

## **The effect of environmental factors on shell growth and repair in *Buccinum undatum***

Colvin, Charlotte; Hollyman, Philip; Richardson, Christopher; Chenery, Simon; Waggitt, James; McCarthy, Ian

**Journal of Experimental Marine Biology and Ecology**

DOI:

[10.1016/j.jembe.2022.151720](https://doi.org/10.1016/j.jembe.2022.151720)

Published: 01/06/2022

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Colvin, C., Hollyman, P., Richardson, C., Chenery, S., Waggitt, J., & McCarthy, I. (2022). The effect of environmental factors on shell growth and repair in *Buccinum undatum*. *Journal of Experimental Marine Biology and Ecology*, 551, Article 151720. <https://doi.org/10.1016/j.jembe.2022.151720>

### **Hawliau Cyffredinol / General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

# The effect of environmental factors on shell growth and repair in *Buccinum undatum*

C.N. Colvin<sup>1\*</sup>, P.R. Hollyman<sup>2</sup>, C.A. Richardson<sup>1</sup>, S.R.N. Chenery<sup>3</sup>, J.J. Waggitt<sup>1</sup>, I.D. McCarthy<sup>1</sup>

<sup>1</sup>School of Ocean Sciences, College of Natural Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

<sup>2</sup>British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

<sup>3</sup>Centre for Environmental Geochemistry, British Geological Survey, Keyworth, Nottingham NG12 5GG, UK

\*Corresponding author c.n.colvin@bangor.ac.uk (C.N. Colvin)

## Abstract

The processes and factors which affect shell growth and repair in molluscs are poorly understood. In this study, the capabilities of shell growth and repair in the marine gastropod *Buccinum undatum* were investigated experimentally by implementing laboratory-controlled mechanical damage to the shell margin/lip. Three key factors, life stage (juvenile or adult), seawater temperature (5-15°C) and food availability (unfed, weekly, or daily feeding), were investigated in a series of controlled laboratory experiments to establish their roles in the processes of shell growth and repair. Significant differences in rates of shell growth and repair between food and temperature regimes were observed, with the greatest difference occurring with different life stages. Rates of shell growth in non-damaged whelks were slightly faster but not significantly different from damaged individuals in any of the experiments. Tank-reared juveniles maintained in the highest seawater temperature regime (15°C) displayed significantly faster rates of shell repair ( $F=6.47$ ,  $p<0.05$ ) than conspecifics held at lower seawater temperatures. Through characterising both biological and environmental factors affecting shell growth and repair, it is demonstrated that there are multiple aspects influencing shell growth and shell repair. It is important to be able to understand and establish differences in rates of growth to better manage this commercial species.

## Keywords

Gastropod mollusc; shell growth; *Buccinum undatum*; fishery; shell damage; repair

27

## 28 1. Introduction

29 Growth is a fundamental process for determining survival and reproductive success within all  
30 taxa and is critical for population growth and resilience, and therefore, understanding what  
31 impacts measurable growth is of key importance (Sebens, 1987; Pepin, 1991). Within living  
32 organisms, growth is primarily defined as a measurable increase in length or mass (e.g., von  
33 Bertalanffy, 1938; France et al., 1996; Ohnishi and Akamine, 2006). For some species, e.g., the  
34 common whelk, *Buccinum undatum*, somatic and shell growth is continuous throughout life  
35 (Kideys et al., 1993). As such, *B. undatum* displays a predictable relationship between size and  
36 age, which has been used to determine growth rates in several studies (Hollyman et al., 2018;  
37 Emmerson et al., 2020; Borsetti et al., 2021).

38 The molluscan shell is vitally important, providing protection and additional support to the  
39 internal body in the form of a calcareous exoskeleton (Ruppert et al., 2004; Bonucci, 2007). As  
40 such, the shell is required to increase as the internal soft tissue grows. The physical process of  
41 shell growth occurs as a result of  $\text{CaCO}_3$  secretions from the mantle epidermis (Findlay et al.,  
42 2011). Damage to the shell can lead to interruptions in growth, with incidents often recorded  
43 in the structure of the shell in the form of shell scarring (Richardson, 2001; Ramsay et al., 2001;  
44 Preston and Roberts, 2007), although there is a paucity of literature surrounding the effects of  
45 shell damage and rates of regrowth in gastropod species. In addition to the normal process of  
46 shell growth with age, it is necessary for gastropods to be able to quickly repair their shells  
47 following predation attacks and to protect them from their local environment and reduce  
48 further predation when vulnerable soft tissues are left exposed following damage. During  
49 periods following damage shell growth can heavily impact on metabolic functioning of the

organism, as energy resources are redirected into shell repair (Ebert, 1968; Ruppert et al., 2004; Melzner et al., 2011; Thomsen et al., 2013).

There are a range of factors that inflict damage to the shells of marine gastropods, including storms and increases in turbulence and exposure (Sepúlveda et al., 2012; Solas et al., 2015). For *B. undatum*, damage to the shell margin often occurs following unsuccessful predatory attacks, both against and inflicted by whelks themselves (Checa, 1993; Mensink et al., 2000; Ramsay et al., 2001). However, one of the key factors leading to shell damage is that caused from fishing gear, both directly from impact with mobile towed fishing gear and indirectly following capture. For example, the process by which whelk are graded for size on a ship's deck can pose additional risk to the shells of under-sized specimens due to the riddling process. Captured whelks are passed through a series of metal riddle bars which sort the catch and retain whelks greater than the minimum legal landing size but allow undersized whelks passage through where the shells may become broken or chipped (Bergman et al., 1994; Cadée et al., 1995; Fahy et al., 1995; De Vooy et al., 1998; Mensink et al., 2000).

This study investigates the impact of environmental factors, seawater temperature, food availability and ontogeny on shell growth and repair in the common neogastropod whelk *Buccinum undatum*. This whelk occurs in British coastal waters and has a widespread distribution throughout North Atlantic shelf waters with records from the Greenland Seas in the north to the Bay of Biscay in the south (Golikov, 1968; De Vooy and van der Meer, 2010; Hayward and Ryland, 2011; Magnúsdóttir et al., 2019). They are the largest edible marine gastropod within the North Atlantic (Fahy et al., 2005) and are of commercial importance. Between January and March 2020, >4000 tonnes were landed by U.K. vessels into U.K. ports (price >£1,200 per tonne) (MMO, 2020). The U.K. shellfish industry has long been of importance economically and historically has relied on sustainable whelk populations that are resilient to

environmental change and harvesting pressures (Clark et al., 2016). Any disruption to an organism's growth through repeated shell damage and repair could potentially result in impacts on the fishery (Hilborn and Minte-Vera, 2008; Biro and Sampson, 2015), for example through reduced growth and longer or failure to reach the minimum landing size (currently in the U.K. MLS = 45 mm McIntyre et al., 2015). Despite the increasing fishery demand for *B. undatum* and need for sustainable management strategies (Fahy et al., 2000), shell damage and repair are understudied and ecologically-important aspects of research.

The aims of this study are to understand both the environmental and biological factors that can affect shell growth rate and repair in *B. undatum*. It is hypothesised that during shell repair, shell growth rate (increase in length) is reduced following a re-direction of energy away from size increase towards shell repair and that this process will be affected by seawater temperature and food availability for whelk of different age (size) groups.

## 2. Materials and Methods

### 2.1 Sample collection and holding

Newly-laid egg masses of *Buccinum undatum* attached to the pier pilings of a small jetty and surrounding rocks at Brynsiencyn, North Wales (UK) 53°09'30.4"N 4°16'46.6"W, were collected during low water of spring tides (November 2014 and November 2017). Large (>45 mm total shell length (TSL), assumed to be adult) and small (<45 mm TSL, assumed to be juvenile) whelks were collected (January & July 2019) using inkwell pots baited with Atlantic mackerel (*Scomber scombrus*), deployed for 24h subtidally at 4m depth off Brynsiencyn. Whelk maturity was probabilistically determined using a previously calculated size of maturity (SOM) estimation to group specimens as either adult whelk (AW) or juvenile wild (JW) (see Haig et al., 2015). This was achieved using the European MLS of 45 mm as opposed to larger, site-specific MLS outlined

in Haig et al. (2015). This smaller size was used to ensure juveniles were juveniles, as a larger TSL could incorporate more mature individuals. Egg masses and whelks were maintained in laboratory tanks, supplied with flowing ambient temperature seawater (8-10°C), and aerated. Ten egg masses were placed in each of three 50L tanks with fine mesh over the outflow pipe to retain any emerging juveniles (tank-reared juvenile whelk (TRJ)). After approximately one-month, juvenile whelks hatched and were transferred daily to smaller 8L tanks (mesh over outflow) supplied with ambient temperature flowing seawater, where they were on-grown and fed daily on a diet of freshly-shucked mussel (*Mytilus edulis*) tissue.

