ) were considered mature (Gendron, 1992). The  $PL_{50}$  morphometric method overestimated maturity (Table 5), although it was determined to be an effective method of identifying mature males which did not show gonad differentiation.

Using an iterative search procedure, an inflection point was identified for morphometric variance in penis length for whelks  $> 65$  mm TSL (Figure 9). This estimate was only slightly higher than the  $L_{50}$  for all pooled males using the gonad assessment method (61.8 mm TSL).

The length frequency distribution of whelks varied between sexes and in each season (Figure 10) and location (Figure 11). The mean size of male whelks was slightly larger than females, with a mean difference of 1 mm TSL (ANOVA,  $F_{1,5042} = 6.90$ ,  $p < 0.01$ ). The length distribution varied among seasons; a bimodal pattern was observed in spring, and a skewed distribution towards smaller whelks was observed in winter. The mean size of whelks varied significantly between locations (ANCOVA,  $F_{3,5042} = 377.56$ ,  $p < 0.001$ ), with an interaction with sex ( $F_{3,5042} = 4.23$ ,  $p < 0.01$ ) and season ( $F_{8,5042} = 324$ ,  $p < 0.001$ ). Whelk size was examined at a site level (the smallest available spatial resolution) and was found to vary significantly ( $F_{7,4732} = 264.6$ ,  $p < 0.001$ , Figure 11). To further explore this relationship between whelk size and site, we included water depth information. Each whelk from a day's catch was assigned to a mean water depth by plotting catches in ArcGIS with bathymetric chart data to determine the 10-m bin. For each location, depth range varied by at least two depth bins between 0–5 and 50–60 m water depth, and at site level, between one and two depth bins occurred. TSL increased with water depth ( $F_{5,4747} = 59.66$ ,  $p < 0.001$ ) with the 0–5 m depth contour having significantly smaller whelks than all other depth bins; whelks at 40–50 m were significantly larger than all shallower depth bins (Tukey HSD,  $p < 0.001$ ). The percentage of animals caught between the



**Figure 6.** Estimated  $L_{50}$  values estimated for sites and plotted for each mean water depth assigned from the “scientific” catches of *B. undatum* landed in Wales between February 2013 and May 2014. The box encloses the interquartile range (IQR, where the middle half of the data lies), the “whiskers” show the range of the data, and the circles represent suspected outliers that are data points  $1.5 \times \text{IQR}$ . The median (or middle) value is represented by the solid line within the box.



**Figure 7.** GSI for whelks (*B. undatum*) caught throughout the sampling season for each location in Wales.

MLS of 45 mm TSL and  $L_{50}$  ranged from 7 to 58% at the site level (Figure 11).

There was a significant linear relationship between minimum and maximum shell widths and TSL producing the following equations suitable for estimating sorting bar widths for any desired TSL:

$$\text{Min width} = 0.411 \times -0.072, \quad r^2 = 0.75, \quad p < 0.001, \quad (3)$$

and

$$\text{Max width} = 0.573 \times 0.627, \quad r^2 = 0.88, \quad p < 0.001. \quad (4)$$

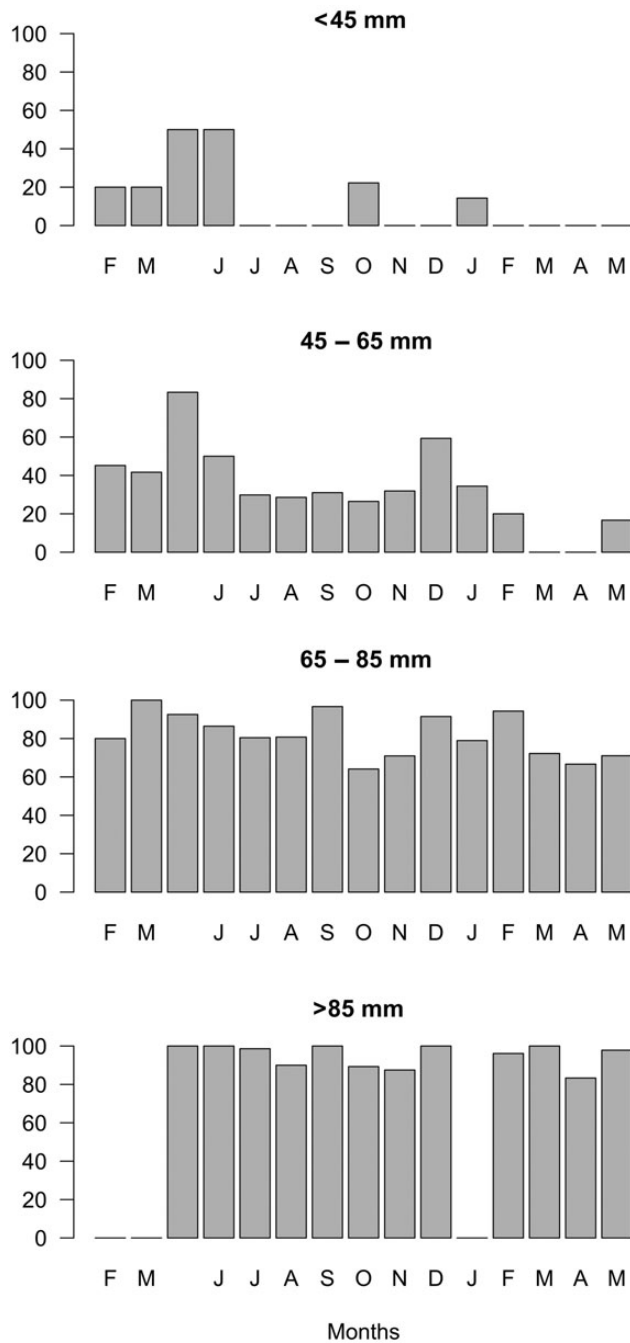
For example, using minimum width, sorting bars would need to be  $\sim 29$  mm apart to retain whelks of  $\sim 70$  mm TSL.

