Using a sclerochronological approach to determine a climate-growth relationship for waved whelk, *Buccinum undatum,* in the U.S. Mid-Atlantic

S. Borsetti [a,*], P.R. Hollyman [b], D. Munroe [a]

[a] *Haskin Shellfish Research Laboratory, Rutgers University, 6959 Miller Ave., Port Norris, NJ, 08349, United States*
[b] *British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom*

ARTICLE INFO

ABSTRACT

Using growth rings observed in statoliths, the size-at-age relationship was modelled for waved whelk (*Buccinum undatum*) populations within the Mid-Atlantic Bight. A total of 45 sites in the Mid-Atlantic were sampled between 2016 and 2019 using a scallop dredge, and a subset of the whelk collected were aged (n = 318). Lab-reared individuals and back-calculation methods were used to fill missing juvenile observations. The Mid-Atlantic Bight population appears to differ in the fit of growth curves, compared to other assessed populations, due to a timing difference in hatching. Growth curves for whelk from the Mid-Atlantic Bight show that maturity is reached between 4 and 6 years of age. A statolith chronology spanning a 10-year period was developed using a mixed-effects modeling approach. The chronology was used to explore the influence of temperature variation on growth during ecologically relevant periods. Growth increased with higher annual temperatures however specific seasonal bottom temperature had varying effects on growth. Increasing bottom temperature during summer, the anticipated egg-development and hatching period in this region, resulted in an age-dependent decline in growth with a positive effect on younger whelk and a negative effect on older whelk growth. Higher summer temperatures provide larger time-windows for growth, facilitating increased growth in early life stages. It appears that whelk in this region possess sufficient growth plasticity to adapt to warmer conditions throughout the year, but increased warming during specific seasons may depress growth in older individuals, potentially affecting fitness and population persistence. Understanding these temperature-growth dynamics are critical for disentangling the effects of climate change on whelk growth, allowing for population predictions in the future.

1. Introduction

To accomplish fisheries management and support fisheries sustainability, data documenting pre-exploitation life-history traits (i.e. growth, reproduction) are key to understanding how a population operates in the absence of fishing. Despite the importance of pre-exploitation data, it is rare that population data is collected prior to the commencement of fishing (Jensen et al., 2012). In the Mid-Atlantic region of the U.S., the waved or common whelk (*Buccinum undatum*) fishery is in its infancy and the U.S. stock is largely unfished, although fishers have begun to explore opportunities to develop the fishery. The Mid-Atlantic whelk fishery is not yet managed, and limited life-history and stock data have been collected (Borsetti et al., 2018, 2020). Internationally, fishing for waved whelk has a long tradition dating back nearly a century in some regions of the United Kingdom (U.K.). Harvest rates have historically remained low in these fisheries, but are now rapidly increasing, more than doubling in some areas over five years (FAO, 2017). In 2018, waved whelk was the fifth most important shellfish species in the U.K., with landings of 17,900 t valued at £21.9 million (MMO, 2019). As interest for this species continues to rise domestically and internationally, it is crucial to collect baseline data to fully understand the spatial variability of the populations prior to heavy exploitation. It is clear, from declines observed in other whelk fisheries, that lack of regionally specific parameters or management practice result in a mix of overfishing and poor regulations (Fahy et al, 1995, 2000, 2006).

The ability to model a stock's dynamic is the foundation for all fisheries management (Hilborn and Walters, 1992). Understanding species population dynamics can be useful in predicting factors affecting changes in these groups. Age studies which assist in understanding local life history traits, such as age, growth, and longevity, are fundamental for understanding characteristics of population dynamics and species

---

biology (Begg et al., 1999; Rodhouse and Hatfield, 1990). *B. undatum* demonstrate geographical variation in size and growth over short distances (Borsetti et al., 2018; Hollyman et al., 2018b; Kenchington and Glass, 1998; Magnúsdóttir, 2010; Magnúsdóttir et al., 2019; Mariani et al., 2012; Thomas and Himmelman, 1988). Therefore, size-at-age estimates derived from geographically distinct whelk populations will not provide reliable global estimates for the purpose of stock assessment in other populations, rather regionally-specific parameters are needed for each exploited and managed population. Due to the lack of growth lines in the shell of this species (Hollyman et al., 2020) and clarity issues in determining growth rings in its operculum (Hollyman et al., 2018b; Kideys, 1996), neither method provides an accurate visual estimate of age. The use of statoliths, calcareous structures (<300 μm) which are contained within the nervous system and are integral to gravitational orientation, have been proven to be the most reliable method to assess age and growth of several gastropod species, such as *B. undatum* (Hollyman 2017; Hollyman et al., 2018b), *Polinices pulchellus* (Richardson et al., 2005), and *Nassarius reticulatus*, (Chatzinikolaou and Richardson 2007). The annual periodicity of statolith growth rings in *B. undatum* has been previously validated using laboratory reared individuals (Hollyman et al., 2018c) and by direct chemical analysis (Hollyman et al., 2019) whereas previous methods that employ the operculum rings as ageing tool have not been validated (Hollyman et al., 2018b). Therefore, using statolith rings is the most suitable method for ageing *B. undatum*, providing increased accuracy, precision, and reliability compared to other age determination methods (Hollyman, 2017; Hollyman et al., 2018b, 2018c).