## 2.2 Experiment set up

A daily frequency of feeding continued throughout the experiments, unless stated otherwise (see Table 1), to ensure food availability was not a limiting factor for shell repair and shell growth. After hatching and collection, whelks were on-grown at a range of seawater temperatures (5, 10 and 15°C) and feeding regimes (unfed, daily fed or weekly fed) (see Table1) and following ten days acclimation, shell growth and repair were investigated under these different environmental conditions. For all experiments carried out under ambient conditions, wild-caught whelks were maintained in a flow-through system in 15L tanks, with TRJ whelk suspended within these in 8L tanks with mesh inserts to prevent escape. For temperature experiments, larger 175L temperature-controlled tanks were used for wild-caught whelk with TRJ again suspended in mesh containers to allow water flow. To achieve acclimation at the upper or lower temperatures, water temperature was raised or lowered incrementally before experimental shell damage was undertaken ten days later. Each whelk was individually labelled with a waterproof paper number adhered with superglue (see Figure 1) so that daily changes in individual shell growth rates could be followed. Although experiments were run over several

different time periods (see Table 1), the size and age of tank-reared juvenile whelks were kept consistent between years, along with all the environmental factors.

### 2.3 Controlled damage and measurements

Following several iterations of method development, the shells of the TRJ, JW and AW whelks were experimentally damaged by cutting out a square portion of the shell lip of each whelk using a Dremel 3000, with a cutting wheel attachment. Each cut was 40% of the aperture diameter (see Figure 1). A proportion of whelks within each experiment were left undamaged to serve as a control comparison. However, for experiments where food and seawater temperature were controlled, due to a limited number of individuals, TRJ did not have undamaged controls. Photographs of each damaged and undamaged whelk shell were taken against a measurable scale and the area of shell removed and regrown and total shell length (TSL) determined (to 3 d.p.) using ImageJ (see Figure 1). Measures of TSL were recorded to monitor growth, not shell repair. The frequency of measurements depended on the rate of visible shell growth and repair and was consequently different between different age groups. Measurements were taken every 3 days for (TRJ), 6 days (JW) and 7 days (AW) respectively until the end of the experiment period to limit disturbance during growth.

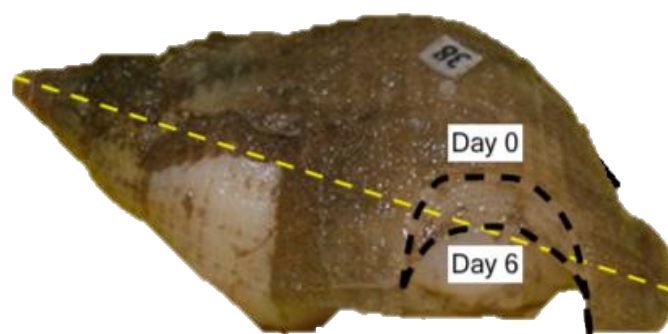
### 2.4 Statistical analysis

From the measurements of TSL and damage area, an individual cumulative value of TSL increase and percentage repair was calculated for the experiment period and daily rates calculated from these final values as percentage repair and growth per day ( $\text{mm}^2.\text{day}^{-1}$  and  $\text{mm}.\text{day}^{-1}$  respectively). General Linear Models (GLM) were used to test whether growth and shell repair were significantly influenced by environmental variables. Depending on experimental treatment (Table 1), response variables were either percentage repair (%) or TSL growth  $\text{day}^{-1}$

(mm); explanatory variables were either age (TRJ, JW, AW), food (unfed, daily, or weekly) or temperature (5, 10 or 15°C). Response variables were modelled as continuous variables, and explanatory variables were modelled as categorical variables. Interactions between life stage and food or temperature were included to test whether relationships between growth rates or percentage repair and food/temperature varied amongst age-groups (TRJ, JW, AW). Statistical significance (p-values) were obtained from F-tests, and backwards model selection based on p-values was applied (Zuur et al., 2009). When interaction terms were non-significant in the full model, they were replaced with a non-interactive term and the process restarted. Diagnostic plots of residuals were checked. For graphical representation, the cumulative values were plotted in place of actual rates for a clearer comparative view of growth and shell repair between treatment groups. TSL was presented graphically using an average cumulative growth, taken as the average increase in shell length, and percentage repair as the average proportion of shell repaired out of 100% for all individuals per measured day.

Due to differences in experiment length, with adult whelk studies run for longer periods than juveniles, and disparity in the degree of shell repair recorded, with some whelks attaining 100% repaired shell long before the end of the experiment, the values have not been taken as a final day measure. To resolve this, for statistical purposes, experiment duration for measures of repair rate have been taken as the day at which the first 75% of individuals from one single experiment have repaired to 100%.





162

163 Figure 1: Experimentally damaged TRJ *Buccinum undatum* (number 38) showing the area of  
 164 shell removed at the shell lip at day 0 and then repaired by day 6 (black dashed lines).  
 165 Percentage repair area measurement calculated through the remaining area to be deposited  
 166 until a value of 0 was reached. Total shell length (TSL) is indicated by the yellow dashed line.

#### 167 2.5 Calcein staining

168 To investigate qualitative changes in shell structure during shell repair, whelks were marked  
 169 with the fluorescent dye Calcein to distinguish the original shell growth prior to damage  
 170 (Kaehler and McQuaid, 1999). Twenty whelks whose shell margins (lips) had been mechanically  
 171 damaged were stained in a 50 mgL<sup>-1</sup> Calcein-seawater solution for 24 hours, to mark the point  
 172 in growth when the shell was damaged. The whelks were then on-grown and fed for 7 days in  
 173 flowing ambient temperature seawater after which the edge of the shell lips of ten of the shells  
 174 that had repaired 50% of their shell were again damaged for a second time and then on-grown  
 175 for a further 7 days. At the end of the experiment, whelks were frozen at -20°C as a means of  
 176 dispatch and upon thawing, the flesh was removed avoiding damage to the shell margin.  
 177 Organic material was removed from the shell surface by immersion for 30 mins in a 0.01M  
 178 NaOH solution, rinsed in fresh water and air-dried before the complete shell was embedded in  
 179 Kleer-set™ polyester casting resin (see Hollyman et al., 2020). The embedded shell lip and area  
 180 of shell damage were sectioned using a precision diamond saw blade (Beuhler isomet 4000)

181 and the cut surface ground on successively finer silicon carbide abrasive papers (FEPA P400 and  
182 P1200 grade) before attaching the dry, cut surface to a microscope slide using superglue. Once  
183 dry, the attached resin and shell were sectioned again using the saw to create a 1 mm thin  
184 section. The thin section was ground with successively finer grades of silicon carbide paper and  
185 polished to a final grade using a 3  $\mu$ m diamond suspension to achieve an approximate 0.2 mm  
186 thick polished section. Low power (10x magnification) images of the shell structure were taken  
187 under transmitted light, using a compound microscope. Matching (10x magnification) images  
188 of the fluorescing Calcein marks were taken using a UV fluorescent light microscope and  
189 photographed using an attached eyepiece camera. This produced comparative composite  
190 images of the repaired shell and structure and Calcein marks.

191

192 Table 1: Summary of experimental design with key differences and experimental conditions outlined

Treatment	Timeframe	Experiment Length (days)	Life Stage	Tank arrangement	Food Availability	Seawater Temperature
Life stage	January 2019	39	Tank Reared Juvenile (TRJ)	8L within 15L tank 20 per tank	Daily	Ambient (8-10°C)
		48	Juvenile Wild (JW)	15L tank 20 per tank	Daily	
		70	Adult Wild (AW)	15L tank 10 per tank	Daily	
Food availability	July 2019	15	Tank Reared Juvenile (TRJ)	8L within 15L tank 15 per tank	Unfed, daily, once weekly	
		21	Adult Wild (AW)	15L tank 10 per tank	Unfed, daily, once weekly	
Temperature	January 2016	15	Tank Reared Juvenile (TRJ)	8L within 175L tank 20 per tank	Daily	5, 10 and 15°C
	January 2019	21	Adult Wild (AW)	175L tank 40 per tank	Daily	5 and 10°C

### 194 3. Results

#### 195 3.1 Effect of age on shell repair and growth.

196 The effect of life stage on shell repair rate is shown in Figure 2A. Mean repair rate with time  
 197 decreased with increase in life stage, with an overall range in rates of 2.1% day<sup>-1</sup> between the  
 198 three measured groups (see Table 2 for rates). Laboratory tank-reared whelks (TRJ) (TSL 11.5-  
 199 21.25mm) repaired their shells rapidly and all shells were repaired within 30 days. Juvenile wild-  
 200 caught (JW) (TSL <45mm) and adult wild-caught (AW) (TSL >45mm) whelks repaired their shells  
 201 more slowly so that by day 40 all the JW whelks had repaired their shells but none of the AW  
 202 whelks had completely repaired their shells by day 65. The cumulative increase in total shell  
 203 length with time (Figure 2B) for the three different whelk age groups showed a similar trend to  
 204 repair rate. Repair rate and increase in total shell length were significantly different between  
 205 age groups (both  $p < 0.001$ ; Table 2). Compared with the experimentally-damaged whelks, the  
 206 undamaged control whelks generally achieved a larger total length (Figure 2B), although this  
 207 was not significantly different ( $p > 0.05$ ; Table 2).