When all available data were combined (from this study and the literature, Table 6), a few patterns emerged. A longitudinal trend occurred; the mean size at maturity for females decreased from west to east ( $r = 0.38, p < 0.001$ ). There was no trend in maturity with latitude or depth (potentially due to insufficient depth observations available from the literature). A negative linear trend was found with female *B. undatum* maturity and mean summer ( $F_{1,28} = 13.47, r^2 = 0.30, p = 0.001$ ) and mean winter ( $F_{1,30} = 8.97, r^2 = 0.21, p < 0.01$ ) SSTs. No similar trends were found for male size at maturity.

## Discussion

Size at maturity for Welsh populations of *B. undatum* varied at a regional scale and within region at a more local scale. This high degree



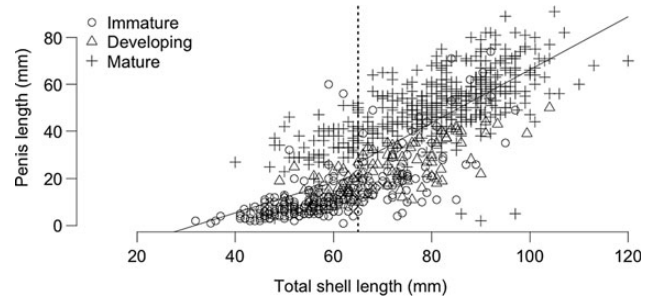


**Figure 8.** Proportion of mature whelks (*B. undatum*) in four size classes caught in each month of the sampling period (starting in February 2013 and running through to May 2014) in Wales. Letters respond to months in chronological order.

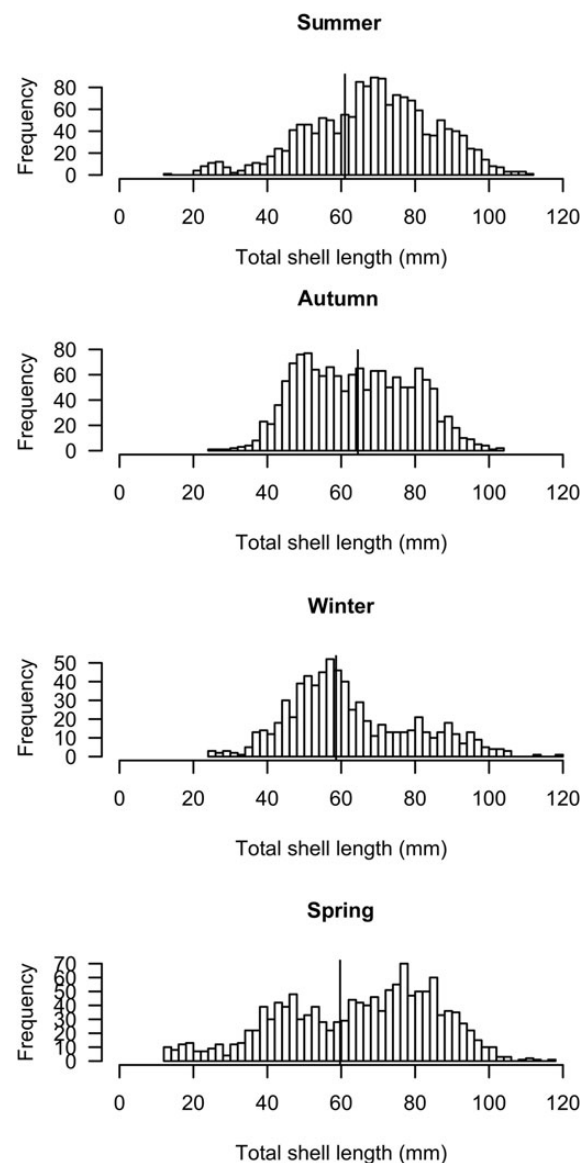
**Table 5.** A comparison between morphometric and gonad estimates of population maturity for the whelk *B. undatum*.