Understanding the impact of a changing climate on species growth can be hampered by the lack of long-term data needed to understand temperature effects on growth in natural environments (Morrongiello et al., 2012). For many species, growth responses to various temperatures are unknown. A sclerochronological approach using widths of periodically deposited increments in animals' calcified structures (shells, bones, teeth, scales, and otoliths) to generate records of growth deviations through time which can be related to environmental records, can overcome the lack of longer-term monitoring (Barrow et al., 2018; Cailliet and Goldman, 2004; Izzo and Gillanders, 2020; Matta et al., 2020; Morrongiello et al., 2015; Wittman et al., 2016). Statolith sclerochronology, combined with mixed-effects modeling, can provide a powerful approach for understanding how past climate variation has affected whelk growth and assist in forecasting how future annual and seasonal warming could affect the population.

Buccinum undatum is a boreal species that experiences a large range of temperatures across its geographical range (0–22 °C; Smith et al., 2013) and warming bottom waters of the Mid-Atlantic could cause mortality and shifts in this range if temperatures warm sufficiently. The Northeast U.S. Shelf (NE Shelf) inhabited by *B. undatum* has undergone enhanced warming – nearly three times faster than the global average (Saba et al., 2016). The NE Shelf has warmed significantly across long-and short-term periods with warming trends increasing from an average rate of 0.24 °C per decade (1968–2018) to 0.95 °C per decade (2004–2018) (Friedland et al., 2020). The Atlantic continental shelf region is characterized by its unique oceanographic conditions including intense stratification in which a strong seasonal thermocline overlies a cold pool of bottom water (typically less than 10 °C). Surface water temperatures rise in response to surface heating while deeper waters are influenced by cold waters from the north (Castelao et al., 2008). The cold pool develops in the spring of each year, reaches peak volume in early summer, and is eroded in early fall of each year (Chen et al., 2018). Due to this seasonally persistent band of cold bottom water in the MAB, large fluctuations in seasonal temperature and warming trends may have impacts on boreal species already at their southern range limit. Studies have further shown that invertebrate communities of the NE Shelf are vulnerable to the impacts of climate change. Particularly sensitive are animals like the waved whelk that are less mobile, dependent upon calcium carbonate shells, and associated with specific habitats

(Gaichas et al., 2014; Hare et al., 2016). Understanding how *B. undatum* can adapt will aid in answering ecological questions about this species' ability to adjust to climate change.

Using an established ageing technique (Hollyman et al., 2018b, 2018c), this study calculates a sex-specific age-length relationship of *B. undatum* in the southern Mid-Atlantic Bight (MAB), the southern-most distributional range of waved whelk range in the northern Atlantic. This unexploited population of waved whelk in the U.S. represents a unique opportunity to collect population baseline data prior to fishery exploitation. Baseline growth data from this unfished population provides an opportunity to explore growth parameters across gradients of fishing effort. To our knowledge, this is the first study to use statolith chronologies to assess growth deviations in whelk to bottom temperature using a mixed-effects modeling approach. We examine the impact of past environmental variation on different life stages of waved whelk as a means of assessing how changes in annual and seasonal bottom temperature have affected growth.