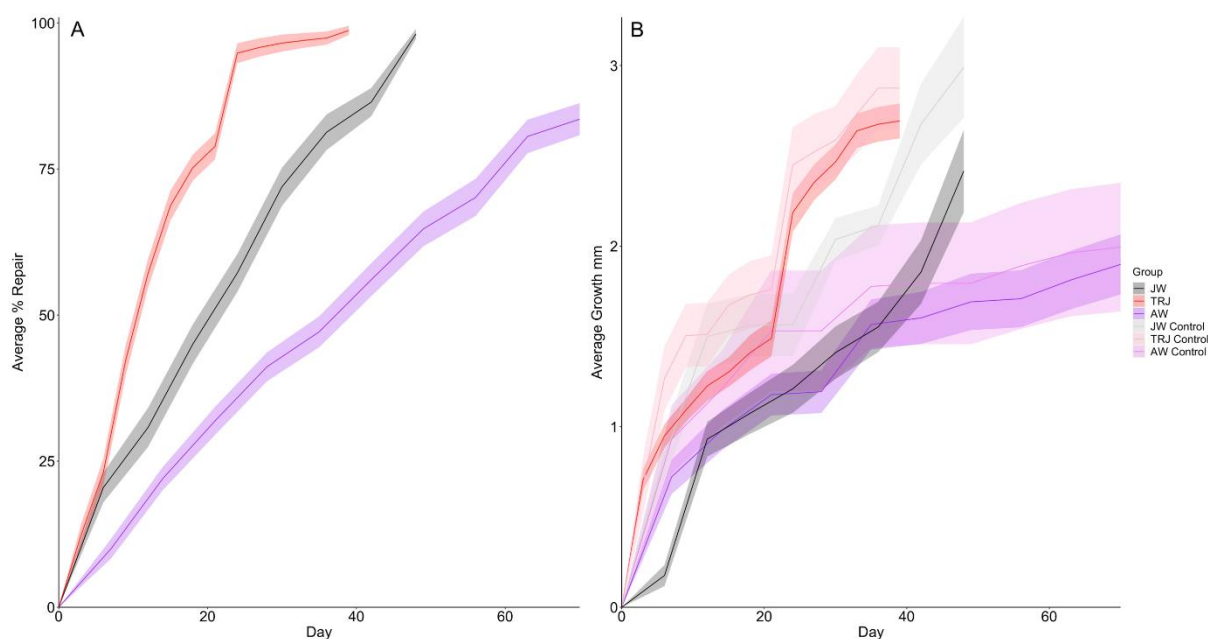


Figure 2: *Buccinum undatum*: A) average cumulative % shell repair ( $\pm$  1S.E. ribbon) with time and B) average cumulative increase in total shell length growth ( $\pm$  1S.E. ribbon) with time for three different age groups during a 70-day (AW – adult wild-collected), 48-day (JW – juvenile wild-collected) and 39-day (TRJ – tank-reared juvenile) laboratory experiment.

### 3.2 Effect of food ration on shell repair and growth.

Damaged juvenile (TRJ) whelks repaired their shells significantly faster than AW whelks ( $p < 0.001$  Table 2) but there were no significant effects of ration or the interaction between age and ration on repair rate (both  $p > 0.05$ ; Table 2). A plot of cumulative repair rate (Figure 3A) showed juveniles that had no food or were fed daily had a faster repair rate than those fed once a week. AW whelks fed once a week repaired their shells at a similar rate to TRW individuals fed a similar ration. However, those AW whelks fed daily or unfed repaired their shells more slowly (Figure 3A). When the effects of ration on cumulative total shell length (Figure 3B) were investigated statistically, TRJ whelks grew significantly faster ( $p < 0.001$ ; Table 2) than damaged and control AW whelks (Figure 3B). Generally, the AW control whelks grew faster than the damaged AW whelks, although the exceptions were the AW control whelks and AW whelks fed daily which grew the slowest,  $0.028 \text{ mm.day}^{-1}$  and  $0.027 \text{ mm.day}^{-1}$  respectively (Table 2 and Figure 3B). Whilst shell growth rate was depressed in AW damaged and control whelks, growth rate was promoted in whelks fed once a week, particularly in TRJ whelks (Figure 3B). The effect of ration and the interaction between ration and age were both significant ( $p < 0.001$  and  $p < 0.05$  respectively; Table 2).

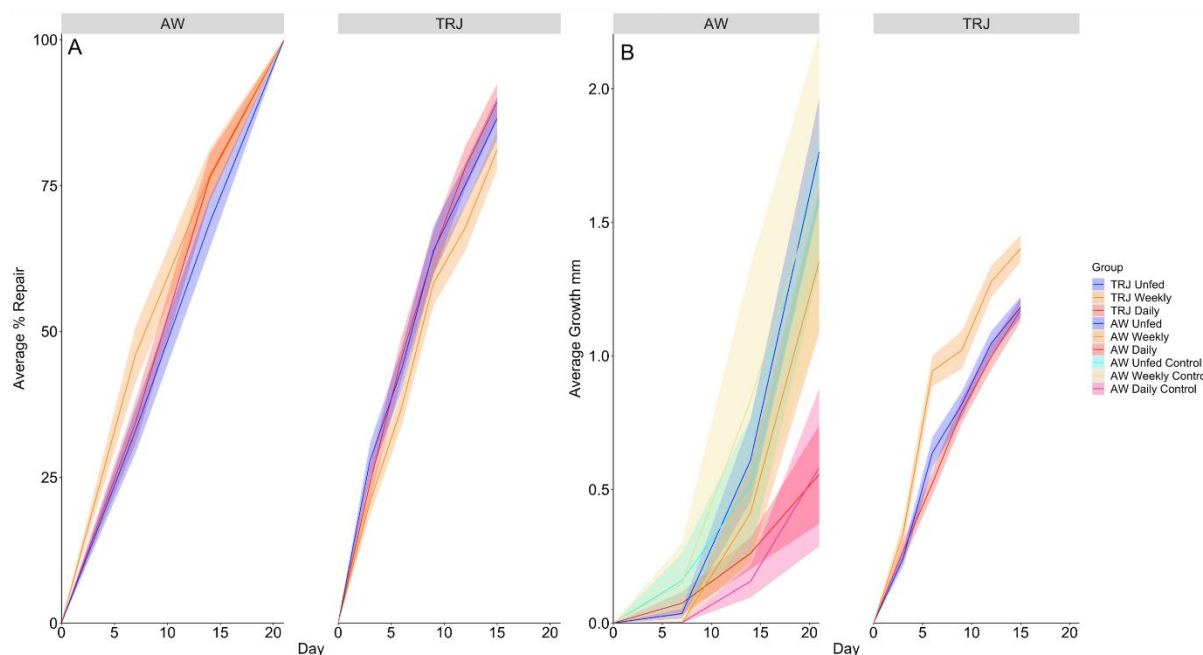
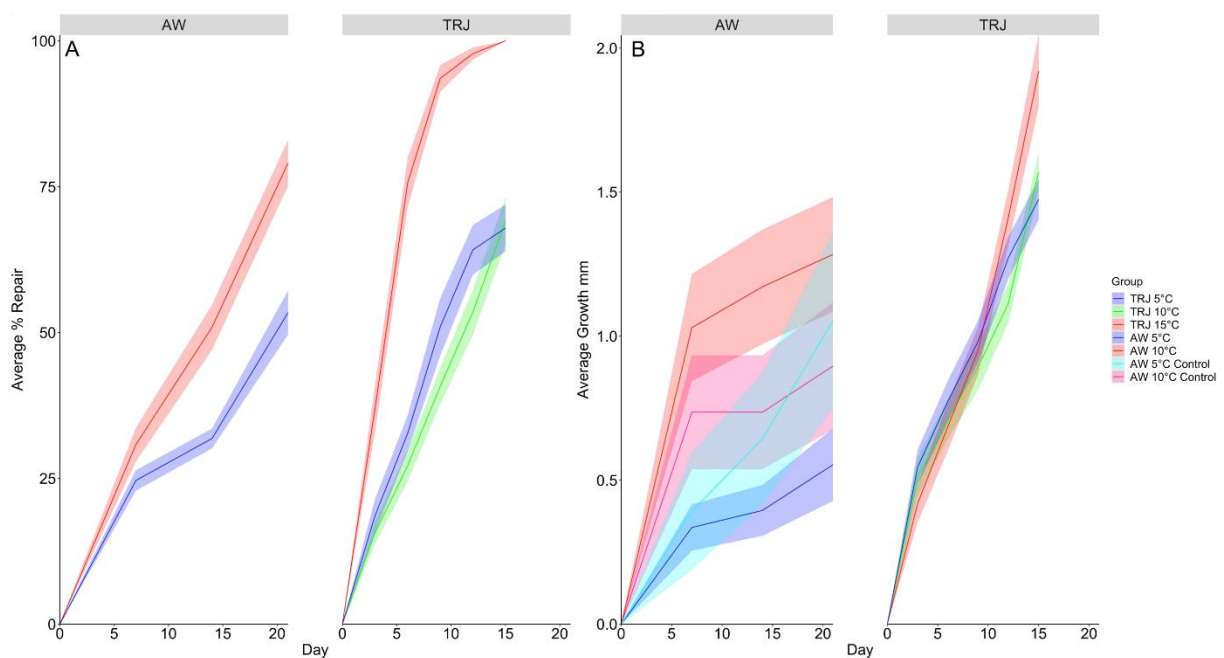