Location	Gonad $L_{50}$	Penis $PL_{50}$	Upper CI	Lower CI
L1	64.3	71.5	75.04	67.11
L2	70.4	82	84.94	79.15
L3	63.3	78.5	81.94	75.03
L4	57.8	67	69.27	64.78

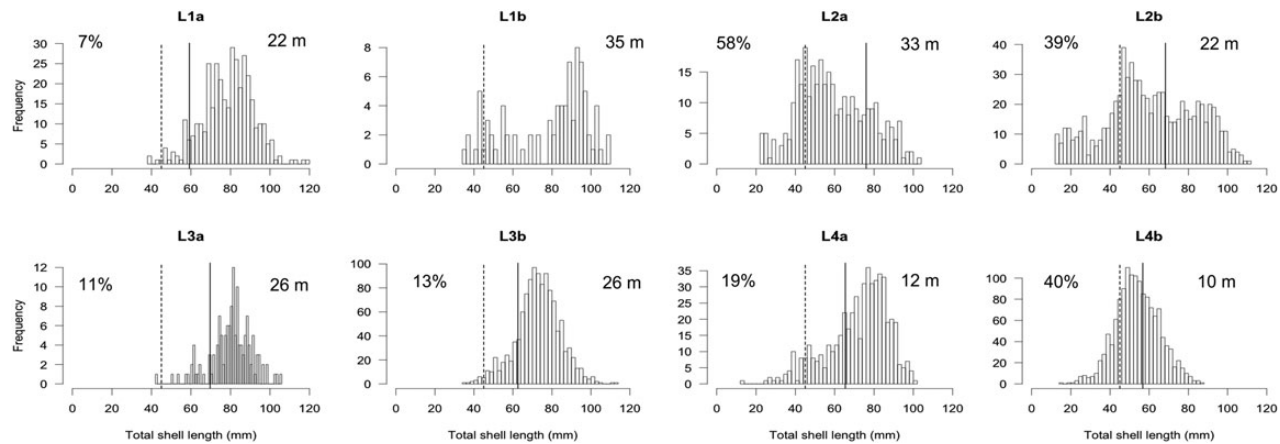
The morphometric measurement was the  $PL_{50}$  (the TSL at which 50% of the population are mature using a morphometric indicator of relative penis length).



**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*. The dotted vertical line is the value with the lowest mean standard error (65 mm TSL). Circles, triangles, and crosses mark the maturity stage, which was determined from visual examination of the gonad.



**Figure 10.** Seasonal TSL distribution of *B. undatum* for all locations in Wales. The vertical solid line indicates the value of  $L_{50}$  estimated for each season on data pooled by location.



**Figure 11.** TSL distribution of all samples of *B. undatum* from sites in Wales. Solid line indicates  $L_{50}$  for the site, and the dashed line indicates current MLS of 45 mm TSL. The value shown is the mean water depth from all samples in that site and also the percentage of the catch between MLS and the  $L_{50}$  value for the individual sites. Site L1b did not have sufficient data to produce an  $L_{50}$ , so no value is shown on this figure.

of variability in size at maturity is consistent with observations in England (McIntyre *et al.*, 2015) and previous published literature for Canada (Gendron, 1992). The greatest difference between two neighbouring populations was found between the two sites in location L4 which were 13 km apart and varied in  $L_{50}$  by 8.7 mm TSL. The whelks caught at these two sites displayed different length frequencies, and the sites had different bathymetry and benthic habitat type (Robson, 2014). Within Swansea Bay, L4a was classified as muddy sand down to a depth of 30 m (Robson, 2014) and was characterized by larger whelks (mean TSL = 72 mm) that had a larger size at maturity ( $L_{50}$  = 65.4 mm). In contrast, site L4b had a mixed sediment of sand, gravel, pebbles, and shells to a depth of 20 m (Robson, 2014), and the whelks were smaller (mean TSL = 54 mm) and matured at a smaller size ( $L_{50}$  = 56.7 mm). A possible explanation for these two populations is that they mature at a similar age, but that growth rate is affected by the different habitats. The driving cause of the variation in  $L_{50}$  between whelk populations at different locations could not be fully resolved using the available literature; however, it is clear that environmental parameters (e.g. depth and temperature) seem to play a significant role. The smaller size in shallow waters suggested that either whelks move off-shore into deeper water as they increase in body size or that the conditions for growth to large body size are better in deeper water than in shallow water. Given the current evidence, it is clear that local conditions have a stronger influence on growth and maturity than broader latitudinal scale influences, which has important implications for the approach to management measures to achieve a sustainable fishery.