2. Methods

2.1. Biological samples

Whelk samples in the MAB were acquired through multiple fishery sampling cruises offshore of New Jersey during 2016–2019, coordinated by the Virginia Institute of Marine Sciences (VIMS) and Rutgers University (Fig. 1). These surveys target Atlantic sea scallops (*Placopecten magellanicus*), although waved whelk is also incidentally caught. Borsetti et al. (2018) showed that whelk and sea scallops commonly co-occur throughout this region. At each sampling station (n = 45), whelk were collected using a scallop dredge (Roman and Rudders, 2019) and were retained and frozen for subsequent analysis. A random subset, representative of all sampled sizes, were used to examine growth (n = 318).
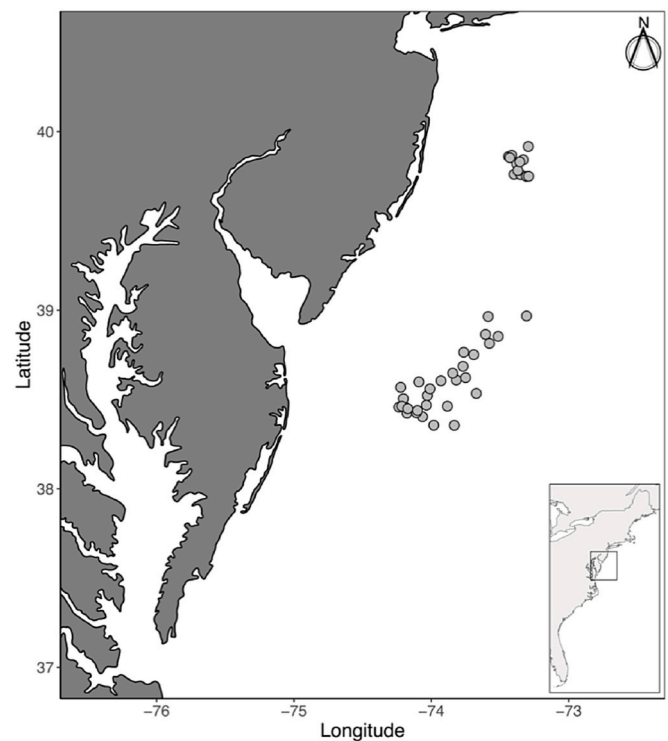

Fig. 1. Map of the MAB region, showing location of the 45 sites sampled from 2016 to 2019. Locations of each dredge sampling station shown with grey circles.

2.2. Statolith sampling and ageing

Whelk were thawed prior to processing. Each specimen was extracted following methods detailed in Borsetti et al. (2018). After the body of each whelk was removed from its shell and sexed, the digestive gland and viscera were discarded and the foot re-frozen in a labeled bag until required for statolith growth ring analysis. Total shell length (TSL) of each whelk was measured to the nearest 0.01 mm, using digital calipers.

Removal and processing of one statolith per individual whelk was performed according to the procedure described by Hollyman (2017). Statoliths were mounted on a microscope slide using Crystalbond™ 509 thermoplastic resin, imaged using a compound microscope (Olympus CX23) at 100X magnification, and photographed using a Celestron HD digital microscope camera. Statoliths were assessed for quality and clarity of rings according to the rankings described by Hollyman et al. (2018b) and only highest ranked specimens (rank 3 or 4) were used for subsequent analysis. Statolith images were interpreted using image analysis software (ImageJ v1.52, Ferreira and Rasband 2012). The number of rings in each statolith were counted and the diameter of the hatching ring and subsequent growth rings were measured (Fig. S1). Statolith growth bands were counted blindly, without knowledge of the size or sex of the individual from which the statolith was extracted. Increment width was calculated using ring diameters as the difference between the diameter of the ring less the previous diameter starting at the hatching ring.

All ages and ring measurements were made by a single reader. To examine precision in age estimates, a subset of 50 statoliths were randomly chosen to be re-aged. The reader had no knowledge of prior age estimates, TSL, or sex. The 'FSA' package (Ogle, 2019) in RStudio version 1.1.435 (R Core Team, 2014) was used to calculate the average coefficient of variation (ACV) and the percent agreement to test for bias in the original age estimates by creating an age-bias plot (Campana, 2001). Because the re-age occurred after the reader had the experience of ageing the whole dataset, estimates from the re-age were treated as reference age (Ogle, 2016).

Annual rings are deposited when temperatures are at their annual minimum (Hollyman, 2017); therefore, March was nominated as the month rings were deposited in individuals from this region (Narváez et al., 2015). Growth year was determined by aligning the calendar year of growth to correspond with appropriate age of life for whelk alive during that year. Increments were assigned to a year by back calculating from the date of capture. The first increment, the hatching ring, was not assigned a year as larval development can last between 10 weeks and 9 months (Kideys et al., 1993; Martel et al., 1986; Smith and Thatje, 2013) and do not comprise a complete year of growth. The growth year was used to link whelk growth and climate data.