Figure 3: *Buccinum undatum* grown during a 21-day (AW) and 15-day (TRJ) laboratory experiment with different feeding regimes. A) average cumulative % shell repair ( $\pm$  1S.E. ribbon) with time for two different groups, tank-reared juveniles (TRJ) and wild-collected adult whelks (AW) provided with three different rations (unfed, daily, weekly) and B) average cumulative increase in total shell length growth ( $\pm$  1S.E. ribbon) with time for three different groups, tank-reared juveniles (TRJ), wild-collected adult whelks (AW) and undamaged wild-collected adult whelks (control) (AW control) provided with three different rations (unfed, daily, weekly).

### 3.3 Effect of Temperature on shell repair and growth.

Experimentally-damaged juvenile whelks (TRJ) repaired their shells faster than adult whelks (AW) at all three seawater (SW) temperatures ( $p < 0.001$ ; Table 2; Figure 4A). TRJ whelks maintained at 15°C repaired their shells at an average of 10.4% day<sup>-1</sup> with >95% of shells being repaired by day 9. A faster initial increase in repair rate (between days 0 and 12) was observed for TRJ whelks maintained at 5°C compared to TRJ whelks maintained at 10°C. At 15°C juveniles repaired their shells completely in 14 days with a repair rate more than double the rate of TRJ whelks held at 10°C and 5°C which repaired 70% of their shell over the same time-period (Figure

245 5A). Adult whelks reared at 10°C and 5°C repaired 75% and 50% of their shell respectively by  
 246 day 20 (Figure 4A). The effects of SW temperature and the interaction between SW  
 247 temperature and age were both significant ( $p < 0.001$  and  $p < 0.05$  respectively; Table 2). When  
 248 the effect of SW temperature on cumulative total shell length (Figure 4B) was investigated  
 249 statistically (Table 2), TSL increased in TRJ whelks independent of SW temperature (Figure 4B).  
 250 In AW whelks TSL generally increased independent of SW temperature for the first 5 days  
 251 whereupon TSL increase slowed down (Figure 4B). Adult whelks increased in TSL the fastest at  
 252 10°C (AW and AW control) whereas TSL increase in adult whelks was slow at 5°C (Figure 4B).  
 253 The effect of SW temperature on TSL was significant ( $F = 3.41$ ,  $p < 0.05$ ) but the interaction  
 254 between SW temperature and age was non-significant ( $p > 0.05$ ; Table 2).



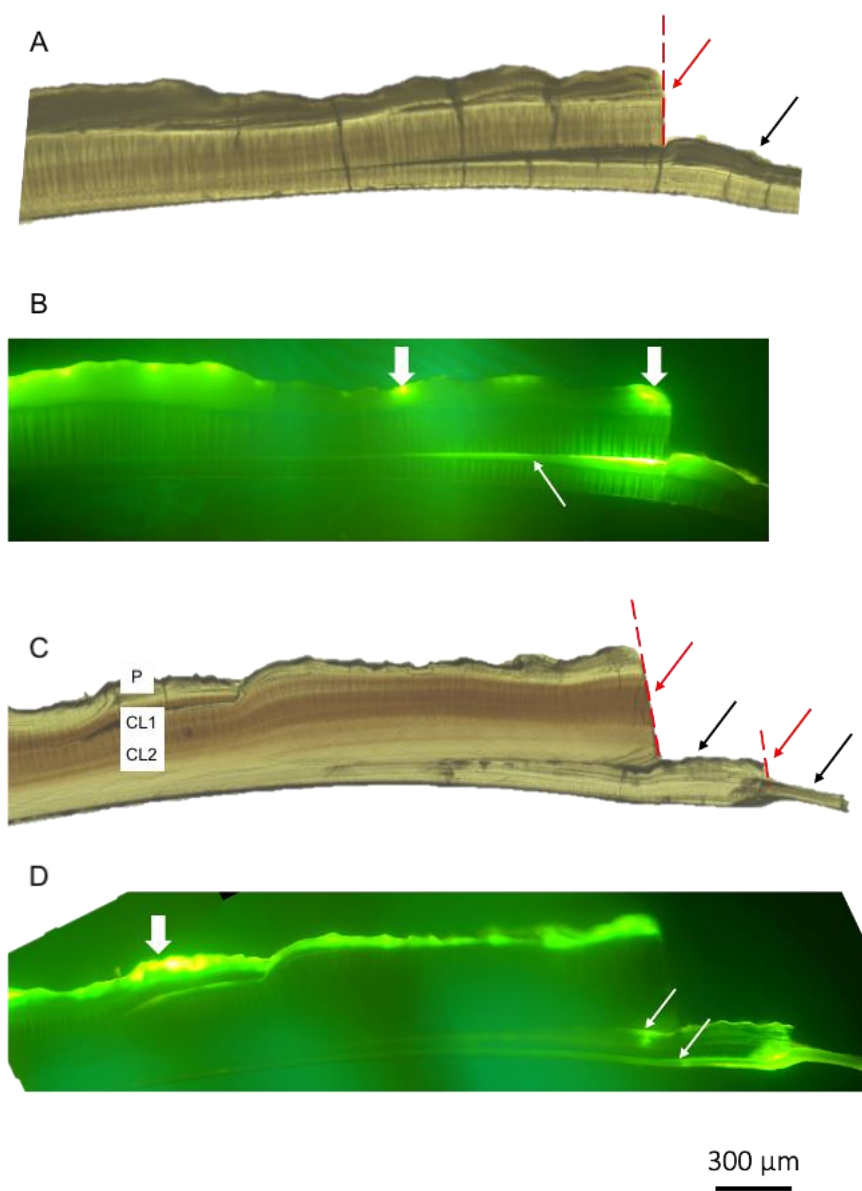
256 Figure 4: Shell repair in *Buccinum undatum* grown during a 21-day (AW), 15-day (TRJ) laboratory  
 257 experiment at different seawater temperatures. A) Average cumulative % shell repair ( $\pm$  1S.E.  
 258 ribbon) with time for juvenile (TRJ) and adult (AW) whelks grown at 5, 10 and 15°C (TRJ) and 5  
 259 and 10°C (AW). All adult whelks died at 15°C. B) Average cumulative increase in total shell  
 260 length ( $\pm$  1S.E. ribbon) with time for juvenile (TRJ) and adult (AW) (damaged and control) whelks

grown at 5, 10 and 15°C (TRJ) and 5 and 10°C (AW). More than 75% mortality was observed within adults in the 15°C experiment within the first 5 days, so it was not continued. Tank-reared juveniles (TRJ), wild-collected adult whelks (AW).