Small-scale spatial variability in growth and size at maturity occurs in other marine molluscs (McShane and Naylor, 1995; Arkhipkin, 1996; Jackson and Moltchanivskyj, 2001). For the marine gastropod *Nucella ostrina*, growth rate is positively related to maternal investment, with maturity occurring earlier for faster-growing individuals (Moran and Emlet, 2001). Other species of marine gastropod have shown variable growth rates in response to environmental conditions over scales of tens of metres (Johnson and Black, 2008) or kilometres (Martone and Micheli, 2012). The Argentinian species *Buccinanops globulosum* is phylogenetically related to *B. undatum* (Ponder and Lindberg, 1997) and shows similar spatial patterns in size at maturity (Narvarte *et al.*, 2008).

Two adjacent populations of *B. globulosum* displayed distinct length frequencies, sex ratios, and size at maturity from two sites with different depths, benthic habitats, exposure, and salinity (Narvarte *et al.*, 2008). Both *B. globulosum* and *B. undatum* present strong cases for local adaptation and phenotypic plasticity over small spatial scales, likely due to their lack of dispersive larval stage and limited adult movement (Behrens Yamada, 1989).

The estimation of  $L_{50}$  varied with season for each location, displaying an increase in  $L_{50}$  in autumn for both males and females. By September and October, whelks had significantly higher GSI values, and there was a greater proportion of mature whelks in catches. By November, mean GSI values had dropped and more immature whelks were caught. Similar patterns were observed in gonad weight of *B. undatum* from the southwestern Irish Sea where gonads were heaviest in autumn and lightest at the end of winter (Fahy *et al.*, 2000). For Canadian populations, although there was variation with season, an inverse pattern of breeding and feeding was observed for *B. undatum* (Martel *et al.*, 1986). The inability to accurately assign maturity in some seasons, for example when female whelks are in a recovery phase or when males are storing sperm, would underestimate the number of mature whelks, thus shifting the curve to the left and underestimating the size at maturity. Given the seasonal nature of reproduction, the ideal season to visually assess size at maturity is when the most individuals display maximum gonad differentiation just before spawning, which for Welsh populations is late summer (July–September). Replication of this study is required to determine if seasonal patterns hold true in other years, particularly if temperature shifts seasonally from year to year (for example, under climate-change influences). In other seasons, it may be necessary to incorporate other indicators for maturity (such as penis length) or undertake histology to confirm visual assessments. Sampling for maturity is best done outside of winter (November–February) as mature whelks cease feeding in November (as indicated by the seasonal decrease in GSI and fewer larger size classes in winter samples); with a greater proportion of immature cohorts caught in winter samples, it would be advised to avoid sampling for maturity between November and February.

Males have been considered mature if the penis length is at least 50% of the TSL (Santarelli, 1985), which was originally based on