2.3. Calculation of missing size classes

A lack of juveniles within samples tends to result in a poor fit of a growth model (Emmerson et al., 2020; Hollyman et al., 2018b; Shelmerdine et al., 2007). The samples in this study were collected using a scallop dredge, which is size-selective in collection of scallops (Roman and Rudders, 2019), and thus likely inefficient at capturing small whelk (Borsetti et al., 2018). Due to the absence of small juveniles (<20 mm) in our samples, it was difficult to identify the lower age and size estimates for the age-length curve. Forcing the growth curve through zero is not appropriate because this species hatches from its egg capsule as a fully formed juvenile resulting in a variable size at hatching depending on a range of factors (i.e. spawner and capsule size) (Nasution et al., 2010; Hollyman et al., 2018a).

To fill this gap of unknown shell lengths for newly hatched and juveniles, a power-trend line, as calculated by Hollyman (2017), was used to back-calculate TSL from observed statolith diameters. Missing size classes were accounted for using back-calculation techniques for ages 0 and 1, in addition to length measurements made on laboratory-hatched juveniles from field-collected egg capsules (Hollyman et al., 2018b). TSL measurements of laboratory-reared juveniles were taken upon the day of hatching, 1-week, 2- and 4-months post-hatching.

2.4. Growth modeling

2.4.1. Growth curve estimation and model selection

Growth of *B. undatum* in the MAB was described using two candidate models namely the von Bertalanffy (1938) and the Gompertz (1825) applied to the length-at-age data, including back-calculated and laboratory-reared juveniles.

The von Bertalanffy growth model was fit using the equation:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

Where L_t is the total shell length at age t (mm), L_∞ is the theoretical asymptotic maximum length (mm), k is the growth coefficient (year^{-1}), and t_0 is the theoretical age (years) at which length is zero.

The Gompertz growth model is sigmoidal in shape and typically performs well for species characterized by slow growth early in life (Griffiths et al., 2010). The Gompertz growth model was fit using the equation:

$$L_t = L_\infty e^{-e^{-gi(t-t_i)}}$$

where gi is the instantaneous growth rate at the inflection point and t_i is the age (years) at the inflection point.

The candidate models were fit using the 'FSA' package (Ogle, 2019) in RStudio version 1.1.435 (R Core Team, 2014), and the 95% confidence intervals of the parameters were estimated using bootstrap resampling (1,000 iterations).

The performance of the growth models was compared by using the corrected Akaike Information Criterion (AICc), calculating the determination coefficient (R^2), and the mean square residual error (MSR$_e$). Model selection was performed using AICc, via the 'AICmodavg' package (Mazerolle, 2015), to identify the best-fit model separately for males, females, and both sexes combined (which included unsexed laboratory hatched individuals). Models were ranked based on the AICc values and whichever had the lowest value was identified as the best fit. AICc difference (ΔAICc) was calculated for each candidate to assess the relative support for each model. Models with ΔAICc values less than 2 are strongly supported, between 2 and 10 have moderate support, and greater than 10 have minimal to no support (Burnham and Anderson, 2002). A likelihood ratio test was performed for the best fitting growth model to determine if sexes should be modelled separately or together (Kimura, 1980).

2.4.2. Meta-analysis of B. undatum growth parameters

Primary literature wherein studies estimated Gompertz growth coefficients using statolith ages were assembled. From these reports, L_∞, gi, Age at maturity, size at sexual maturity, and study location were compiled and used to explore preliminary trends among these growth parameters.

The Gompertz growth parameters from this present study and size at maturity (L_{50}) estimates from Borsetti et al. (2020) were compared to two studies in the U.K. (Emmerson et al., 2020; Hollyman, 2017). Pearson's correlation coefficient was used to examine the pairwise comparisons between various growth coefficients.

2.5. Biochronology modeling

To analyze the statolith growth-increment data, mixed-effect models were used due to their ability to account for the hierarchical nature of growth data, which consists of repeated measures within individuals and multiple individuals' samples from different years (Weisberg et al.,

2010). A series of mixed-effects models that use a two-step procedure (Morrongiello et al., 2015) were developed to examine intrinsic and extrinsic drivers of whelk growth using statolith rings (in μm). Analyses were performed in R using packages lme4 (Bates et al., 2015), AICc-modavg (Mazerolle, 2015), and effects (Fox, 2003). *Statolith increment widths*, *age*, and *age-at-capture* (*AAC*) were log-transformed to meet model assumptions and all intrinsic and extrinsic variables were mean-centered to assist model convergence and random slope interpretation (Morrongiello et al, 2012, 2015). *AAC* was included to account for potential age sampling bias in the dataset (Morrongiello et al., 2015)