### 3.4 Structure of shell growth

Figure 5 shows the appearance of *B. undatum* thin shell lip sections viewed in transmitted light (A and C) and the same sections illuminated with U.V. light (B and D). The point where the shell was damaged is a truncated cut perpendicular to the growing shell (red arrow), with the subsequently deposited thinner post-repaired shell (black arrow). Following exposure to Calcein, post-shell damage, a bright fluorescent line is visible under U.V. light (small white arrow Figure 5B). A similar response to shell damage and Calcein incorporation is visible in shells that were damaged twice followed by Calcein exposure. Figure 5C shows two truncated cuts (red arrows) and subsequent thinner shell re-growth (black arrows). The same section viewed in U.V. shows two fluorescent lines corresponding to the two periods of Calcein exposure (small white arrows Figure 5D). The thin sections show that following shell damage, new shell deposition begins rapidly following Calcein incorporation on the inner surface of the crossed lamellar layer with newly forming outer prismatic layer developing approximately 1mm inside the point of shell damage (Figure 5A). Shell extension occurs rapidly as the removed shell is quickly replaced to repair the missing shell at the lip and is thickened on the inner surface with crossed lamellar shell structure. The extension of repaired shell following the second damage incident however appears to be less than when the shell was first damaged (Figure 5C).





281  
 282 Figure 5: Thin shell sections of *Buccinum undatum* viewed in transmitted light (A and C) and in  
 283 U.V. light (B and D). A) section to show the appearance of the damaged shell (red arrow) and  
 284 subsequent shell repair (black arrow), B) shell section in (A) to show damage and incorporation  
 285 of Calcein (bright fluorescent line – thin white arrow (incorporation), thick white arrow  
 286 (absorption)), C) section to show appearance of a double damaged shell (red arrows mark the  
 287 first and second incidents of damage. Black arrows indicate post-damage re-growth) and D)  
 288 shell section in (C) to show damage and incorporation of Calcein (bright fluorescent line – white  
 289 arrows). P = periostracum, CL1 and CL2 = crossed lamellar layer. The outer periostracum  
 290 absorbs the Calcein and fluoresces under U.V. light (Large white arrow). Scale bars = 300μm.

Table 2: Summary of repair rates ( $\text{mm}^2.\text{day}^{-1}$ ) and growth rates ( $\text{mm}.\text{day}^{-1}$ ) of experimentally-damaged *Buccinum undatum* grown under different food rations and seawater temperatures.

Life Stage		Mean ± Standard Error						ANOVA		Where within Group	Fig.	
Group	Tank Reared Juvenile (TRJ)			Juvenile Wild (JW)			Adult Wild (AW)					
	Damaged	Control		Damaged	Control		Damaged	Control				
Repair Rate	3.951 ±0.071	-		2.044 ±0.017	-		1.933 ±0.039	-		Group: F= 865, p<0.001	All	2A
Growth Rate	0.091 ±0.004	0.102 ±0.009		0.050 ±0.005	0.062 ±0.006		0.027 ±0.002	0.029 ±0.005		Group: F= 90.6, p<0.001	All	2B
Food ration		Mean ± Standard Error						ANOVA		Where within Group	Fig.	
Group	Unfed			Weekly			Daily					
	TRJ Damaged	AW Damaged	AW Control	TRJ Damaged	AW Damaged	AW Control	TRJ Damaged	AW Damaged	AW Control			
Repair Rate	5.765 ±0.025	4.756 ±0.002	-	5.405 ±0.226	4.760 ±0.001	-	5.954 ±0.203	4.761 ±0.001	-	Age: F= 54.6, p<0.001 Group: F= 1.87, p>0.05 Age*Group: F= 2.01, p>0.05	None	3A
Growth Rate	0.079 ±0.003	0.084 ±0.010	0.075 ±0.012	0.093 ±0.003	0.065 ±0.013	0.079 ±0.026	0.078 ±0.003	0.027 ±0.009	0.028 ±0.014	Age: F= 17.2, p<0.001 Group: F= 11.1, p<0.001 Age*Group: F= 6.53, p<0.05	Daily/ Unfed Daily/ Weekly	3B
Temperature		Mean ± Standard Error						ANOVA		Where within Group	Fig.	
Group	5°C			10°C			15°C					
	TRJ Damaged	AW Damaged	AW Control	TRJ Damaged	AW Damaged	AW Control	TRJ Damaged	AW Damaged	AW Control			
Repair Rate	4.527 ±0.266	2.545 ±0.179	-	4.605 ±0.269	3.766 ±0.186	-			10.397 ±0.253	Age: F= 296, p<0.001 Group: F= 183, p<0.001 Age*Group: F= 6.47, p<0.05	All	4A
Growth Rate	0.098 ±0.005	0.026 ±0.006	0.050 ±0.014	0.105 ±0.004	0.061 ±0.009	0.045 ±0.010			0.106 ±0.009	Age: F= 72.7, p<0.001 Group: F= 3.41, p<0.05 Age*Group: F= 1.05, p>0.05	All	4B

## 294 4. Discussion

295 This study used a series of controlled laboratory experiments to investigate the rate of shell  
296 repair and shell growth in juvenile and adult common whelk, *Buccinum undatum* following  
297 damage to the shell lip and examined how these rates are affected by food availability and  
298 seawater temperature. The responses to shell damage recorded help provide an insight into  
299 the factors involved in the recovery process of damaged individuals in wild populations  
300 following shell damage as a result of storms, predation or demersal fishing activities. Our  
301 findings reveal significant variation in responses between juvenile and adult *B. undatum*, with  
302 these differences synchronous under all tested conditions for both rates of shell repair and  
303 growth (i.e., TSL increase). Responsiveness to changing temperature and food availability  
304 presented further differences in growth and repair rates, suggesting that there are multiple  
305 factors influencing these rates in gastropod molluscs. The study therefore provides insight into  
306 the key environmental drivers influencing shell repair in the wild.

307 Results from calcein staining showed that a damaged area did not only fill in with new shell  
308 growth but continued the build-up of new shell layers on the inner surface of the shell and back  
309 into the shell whorls throughout periods of damage and repair. The re-building of shell layers  
310 by depositing beneath existing layers, although strengthening the repaired section, is likely to  
311 result in heavier shells occurring within natural populations of areas with increased damage  
312 incidents (Thomas and Himmelman, 1988; Ramsay et al., 2001; Stafford et al., 2015). Such  
313 variation is often observed within wild whelk populations, with shell thickening and scarring  
314 occurring more in certain geographical areas than others (Ramsay et al., 2001; Preston and  
315 Roberts, 2007). In addition, this variation in shell scarring due to fishery disturbance has been  
316 noted for other species, for example in the dog cockle *Glycymeris glycymeris*, with areas of  
317 higher fishing seeing higher rates of damage and consequent repair (Kaiser et al., 2000;

Mensink et al., 2000). Additionally, predation pressures and wave action see further shell variation in scarring events, as seen within the painted top shell *Calliostoma zizyphinum* (Preston and Roberts, 2007) and the hydrothermal whelk species *Buccinum thermophilum* (Martell et al., 2002), through incidents of shell chipping. Although the thickening of the shell would increase resistance to a re-break, the process itself leaves the individual vulnerable to its surroundings immediately post-damage, due to the large metabolic implications of shell growth along with the damaged shell leaving the soft tissues exposed (Palmer, 1992; Frieder et al., 2017).

Total shell length was found to continue to increase throughout periods of repair and, although a significant difference in the rate of TSL increase was not observed, shell damage did result in some deviation in daily growth trends of repairing animals, when compared with control groups. It was expected that due to the high metabolic cost of shell growth and biomineralization, the rate of TSL increase would dramatically reduce due to the shell repair process in damaged whelks (Ebert, 1968; Ruppert et al., 2004; Melzner et al., 2011; Thomsen et al., 2013). However, the results indicate the importance of continual shell growth even when the shell is damaged, with little difference in TSL between the control and damaged groups. This is likely an evolutionary development to ensure that whelks continue to increase in size so that they reach a spatial size refuge from a range of predators as quickly as possible. Although there has been limited research into this, continual shell growth has recently been observed in the brachiopod *Liothyrella uva* (Cross et al., 2015). This build-up occurring, with the complete re-growing of new shell layers could further be an influencing factor in the continued TSL increase due to increased shell deposition and biomineralization.

The influence of age on an individual's growth trajectory has long been studied across a range of animal taxa (von Bertalanffy, 1938; Richardson, 2001; West et al., 2001; Sibley et al., 2015).