**Table 6.** Data included in analysis to determine trends in size at maturity for *B. undatum*.

Country	Site reference	DDLat	DDLong	TSL	Male SAM	Female SAM	Female method	Male method	Summer SST	Winter SST	Mean depth	Reference
Canada	Archipel de Mingan	50.23333333	63.6	NA	70	70	Visual	Visual	4	4	10	Martel <i>et al.</i> (1986)
Canada	La Tabat	50.83880278	58.93779722	NA	61.87	73.67	GSI	PL	NA	1.89	NA	Gendron (1992)
Canada	Magdalen Island	47.29043889	61.88001389	NA	49.09	60.29	GSI	PL	4.52	3.13	127	Gendron (1992)
Canada	Magpie	50.30487222	64.49681389	NA	67.06	73.61	GSI	PL	2.82	2.09	73	Gendron (1992)
Canada	Mingan	50.23331667	63.56741944	NA	75.55	78.33	GSI	PL	2.82	2.09	73	Gendron (1992)
Canada	Moisie	50.17118333	66.08427778	NA	58.94	79.54	GSI	PL	2.82	2.09	73	Gendron (1992)
Canada	Mont Louis	49.32502222	65.62953333	NA	71.78	73.76	GSI	PL	2.82	2.09	73	Gendron (1992)
Canada	Sept Lles	50.204175	66.44583333	NA	69.22	80.76	GSI	PL	2.82	2.09	73	Gendron (1992)
Canada	St Joachim	48.01639167	69.59500278	NA	76.38	75.62	GSI	PL	NA	2.55	NA	Gendron (1992)
England	Eastbourne	50.76596389	0.302491667	NA	51.2	56.7	Visual	Visual	16.85	7.32	NA	McIntyre <i>et al.</i> (2015)
England	Exmouth	50.58574167	3.413344444	NA	69.2	72.4	Visual	Visual	16.4	8.15	NA	McIntyre <i>et al.</i> (2015)
England	Inner Cromer Knoll	53.21555833	1.449794444	NA	76.2	77.8	Visual	Visual	NA	NA	NA	McIntyre <i>et al.</i> (2015)
England	Lundy	51.17146389	4.653416667	NA	75.5	75.5	Visual	Visual	16.4	8.15	NA	McIntyre <i>et al.</i> (2015)
England	Poole	50.69674722	1.999144444	NA	66	63.5	Visual	Visual	17.03	7.59	NA	McIntyre <i>et al.</i> (2015)
England	Portsmouth	50.8217	1.126333333	NA	46.4	44.8	Visual	Visual	17.16	8.62	NA	McIntyre <i>et al.</i> (2015)
England	Ramsgate	51.33082778	1.428852778	NA	49.5	52.8	Visual	Visual	16.02	6.24	NA	McIntyre <i>et al.</i> (2015)
England	Selsey	50.72575556	0.805602778	NA	64.6	59.6	Visual	Visual	NA	NA	NA	McIntyre <i>et al.</i> (2015)
England	Wells-next-the-sea	52.98965556	0.785258333	NA	62.5	60.6	Visual	Visual	17.08	4.16	NA	McIntyre <i>et al.</i> (2015)
England	Weymouth	50.60921389	2.850527778	NA	59.1	54.7	Visual	Visual	16.1	7.94	NA	McIntyre <i>et al.</i> (2015)
England	Whitehaven	54.54995556	3.602969444	NA	74	69.5	Visual	Visual	16.58	5.4	NA	McIntyre <i>et al.</i> (2015)
England	Whitstable	51.36278056	1.018461111	NA	61.9	60.7	Visual	Visual	NA	NA	NA	McIntyre <i>et al.</i> (2015)
France	Cotentin	49.43714722	1.901186111	NA	49	52	Visual	Visual	NA	NA	NA	Heude-Berthelin <i>et al.</i> (2011)
France	Normandy	49.42068333	0.253733333	NA	55	55	GSI	GSI	17.12	7.35	30	Santarelli (1985)
Iceland	Flikrusker	65.4500913	23.0594911	50.5	63.5	NA	NA	PL	9.3	1.3	18	Gunnarsson and Einarsson (1995)
Iceland	Hnallar	65.4500913	23.0594911	49.9	57.5	NA	NA	PL	9.3	1.3	18	Gunnarsson and Einarsson (1995)
Iceland	Hrappsey	65.06583333	22.26130556	53.2	57.5	NA	NA	PL	9.3	1.3	10	Gunnarsson and Einarsson (1995)
Iceland	Lagmuli	65.17642778	23.98986389	49.6	57.5	NA	NA	PL	9.3	1.3	40	Gunnarsson and Einarsson (1995)
Iceland	Midjanesvik	65.4500913	23.0594911	58.5	75.5	NA	NA	PL	9.3	1.3	10	Gunnarsson and Einarsson (1995)
Iceland	Mulanes	66.05873889	23.14561111	61.5	63.5	NA	NA	PL	9.3	1.3	8	Gunnarsson and Einarsson (1995)
Iceland	Mulanes	66.05873889	23.14561111	62.8	73.5	NA	NA	PL	9.3	1.3	18	Gunnarsson and Einarsson (1995)
Iceland	Sandsker	65.4500913	23.0594911	52.8	73.5	NA	NA	PL	9.3	1.3	20	Gunnarsson and Einarsson (1995)
Iceland	Stadur	65.4500913	23.0594911	49.5	47.5	NA	NA	PL	9.3	1.3	18	Gunnarsson and Einarsson (1995)
Iceland	Stadur	65.4500913	23.0594911	61.3	73.5	NA	NA	PL	9.3	1.3	10	Gunnarsson and Einarsson (1995)
Iceland	Svidhnur	65.40689444	22.63934722	60.8	57.5	NA	NA	PL	9.3	1.3	8	Gunnarsson and Einarsson (1995)
Iceland	Svidhnur	65.40689444	22.63934722	61.2	67.5	NA	NA	PL	9.3	1.3	18	Gunnarsson and Einarsson (1995)
Ireland	Dublin	53.329375	6.098802778	NA	83	NA	NA	PL	14.62	9.68	74	Fahy <i>et al.</i> (2000)
Ireland	Southeast Ireland	52.20057778	6.298088889	NA	63	NA	NA	PL	14.62	9.68	74	Fahy <i>et al.</i> (2000)
Shetland	Scalloway	60.13333333	1.276944444	91.95	NA	NA	NA	NA	10.82	8.52	NA	Shelmerdine <i>et al.</i> (2007)
Shetland	South England	51.21111111	0.02335	54.3	NA	NA	NA	NA	17.31	6.72	NA	Shelmerdine <i>et al.</i> (2007)
Shetland	Whalsay	60.33897222	1.028611111	76.24	NA	NA	NA	NA	10.82	8.52	NA	Shelmerdine <i>et al.</i> (2007)
Sweden	Brattebergssund, Skagerrak	58.88333333	11.16694444	NA	53.5	51.5	Visual	Visual	12.12	4.38	316	Valentinsson <i>et al.</i> (1999)
Sweden	Tjarno, Skagerrak	58.88333333	11.13333333	NA	NA	NA	NA	NA	15.42	4.9	11	Valentinsson (2002)
Sweden	Usto, Kattegatt	57.28333333	12.05027778	NA	68.7	67.5	Visual	Visual	13.76	3.87	50	Valentinsson <i>et al.</i> (1999)