2.5.1. Intrinsic predictors

First, the optimal random model with fixed intrinsic predictors (within-individual) (including *age*, *sex*, and *AAC*) was determined (Morrongiello et al., 2012). Random effects structures contained random intercepts for *individual whelk ID* and *year* in combination with random slopes for *age* (Table S1). Both the *individual whelk ID* and *year* sampled were introduced as random intercepts, allowing for individual-specific or year-specific differences in growth (Morrongiello et al., 2015). Random *age* slope for *individual whelk ID* and *year* were included to allow for individual whelk differences in the growth-age relationship, and year-dependent differences in age-specific growth. The random effect structures were fit with restricted maximum likelihood (REML) and then compared with the Akaike information criterion corrected (AICc) for small sample sizes (Burnham and Anderson, 2002).

The model that best supported the data was then used to optimize the fixed effect structure using maximum likelihood (ML). The most parsimonious model based on the AICc, with the optimal random and fixed structures, was refit using REML to obtain unbiased parameter estimates (Zuur et al., 2009). For each model, conditional R^2 (the proportion of variance explained by the fixed and random effects) were calculated (Nakagawa and Schielzeth, 2013). The growth chronology was developed by extracting random *year* effects from the model which contained the optimal random and fixed effects structure. These random *year* effects represent the mean inter-annual deviations in population growth which centers around an overall chronology mean of zero.

2.5.2. Extrinsic predictors

The optimal annual growth model determined above was extended to relate patterns of inter-annual growth variation (increment width in μm) to changes in fixed extrinsic factors such as bottom temperature. The influence of bottom temperature on whelk growth was assessed by relating temperature over five ecologically relevant periods: a. Annual growth cycle (January–December); and four seasons including b. Winter (December–February), coinciding with the breeding season (Borsetti et al., 2020); c. Spring (March–May), coinciding with the egg-laying period (Borsetti et al., 2020); d. Summer (June–August), coinciding with anticipated egg-development and hatching period; e. Fall (September–November) coinciding with anticipated hatching season. A 10-year (2009–2018) time series of daily average bottom temperatures (Fig. S2) were obtained for model grids coincident with the sample sites from "DOPPIO", a data-assimilative Regional Ocean Modeling System (ROMS) ocean circulation model (Levin et al., 2019; Wilkin et al., 2018). Daily bottom temperature data were averaged over the five ecological time periods before inclusion in the optimal model.

To test the potential influence of each ecologically relevant period on statolith growth, individual periods were included in the optimal model as additional fixed effects. A series of models were fit with different combinations of yearly and seasonal bottom temperatures and their interactions with age. These added interaction terms allowed for age-dependent growth responses to temperature. Seasonal bottom temperatures which were highly correlated (Pearson coefficient $p < 0.05$) were not simultaneously included in the model. The conditional R^2 for each model was calculated and the optimal model, based on AICc, was fit with REML for unbiased parameter estimates (Nakagawa and Schielzeth, 2013; Zuur et al., 2009). If the difference between the subsequent

ranked model's AICc value and that of the best model was less than 2, then those models were selected (Burnham and Anderson, 2002), inferring that temperature drivers in those selected models influence whelk growth (Izzo et al., 2016).

3. Results

3.1. Biological samples

Statoliths were collected from 318 *B. undatum* consisting of 163 females (21.9–87.0 mm TSL) and 111 males (34.1–80.0 mm TSL) ranging from 1–8 and 2–8 years old respectively. A total of 44 statoliths had a poor clarity rating (1 or 2) and were not included in subsequent analysis. Minimum – maximum and mean statolith diameter were 193–341 μm and 253.7 ± 27.6 μm respectively.

3.2. Statolith sampling and ageing

The ACV score for the reassessment of 50 randomly selected statoliths was 2.9%, and thus within acceptable bounds (i.e. ACV<5%) which indicates a reliable age estimation structure. The percent agreement between both ages was 80%. There was no systematic bias across the entire age range between the two reads (Bowker's test of symmetry: df = 5, $\chi^2 = 10.0$, p = 0.08).

3.3. Calculation of missing size classes

A total of 50 juvenile shell lengths were back-calculated using model-based methods. These back-calculated sizes included 24 females (1.35–24.4 mm TSL) and 26 males (2.24–26.9 mm TSL). In addition, 233 laboratory-hatched juveniles were measured, with sizes ranging from 1.3 – 5.6 mm TSL. Sex of the laboratory-hatched juveniles was indistinguishable and therefore these individuals' sizes could not be used in sexually specific growth curves.