342 As expected from theory, the results of this study show ontogenetic differences in rates of shell  
343 growth and repair, with slower rates for both processes observed in older individuals; tank-  
344 reared juvenile whelks repairing their damaged shell at a rate almost twice that of adult whelks.  
345 These responses have often been seen as a result of constraints to body size and development,  
346 with larger older individuals seeing reduced rates of growth (Tanabe, 1988; Richardson, 2001).  
347 With an increased body size, the trade-off between additional metabolic costs, including  
348 maturation and reproductive success, outweighs the requirement of further shell production  
349 resulting in a further decline in growth rates, as energy allocation is shifted from growth to  
350 reproduction (Tanabe, 1988; Palmer, 1990; Kideys, 1996; Richardson, 2001; Thomsen et al.,  
351 2013). In addition, an increased need for protection at a smaller size would further require  
352 faster rates of growth and repair, as an individual needs to grow until they reach a size  
353 threshold at which predation vulnerability is reduced, i.e., a size refuge is reached (Chase, 1999;  
354 Karythis et al., 2020). Nonetheless, the capacity for retraction into and protection from the shell  
355 is of key importance for increased rapid escape capabilities from a surrounding threat (Tanabe,  
356 1988; Palmer, 1990; Seed and Hughes, 1995; Kideys, 1996).

357 Metabolic cost is a fundamental part of growth, with energy consumption vital for development  
358 and survival. It is interesting to note that the results of this study indicate that food availability  
359 had no significant effect on shell repair rates with unfed individuals and those fed daily showing  
360 similar rates of shell repair. However, differences in growth (as indicated by changes in TSL)  
361 were observed between the different feeding groups. Under unfed or daily feeding conditions,  
362 juvenile whelks displayed faster repair rates than those offered food once per week, whereas  
363 for TSL growth, weekly food conditions for juvenile and non-damaged adult whelks saw the  
364 fastest overall rates. Although the response to a lack of food did not follow expected responses,  
365 whereby for many marine organisms, energy is often saved for increased survival capabilities,

366 or processes are reduced until more favourable conditions arise (Tomanek and Somero, 1999;  
367 Stillman, 2003; Melzner et al., 2011). The observed response in our experiments likely suggests  
368 that the need to repair the shell is overwhelmingly important for protection and growth. Palmer  
369 (1983) however, showed that starved gastropods used body reserves and supplementary  
370 energy sources to fulfil the needs of shell formation, often through protein catabolism, a  
371 process that continues throughout normal feeding but is relied upon more heavily when food  
372 becomes scarce or unavailable. Without knowledge of the whelk's feeding behaviour in the  
373 wild prior to capture, we do not know whether sufficient energy reserves may still have been  
374 available to the unfed whelks or they were using protein catabolism to provide energy to repair  
375 their shells and increase their TSL during their laboratory experimental conditions. Our initial  
376 hypothesis was that there would be a link between food supply and shell repair rate, i.e., whelks  
377 fed daily would repair their shells faster than those fed weekly and those with no food supply.  
378 Our results demonstrated that there was no difference in repair rates between the three  
379 different feeding regimes although there was a significant difference in growth rate between  
380 the three groups of whelks. The daily fed whelks grew the slowest possibly because they over  
381 ate as they had access to an unlimited food supply and were subsequently stressed. However,  
382 throughout all daily feeding conditions no sign of distress to the whelks was observed and the  
383 highest number of mortalities were in the unfed whelk groups and not those fed daily. We  
384 postulate that during the summer the daily fed whelks may have allocated surplus energy from  
385 their food intake to gametogenesis, a few months prior to when individuals would be engaging  
386 in reproduction in the autumn, at the expense of increasing their TSL. Likewise, shell deposition

and rates of biomineralization are further affected through gene expression, and further through temperature changes (Joubert et al., 2014).

Temperature is a key environmental factor, with fluctuations in seawater temperature dramatically affecting physiological processes within marine organisms, with a range of responses and metabolic adjustments seen (Page and Hubbard, 1987; Prosser, 1991; Sokolova and Portner, 2003; Harley et al., 2006). Benthic organisms have an increased susceptibility to thermal stress (Foster, 1971; Harley et al., 2006) with greater impacts/effects observed in juvenile/ smaller individuals (Pechenik et al., 2019; Levinton, 2020), a response observed within this study. Temperature was found to have a significant effect on both rates of growth and repair with juvenile whelks reared at 15°C presenting the highest rates observed. A similar result was observed for adult whelks that showed increased rates at 10°C compared to 5°C but could not be tested at 15°C due to their mortality rates increasing as their thermal limit was reached and exceeded. It appears that juvenile whelk can handle much warmer seawater temperatures demonstrated by the 15°C degree TRJ whelks that showed the fastest growth. The observed responses would allow for early life development of whelks at shallower depth, although as adult whelks (AW) are generally found in deeper, cooler waters, this could be further reflective of the metabolic changes occurring (Valentinsson et al., 1999; McIntyre et al., 2015).

In some gastropod species certain environmental conditions (e.g., a combined change in pH and elevated seawater temperature) have been observed to reduce morphological size and have a negative effect on growth, as observed, for example, in the periwinkle (*Littorina saxatilis*) and gold-ringed cowry (*Monetaria annulus*) (Sokolova and Pörtner, 2000; Irie and Fischer, 2009; Melatunan et al., 2013). Observations from our study support previous work into

metabolism and temperature, with increased temperatures causing an increased rate of growth, up until the thermal tolerance is reached (Emmerson et al., 2020; Borsetti et al., 2021). In these studies, elevated temperature resulted in increased rates of calcification, due to heightened enzyme activity associated with the biomineralization process and consequently raised uptake of  $\text{Ca}^{2+}$  ions (Bevelander and Nakahara, 1969; Pons et al., 2002; Thomsen et al., 2010; Lervik et al., 2013). Although the results from our study showed a difference in response to changing temperatures. Plasticity to surrounding temperature has been seen to be dependent on pH, and external stimuli in other marine molluscs (Melatunan et al., 2013).

In conclusion, our study has shown that shell growth and shell repair rates in *B. undatum* are strongly influenced by factors such as age, seawater temperature, and food availability. The growth and repair of shells of marine gastropods can vary greatly both within and between species (Palmer, 1990). This variability is not only a result of phenotypic differences, such as shell thickness and shape (Brookes and Rochette, 2007; Magnúsdóttir et al., 2018), but also as a response to individual genotype (Magnúsdóttir et al., 2019; Goodall et al., 2021) and environmental cues such as predator presence and seawater temperature changes (Zdelar et al., 2018). It is important to understand how a combination of these factors impact the populations of *B. undatum*, particularly given their current commercial importance, and interest in fishery management strategies. In understanding how shell growth and repair occurs in the whelk, and its impacts on the organism, we can better understand its resilience to both direct and indirect fishery impacts.

#### Acknowledgements

This work was funded by the family of C.N.C. and Bangor University, and we would like to thank Mark and Lina Colvin for their support and reviewing of this manuscript. We are grateful to



434 Berwyn Roberts for collecting *Buccinum undatum* and for his invaluable help with maintaining  
435 aquaria and animal husbandry. We also thank Stef Kraft, Helène Bonici-Strohmer, and George  
436 Collinson for their assistance during this project.

## 437 References

- 438 Bergmann, M., Beare, D.J., Moore, P.G., 2001. Damage sustained by epibenthic invertebrates  
439 discarded in the Nephrops fishery of the Clyde Sea area, Scotland. *Journal of Sea Research*,  
440 45(2), pp. 105-118.
- 441 Bevelander, G., Nakahara, H., 1969. An electron microscope study of the formation of the  
442 nacreous layer in the shell of certain bivalve molluscs. *Calcified Tissue Research*, 3(1), pp. 84-  
443 92.
- 444 Biro, P.A., Sampson, P., 2015. Fishing directly selects on growth rate via behaviour: implications  
445 of growth-selection that is independent of size. *Proceedings of the Royal Society B: Biological*  
446 *Sciences*, 282(1802), p.20142283.
- 447 Bonucci, E., 2007. Biological calcification. Normal and pathological processes in the early stages.  
448 Springer-Verlag, Berlin, Germany.
- 449 Borsetti, S., Hollyman, P.R., Munroe, D., 2021. Using a sclerochronological approach to  
450 determine a climate-growth relationship for waved whelk, *Buccinum undatum*, in the US Mid-  
451 Atlantic. *Estuarine, Coastal and Shelf Science*, 252, p.107255.
- 452 Brookes, J.I., Rochette, R., 2007. Mechanism of a plastic phenotypic response: predator-  
453 induced shell thickening in the intertidal gastropod *Littorina obtusata*. *Journal of Evolutionary*  
454 *Biology*, 20(3), pp.1015-1027.
- 455 Cadée, G.C., Boon, J.P., Fischer, C.V., Mensink, B.P., Ten Hallers-Tjabbes, C.C., 1995. Why the  
456 whelk (*Buccinum undatum*) has become extinct in the Dutch Wadden Sea. *Netherlands Journal*  
457 *of Sea Research*, 34(4), pp. 337-339.