Data were obtained from the published literature where possible; other data (latitude, longitude, and sea surface temperatures) were obtained from other sources, which are referenced in the methods. Female and Male method refers to the method used in the publication to determine  $L_{50}$  or minimum size at maturity.

DD, decimal degrees; Lat, latitude; Long, longitude; TSL, total shell length; SAM, size at maturity; SST, sea surface temperature.

early observations of male maturity (Koie, 1969), and has been continually used to either confirm or identify male maturity for *B. undatum* (Martel et al., 1986; Gendron, 1992; Fahy et al., 2000; McIntyre et al., 2015). In this study, a total of 16 male whelks measuring 51–97 mm TSL had no differentiation in the digestive whorl and thus were classed as immature, although they had a penis index > 50% and, therefore according to the literature, were mature. There was no discernible seasonal pattern when large immature whelks were detected, as they were found in all seasons and all locations, did not have extensive damage, and displayed no obvious signs of disease (evident from a mottled pattern in the gonad). At larger sizes, whelks are thought to skip years in reproductive activity (Martel et al., 1986), which is the likely explanation for the presence of these individuals. The iterative process identified an inflection point relatively close to the  $L_{50}$  value (morphometric inflection = 65 mm TSL;  $L_{50}$  = 61.8 mm TSL), which confirms that a penis length 50% of TSL is a reasonable method of identifying mature males which do not display typical gonad differentiation. Other studies have found that  $PL_{50}$  closely resembles  $L_{50}$  (McIntyre et al., 2015), although  $PL_{50}$  consistently overestimated maturity in our dataset. As there is no detailed methodology for measuring a whelk penis, perhaps methods are not consistent between studies.

Length frequency of harvested whelks varied with water depth at each site. The MLS is 45 mm for Wales, which is too small to protect whelk populations, although the proportion of immature whelks landed varies over small spatial scales (7–58% of the catch from scientific pots were immature whelks). That whelk demographics vary over such small scales presents some difficulties for management as a broadscale application of MLS may be suitable for some populations while rendering others vulnerable to overfishing. A broad-brush approach to MLS disproportionately impacts fishers reliant on the smaller whelk populations and, under a scenario of a 25-mm increase, may result in decreased landings of up to 50% for some fishers.

The *B. undatum* fishery is considered “data poor” and for both Wales and England, stock assessments are not available to inform total allowable catch limits (McIntyre et al., 2015). Unmanaged effort and overfishing has decreased size at maturity for other commercially targeted marine gastropods (Torroglosa and Giménez, 2010), although recent studies did not find supporting evidence of this scenario for *B. undatum* (McIntyre et al., 2015). With an increase in fishing effort over the last few decades, there has been increasing concern for whelk stocks, yet no management measures have been put in place in Wales beyond the introduction of an MLS. Mandatory sorting using known length–width relationships, restrictive measures on gear and effort, and closed seasons are all viable management options for protecting whelk stocks. A further increase in MLS has been suggested, which would have negative short-term impacts on fishers targeting naturally occurring small whelk populations. For this reason, a stepped approach followed by population monitoring may be more acceptable than a single increase in MLS. The current use of operculum rings for ageing is at best unreliable (Kideys, 1996), which is why ageing was not attempted in this study. Current research is developing more reliable ageing techniques (P. Hollyman, pers. comm.), which will be crucial to understanding the relationship between the habitat, maturity, and growth.