- 458 Chase, J.M., 1999. Food web effects of prey size refugia: variable interactions and alternative  
459 stable equilibria. *The American Naturalist*, 154(5), pp.559-570.
- 460 Checa, A., 1993. Non-predatory shell damage in recent deep-endobenthic bivalves from Spain.  
461 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 100(3), 309-331.
- 462 Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2016. The  
463 impacts of deep-sea fisheries on benthic communities: a review. *ICES Journal of Marine*  
464 *Science: Journal Du Conseil*, 73(suppl 1), i51-i69.
- 465 Cross, E.L., Peck, L.S., Harper, E.M., 2015. Ocean acidification does not impact shell growth or  
466 repair of the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). *Journal of Experimental*  
467 *Marine Biology and Ecology*, 462, pp.29-35.
- 468 De Vooy, C., Van der Meer, J., 1998. Changes between 1931 and 1990 in by-catches of 27  
469 animal species from the southern North Sea. *Journal of Sea Research*, 39(3-4), pp. 291-298.
- 470 De Vooy, C.G.N., Van Der Meer, J., 2010 The whelk (*Buccinum undatum* L.) in the western  
471 Dutch Wadden Sea in the period 1946–1970: Assessment of population characteristics and  
472 fishery impact. *J Sea Res* 63:11–16.
- 473 Ebert, T.A., 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food  
474 availability and spine abrasion. *Ecology*, 49(6), pp. 1075-1091.
- 475 Emmerson, J.A., Hollyman, P.R., Bloor, I.S.M., Jenkins, S.R., 2020. Effect of temperature on the  
476 growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis  
477 within the Irish Sea. *Fisheries Research*, 223, p.105437.

- 478 Fahy, E., Carroll, J., Hother-Parkes, L., O'Toole, M., Barry, C., 2005. Fishery associated changes  
479 in the Whelk *Buccinum undatum* stock in the southwest Irish Sea, 1995-2003. Dublin: Fisheries  
480 Science Services.
- 481 Fahy, E., Masterson, E., Swords, D., Forrest, N., 2000. A Second Assessment of the whelk fishery  
482 *Buccinum undatum* in the southwest Irish Sea with particular reference to its history of  
483 management by size limit. Dublin: Fisheries Science Services.
- 484 Fahy, E., Yalloway, G., Gleeson, P., 1995. Appraisal of the whelk *Buccinum undatum* fishery of  
485 the southern Irish sea with proposals for a management strategy. Irish Fisheries Investigations,  
486 Series B (Marine), 42.
- 487 Findlay, H.S., Wood, H.L., Kendall, M.A., Spicer, J.I., Twitchett, R.J., Widdicombe, S., 2011.  
488 Comparing the impact of high CO<sub>2</sub> on calcium carbonate structures in different marine  
489 organisms. Marine Biology Research, 7(6), pp. 565-575.
- 490 Foster, B., 1971. On the determinants of the upper limit of intertidal distribution of barnacles  
491 (Crustacea: Cirripedia). The Journal of Animal Ecology, 40(1), pp. 33-48.
- 492 France, J., Dijkstra, J., Thornley, J.H., Dhanoa, M.S., 1996. A simple but flexible growth  
493 function. Growth, development, and aging: GDA, 60(2), pp.71-83.
- 494 Frieder, C.A., Applebaum, S.L., Pan, T.C.F., Hedgecock, D., Manahan, D.T., 2017. Metabolic cost  
495 of calcification in bivalve larvae under experimental ocean acidification. ICES Journal of Marine  
496 Science, 74(4), pp.941-954.
- 497 Golikov, A. N., 1968. Distribution and variability of long-lived benthic animals as indicators of  
498 currents and hydrological conditions. Sarsia. 34, pp. 199-208.

- 499 Goodall, J., Westfall, K.M., Magnúsdóttir, H., Pálsson, S., Örnólfssdóttir, E.B., Jónsson, Z.O., 2021.  
500 RAD sequencing of common whelk, *Buccinum undatum*, reveals fine-scale population  
501 structuring in Europe and cryptic speciation within the North Atlantic. *Ecology and*  
502 *evolution*, 11(6), pp.2616-2629.
- 503 Harley, C.D., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S.,  
504 Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal  
505 marine systems. *Ecology Letters*, 9(2), pp. 228-241.
- 506 Hayward, P.J., Ryland, J.S. (eds.), 2011 (reprinted). *Handbook of the Marine Fauna of North-*  
507 *West Europe*, Chapter 10: Molluscs, p. 535. Oxford: Oxford University Press.
- 508 Hilborn, R., Minte-Vera, C.V., 2008. Fisheries-induced changes in growth rates in marine  
509 fisheries: are they significant? *Bulletin of Marine science*, 83(1), pp.95-105.
- 510 Hollyman, P.R., Chenery, S.R., Leng, M.J., Laptikhovsky, V.V., Colvin, C.N., Richardson, C.A.,  
511 2018. Age and growth rate estimations of the commercially fished gastropod *Buccinum*  
512 *undatum*. *ICES Journal of Marine Science*, 75(6), pp.2129-2144.
- 513 Hollyman, P.R., Leng, M.J., Chenery, S.R., Sloane, H.J., Richardson, C.A., 2020. Calibration of  
514 shell  $\delta^{18}\text{O}$  from the common whelk *Buccinum undatum* highlights potential for  
515 palaeoenvironmental reconstruction. *Palaeogeography, Palaeoclimatology,*  
516 *Palaeoecology*, 560, p.109995.
- 517 Irie, T., Fischer, K., 2009. Ectotherms with a calcareous exoskeleton follow the temperature-  
518 size rule-evidence from field survey. *Marine Ecology Progress Series*, 385, pp.33-37.

- 519 Joubert, C., Linard, C., Le Moullac, G., Soye, C., Saulnier, D., Teaniniuraitemoana, V., Ky, C.L.,  
520 Gueguen, Y., 2014. Temperature and food influence shell growth and mantle gene expression  
521 of shell matrix proteins in the pearl oyster *Pinctada margaritifera*. PLoS One, 9(8), p.e103944.
- 522 Kaehler, S., McQuaid, C.D., 1999. Use of the fluorochrome calcein as an in situ growth marker  
523 in the brown mussel *Perna perna*. Marine Biology 133:455-460.
- 524 Kaiser, M.J., Ramsay, K., Richardson, C.A., Spence, F.E., Brand, A.R., 2000. Chronic fishing  
525 disturbance has changed shelf sea benthic community structure. Journal of Animal  
526 Ecology, 69(3), pp.494-503.
- 527 Karythis, S., Cornwell, T.O., Noya, L.G., McCarthy, I.D., Whiteley, N.M., Jenkins, S.R., 2020. Prey  
528 vulnerability and predation pressure shape predator-induced changes in O<sub>2</sub> consumption and  
529 antipredator behaviour. Animal Behaviour, 167, pp.13-22.
- 530 Kideys, A.E., Nash, R.D.M., Hartnoll, R.G., 1993. Reproductive cycle and energetic cost of  
531 reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. Journal of the Marine  
532 Biological Association of the United Kingdom, 73(02), pp. 391-403.
- 533 Kideys, A.E., 1996. Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off  
534 Douglas, Isle of Man. Helgoländer Meeresuntersuchungen, 50(3), pp. 353-368.
- 535 Lervik, A., Bedeaux, D., Kjølstrup, S., 2013. Active transport of the Ca<sup>2+</sup>- pump: introduction of  
536 the temperature difference as a driving force. European Biophysics Journal, 42(5), pp. 321-331.
- 537 Levinton, J., 2020. Thermal stress: The role of body size and the giant major claw in survival and  
538 heat transfer of a fiddler crab (*Leptuca pugilator*). Journal of Experimental Marine Biology and  
539 Ecology, 530, p.151428.

- 540 Magnúsdóttir, H., Pálsson, S., Westfall, K.M., Jónsson, Z.O., Örnólfsson, E.B., 2018. Shell  
541 morphology and colour of the subtidal whelk *Buccinum undatum* exhibit fine-scaled spatial  
542 patterns. *Ecology and evolution*, 8(9), pp.4552-4563.
- 543 Magnúsdóttir, H., Pálsson, S., Westfall, K.M., Jónsson, Z.O., Örnólfsson, E.B., 2019.  
544 Morphological variation in genetically divergent populations of the common whelk, *Buccinum*  
545 *undatum* (Gastropoda: Buccinidae), across the North Atlantic. *Biological Journal of the Linnean*  
546 *Society*, 128(1), pp.93-106.
- 547 Marine Management Organisation., 2020. UK Sea Fisheries Statistics 2020. Office for National  
548 Statistics, London.
- 549 Martell, K.A., Tunnicliffe, V., Macdonald, I.R., 2002. Biological features of a buccinid whelk  
550 (Gastropoda, Neogastropoda) at the Endeavour ventfields of Juan de Fuca Ridge, Northeast  
551 Pacific. *Journal of Molluscan Studies*, 68(1), pp.45-53.
- 552 McIntyre, R., Lawler, A., Masfield, R., 2015. Size of maturity of the common whelk, *Buccinum*  
553 *undatum*: is the minimum landing size in England too low? *Fisheries Research*, 162, pp.53-57.
- 554 Melatunan, S., Calosi, P., Rundle, S.D., Widdicombe, S., Moody, A.J., 2013. Effects of ocean  
555 acidification and elevated temperature on shell plasticity and its energetic basis in an intertidal  
556 gastropod. *Marine Ecology Progress Series*, 472, pp.155-168.
- 557 Melzner, F., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U., Gorb, S.N.,  
558 Gutowska, M.A., 2011. Food supply and seawater pCO<sub>2</sub> impact calcification and internal shell  
559 dissolution in the Blue Mussel *Mytilus edulis*. *PloS One*, 6(9), e24223.

- 560 Mensink, B.P., Fischer, C.V., Cadée, G.C., Fonds, M., Ten Hallers-Tjabbes, C.C., Boon, J.P., 2000.  
561 Shell damage and mortality in the common whelk *Buccinum undatum* caused by beam trawl  
562 fishery. Journal of Sea Research, 43(1), pp. 53-64.
- 563 Ohnishi, S., Akamine, T., 2006. Extension of von Bertalanffy growth model incorporating growth  
564 patterns of soft and hard tissues in bivalve molluscs. Fisheries Science, 72(4), pp.787-795.
- 565 Page, H.M., Hubbard, D.M., 1987. Temporal and spatial patterns of growth in mussels *Mytilus*  
566 *edulis* on an offshore platform: relationships to water temperature and food availability. Journal  
567 of Experimental Marine Biology and Ecology, 111(2), pp. 159-179.
- 568 Palmer, A.R., 1983. Relative cost of producing skeletal organic matrix versus calcification:  
569 Evidence from marine gastropods. Marine Biology, 75(2-3), pp. 287-292.
- 570 Palmer, A.R., 1990. Effect of crab effluent and scent of damaged conspecifics on feeding,  
571 growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). Hydrobiologia,  
572 193(1), pp. 155-182.
- 573 Palmer, A.R., 1992. Calcification in marine molluscs: how costly is it?. Proceedings of the  
574 National Academy of Sciences, 89(4), pp.1379-1382.
- 575 Pechenik, J.A., Chaparro, O.R., Franklin, A., Mardones, M.L., Montory, J.A., 2019. Thermal  
576 tolerance of intertidal and subtidal adults and embryos of the marine gastropod *Crepipatella*  
577 *peruviana*. Marine Ecology Progress Series, 616, pp.67-81.
- 578 Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival rates  
579 of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic  
580 Sciences, 48(3), pp.503-518.



- 581 Pons, G., Evangelisti, V., Capri, F., Mozzone, S., Viarengo, A., 2002. Cytochemical localization  
582 and quantification of plasma membrane Ca<sup>2+</sup>-ATPase activity in mollusc digestive gland cells.  
583 European Journal of Histochemistry, 46(1), p. 31-40.
- 584 Preston, S.J., Roberts, D., 2007. Variation in shell morphology of *Calliostoma zizyphinum*  
585 (Gastropoda: Trochidae). Journal of Molluscan Studies, 73(1), pp.101-104.
- 586 Prosser, C.L., Graham, G., Galton, V., 1991. Hormonal regulation of temperature acclimation in  
587 catfish hepatocytes. Journal of Comparative Physiology B, 161(1), pp.117-124.
- 588 Ramsay, K., Richardson, C.A., Kaiser, M.J., 2001. Causes of shell scarring in dog cockles  
589 *Glycymeris glycymeris* L. Journal of Sea Research, 45(2), pp. 131-139.
- 590 Richardson, C.A., 2001. Molluscs as archives of environmental change. Oceanography and  
591 Marine Biology: an Annual Review, 39, pp. 103-164.
- 592 Ruppert, E.E., Fox, R.S, Barnes, R.D., 2004. Invertebrate Zoology. Delhi: Cengage Learning,  
593 Chapter 12: Mollusca, pp. 269-301.
- 594 Sebens, K.P., 1987. The ecology of indeterminate growth in animals. Annual review of ecology  
595 and systematics, 18(1), pp.371-407.
- 596 Seed, R., Hughes, R.N., 1995. Criteria for prey size-selection in molluscivorous crabs with  
597 contrasting claw morphologies. Journal of Experimental Marine Biology and Ecology, 193(1-2),  
598 pp. 177-195.
- 599 Sepúlveda, R.D., Jara, C.G., Gallardo, C.S., 2012. Morphological analysis of two sympatric  
600 ecotypes and predator-induced phenotypic plasticity in *Acanthina monodon* (Gastropoda:  
601 Muricidae). Journal of Molluscan Studies, 78(2), pp.173-178.

- 602 Sibly, R. M., Baker, J., Grady, J. M., Luna, S. M., Kodric-Brown, A., Venditti, C., Brown, J. H., 2015.  
603 Fundamental insights into ontogenetic growth from theory and fish. Proceedings of the  
604 National Academy of Sciences 112, 13934-13939.
- 605 Sokolova, I.M., Pörtner, H.O., 2003. Metabolic plasticity and critical temperatures for aerobic  
606 scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda: Littorinidae) from  
607 different latitudes. Journal of Experimental Biology, 206(1), pp.195-207.
- 608 Sokolova, I.M., Bock, C., Pörtner, H.O., 2000. Resistance to freshwater exposure in White Sea  
609 *Littorina* spp. I: Anaerobic metabolism and energetics. Journal of Comparative Physiology B,  
610 170(2), pp.91-103.
- 611 Solas, M.R., Hughes, R.N., Márquez, F., Brante, A., 2015. Early plastic responses in the shell  
612 morphology of *Acanthina monodon* (Mollusca, Gastropoda) under predation risk and water  
613 turbulence. Marine Ecology Progress Series, 527, pp.133-142.
- 614 Stillman, J.H., 2003. Acclimation capacity underlies susceptibility to climate change. Science  
615 (New York), 301(5629), p. 65.
- 616 Tanabe, K., 1988. Age and growth rate determinations of an intertidal bivalve, *Phacosoma*  
617 *japonicum*, using internal shell increments. Lethaia, 21(3), pp. 231-241.
- 618 Thomsen, J., Casties, I., Pansch, C., Körtzinger, A., Melzner, F., 2013. Food availability outweighs  
619 ocean acidification effects in juvenile *Mytilus edulis*: Laboratory and field experiments. Global  
620 Change Biology, 19(4), pp. 1017-1027.
- 621 Thomsen, J., Gutowska, M., Saphörster, J., Heinemann, A., Trübenbach, K., Fietzke, J.,  
622 Hiebenthal, C., Eisenhauer, A., Körtzinger, A., Wahl, M., Melzner, F., 2010. Calcifying

623 invertebrates succeed in a naturally CO<sub>2</sub> enriched coastal habitat but are threatened by high  
624 levels of future acidification. *Biogeosciences*, 7(11), pp. 3879-3891.

625 Tomanek, L., Somero, G.N., 1999. Evolutionary and acclimation-induced variation in the heat-  
626 shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats:  
627 implications for limits of thermotolerance and biogeography. *The Journal of Experimental*  
628 *Biology*, 202(21), pp. 2925-2936.

629 Valentinsson, D., Sjödin, F., Jonsson, P.R., Nilsson, P., Wheatley, C., 1999. Appraisal of the  
630 potential for a future fishery on whelks (*Buccinum undatum*) in Swedish waters: CPUE and  
631 biological aspects. *Fisheries research*, 42(3), pp.215-227.

632 Von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws. II).  
633 *Human Biology*, 10(2), pp. 181-213.

634 West, G. B., Brown, J. H., Brian J. Enquist, B. J., 2012. A general model for ontogenetic growth.  
635 *Nature* 413, 628-631.

636 Zdelar, M., Mullin, F., Cheung, C., Yousif, M., Baltaretu, B., Stone, J.R., 2018. Pollution-,  
637 temperature-and predator-induced responses in phenotypically plastic gastropod shell  
638 traits. *Molluscan Research*, 38(1), pp.34-40.

639 Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., Smith, G. M., 2009. Mixed effects models and  
640 extensions in ecology with R. New York, USA: Springer.

641