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## References

- Arkipkin, A. 1996. Geographical variation in growth and maturation of the squid *Illex coindetii* (Oegopsida, Ommastrephidae) off the north-west African coast. *Journal of the Marine Biological Association of the United Kingdom*, 76: 1091–1106.
- Behrens Yamada, S. 1989. Are direct developers more locally adapted than planktonic developers? *Marine Biology*, 103: 403–411.
- Bell, M. C., and Walker, P. 1998. Size at Maturity in Common Whelks *Buccinum undatum* L. in England and Wales. ICES Document CM 1998/CC: 9.
- Cefas. 2015. Coastal Temperature Network. <http://cefas.defra.gov.uk/our-science/observing-and-modelling/monitoring-programmes/sea-temperature-and-salinity-trends/station-positions-and-data-index.aspx> (last accessed 28 April 2015).
- Crawley, M. J. 2007. *The R Book*. Wiley, Blackwell, West Sussex, UK.
- Dakin, W. J. 1912. L. M. B. C. Memoirs on Typical British Marine Plants and Animals: *Buccinum* (the Whelk). Liverpool Marine Biology Committee, London. 107 pp.
- De Vooys, C. G. N., and van der Meer, J. 2010. The whelk (*Buccinum undatum* L.) in the western Dutch Wadden Sea in the period 1946–1970: Assessment of population characteristics and fishery impact. *Journal of Sea Research*, 63: 11–16.
- ESRI. 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, CA, USA.
- Fahy, E., Masterson, E., Swords, D., and Forrest, N. 2000. A Second Assessment of the Whelk Fishery *Buccinum undatum* in the Southwest Irish Sea with Particular Reference to its History of Management by Size Limit. Marine Institute, Dublin. 52 pp.
- Fredensborg, B. L., and Poulin, R. 2006. Parasitism shaping host life-history evolution: Adaptive responses in a marine gastropod to infection by trematodes. *Journal of Animal Ecology*, 75: 44–53.
- French, C. 2011. Informing the management and conservation of the whelk (*Buccinum undatum*) fishery in South Wales. MSc thesis. Swansea University, Wales. 68 pp.
- Gendron, L. 1992. Determination of the size at sexual maturity of the waved whelk *Buccinum undatum* Linnaeus, 1758, in the Gulf of St Lawrence, as a basis for the establishment of a minimum catchable size. *Journal of Shellfish Research*, 11: 1–7.
- Gunnarsson, K., and Einarsson, S. 1995. Observations on Whelk Populations (*Buccinum undatum* L., Mollusca; Gastropoda) in Breidifjörður, Western Iceland. ICES Document CM 1995/K: 20. 13 pp.
- Hancock, D., and Urquhart, A. 1959. Methods for marking whelks (*Buccinum undatum* L.). *Journal du Conseil International pour l'Exploration de la Mer*, 24: 494–496.
- Hanna, E., Jónsson, T., Ólafsson, J., and Valdimarsson, H. 2006. Icelandic coastal sea surface temperature records constructed: Putting the pulse on air-sea-climate interactions in the northern North Atlantic. Part I: Comparison with HadISST1 open ocean surface temperatures and preliminary analysis of long-term patterns. *Journal of Climate*, 19: 5652–5666.
- Harry, A. V. 2013. Maturity ogive R. <https://gist.github.com/alharry/4576675> (last accessed 16 February 2015).
- Heude-Berthelin, C., Hégon-Macé, L., Legrand, V., Jouaux, A., Adeline, B., Mathieu, M., and Kellner, K. 2011. Growth and



- reproduction of the common whelk *Buccinum undatum* in west Cotentin (Channel), France. *Aquatic Living Resources*, 24: 317–327.
- Himmelman, J. H., and Hamel, J. R. 1993. Diet, behaviour and reproduction of the whelk *Buccinum undatum* in the northern Gulf of St Lawrence, eastern Canada. *Marine Biology*, 430: 423–430.
- ICES. 2015. Oceanography. <http://ocean.ices.dk/HydChem.aspx?plot=yes> (last accessed 27 April 2015).
- Jackson, G. D., and Moltschaniwskyj, N. A. 2001. Temporal variation in growth rates and reproductive parameters in the small near-shore tropical squid *Loliolus noctiluca*; is cooler better? *Marine Ecology Progress Series*, 218: 167–177.
- Johnson, M. S., and Black, R. 2008. Effects of contrasting tidal habitats on growth, survivorship and dispersal in an intertidal snail. *Journal of Experimental Marine Biology and Ecology*, 363: 96–103.
- Kideys, A. E. 1996. Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgoländer Meeresuntersuchungen*, 50: 353–368.
- Kideys, A. E., Nash, R. D. M., and Hartnoll, R. G. 1993. Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. *Journal of the Marine Biological Association of the United Kingdom*, 73: 391–403.
- Koie, M. 1969. On the endoparasites of *Buccinum undatum* L. with special reference to the trematodes. *Ophelia*, 6: 251–279.
- Martel, A., Larrivee, D. H., Klein, K. R., and Himmelman, J. H. 1986. Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. *Marine Biology*, 92: 211–221.
- Martone, R. G., and Micheli, F. 2012. Geographic variation in demography of a temperate reef snail: Importance of multiple life-history traits. *Marine Ecology Progress Series*, 457: 85–99.
- McIntyre, R., Lawler, A., and Masefield, R. 2015. Size of maturity of the common whelk, *Buccinum undatum*: Is the minimum landing size in England too low? *Fisheries Research*, 162: 53–57.
- McShane, P. E., and Naylor, J. R. 1995. Small-scale spatial variation in growth, size at maturity, and yield- and egg-per-recruit relations in the New Zealand abalone *Haliotis iris*. *New Zealand Journal of Marine and Freshwater Research*, 29: 603–612.
- Marine Management Organisation. 2014. UK Sea Fisheries Statistics 2013. Marine Management Organisation, London. 178 pp.
- Montory, J. A., Chaparro, O. R., Pechenik, J. A., Diederich, C. M., and Cubillos, V. M. 2014. Impact of short-term salinity stress on larval development of the marine gastropod *Crepidatella fecunda* (Calyptreidae). *Journal of Experimental Marine Biology and Ecology*, 458: 39–45.
- Moran, A. L., and Emler, R. B. 2001. Offspring size and performance in variable environments: Field studies on a marine snail. *Ecology*, 82: 1597–1612.
- Narvarte, M., Willers, V., Avaca, M. S., and Echave, M. E. 2008. Population structure of the snail *Buccinanops globulosum* (Prosobranchia, Nassariidae) in San Matías Gulf, Patagonia Argentina: Isolated enclaves? *Journal of Sea Research*, 60: 144–150.
- NEODAAS. 2015. NERC Earth Observation Data Acquisition and Analysis Service. [www.neodaas.ac.uk](http://www.neodaas.ac.uk) (last accessed 1 April 2015).
- Nicholson, G. J., and Evans, S. M. 1997. Anthropogenic impacts on the stocks of the common whelk *Buccinum undatum* (L.). *Marine Environmental Research*, 44: 305–314.
- Pálsson, S., Magnúsdóttir, H., Reynisdóttir, S., Jónsson, Z. O., and Örnólfssdóttir, E. B. 2014. Divergence and molecular variation in common whelk *Buccinum undatum* (Gastropoda: Buccinidae) in Iceland: A trans-Atlantic comparison. *Biological Journal of the Linnean Society*, 111: 145–159.
- Pardo, L. M., and Johnson, L. E. 2005. Explaining variation in life-history traits: Growth rate, size, and fecundity in a marine snail across an environmental gradient lacking predators. *Marine Ecology Progress Series*, 296: 229–239.
- Ponder, W. F., and Lindberg, D. R. 1997. Towards a phylogeny of gastropod molluscs: An analysis using morphological characters. *Zoological Journal of the Linnean Society*, 119: 83–265.
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Roa, R., Ernst, B., and Tapia, F. 1999. Estimation of size at sexual maturity: An evaluation of analytical and resampling procedures. *Fishery Bulletin US*, 97: 570–580.
- Robson, G. 2014. The distribution, abundance and movement of the adult whelk *Buccinum undatum* (L. 1758) in South Wales, UK. MSc thesis. Bangor University, Wales. 94 pp.
- Santarelli, C. H. L. 1985. Les Pecheries de Buccin (*Buccinum undatum* L.: Gastropoda) du Golfe Normand-Breton. Université d'Aix-Marseille II, France. 194 pp.
- Shelmerdine, R. L., Adamson, J., Laurenson, C. H., and Leslie, B. 2007. Size variation of the common whelk, *Buccinum undatum*, over large and small spatial scales: Potential implications for micro-management within the fishery. *Fisheries Research*, 86: 201–206.
- Shrives, J. P., Pickup, S. E., and Morel, G. M. 2015. Whelk (*Buccinum undatum* L.) stocks around the Island of Jersey, Channel Islands: Reassessment and implications for sustainable management. *Fisheries Research*, 167: 236–242.
- Stearns, S. C., and Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution*, 40: 893–913.
- Torroglosa, E. M., and Giménez, J. 2010. Temporal variation in size at maturity of the snail *Zidona dufresnei* from the southwestern Atlantic Ocean after ten years of fishery exploitation. *Aquatic Biology*, 11: 163–167.
- Valentinsson, D. 2002. Reproductive cycle and maternal effects on offspring size and number in the neogastropod *Buccinum undatum* (L.). *Marine Biology*, 140: 1139–1147.
- Valentinsson, D., Sjödin, F., Jonsson, P. R., Nilsson, P., Wheatley, C., Sjödin, F., Jonsson, P. R., et al. 1999. Appraisal of the potential for a future fishery on whelks (*Buccinum undatum*) in Swedish waters: CPUE and biological aspects. *Fisheries Research*, 42: 215–227.
- Walker, T. I. 2005. Reproduction in fisheries science. In *Reproductive Biology and Phylogeny of Chondrichthyans: Sharks, Batoids, and Chimaeras*, pp. 81–127. Ed. by W. C. Hamlett. Science Publishers, Inc., Enfield, NH.
- Weetman, D., Hauser, L., Bayes, M., Ellis, J., and Shaw, P. 2006. Genetic population structure across a range of geographic scales in the commercially exploited marine gastropod *Buccinum undatum*. *Marine Ecology Progress Series*, 317: 157–169.

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