3.4. Growth modeling

3.4.1. Growth curve estimation and model selection

Both candidate growth models were successfully fit to age-at-length data which included back-calculated sizes and laboratory-hatched juveniles from the Mid-Atlantic population. The VBGF had the lowest AIC$_c$, R^2, and MSR$_e$ values, which suggests it provides a better fit for all curves tested (Table 1). Growth curves for males and females (Fig. 2) did not differ significantly (VBGF likelihood ratio test: df = 3, $\chi^2 = 4.45$, p = 0.22). However, larger L_∞ and t_0 were recorded for females, whereas the growth coefficient (k) was higher for males (Table 2). A pronounced asymptote was not observed in the VBGF for either sex, and the asymptotic lengths were greater than the largest individual observed in both males and females (L_∞- Male: 87.6; Female: 104.3).

3.4.2. Meta-analysis of B. undatum growth parameters

There was a positive trend and significant correlation between location and the mean asymptotic length (L_∞, mm) for U.K. populations (r = 0.75; p = 0.008) and the inclusion of U.S. whelk population resulted in an insignificant relationship (Fig. 3a). For all populations, a strong negative relationship exists between L_∞ and instantaneous growth rate (gi) (r = −0.75; p = 0.005), however, this correlation between these two growth parameters increases with the removal of the U.S. data (r = −0.85; p = 0.0008) (Fig. 3b). Growth curves for whelk from the Mid-Atlantic Bight show that maturity is reached between 4 and 6 years of age, depending on sex. Age-at-maturity ranges from 3 to 5 years for exploited U.K. whelk populations (Fig. 3c). There appears to be a trend between the size and age of maturity for the exploited U.K. populations that the unexploited U.S. population deviates from.

Table 1

n is the sample size, AIC_C is the small-sample bias adjusted form of Akaike's Information Criteria, Δ is the difference in AIC_C values between models, Determination coefficient (R^2), mean square residual error (MSR_e), L_∞ is asymptotic length parameter in mm, t_0 is the theoretical age (years) at which length is zero, k is the growth rate parameter in yr^{-1} for the VBGF, gi is the instantaneous growth rate at the inflection point and t_i is the age (years) at the inflection point for the Gompertz model.

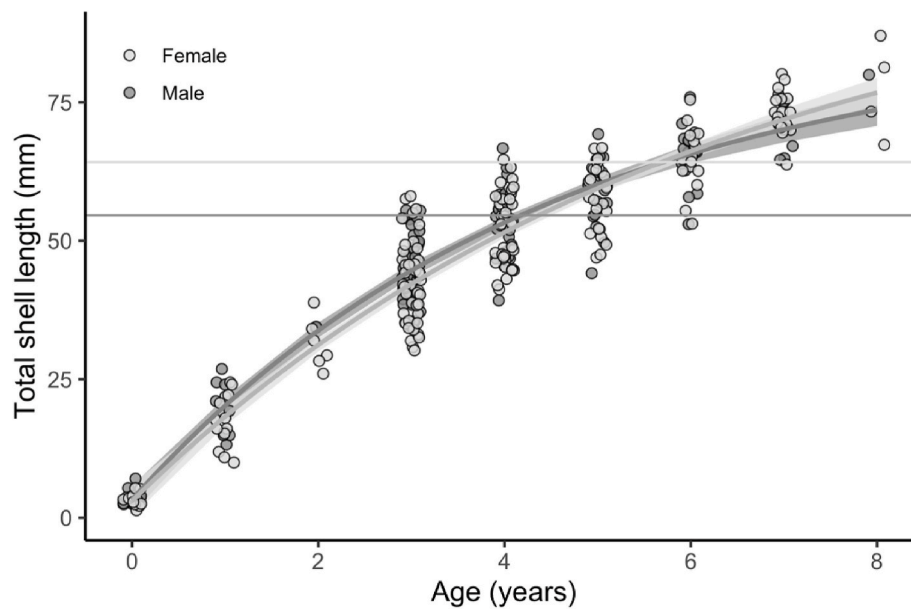| Sex	Model	n	AIC_c	ΔAIC	R^2	MSRe	L_∞	t_0	k	g_i	t_i
Sexes combined	**VBGF**	559	3292.9		0.969	4.57	94.4	−0.009	0.20	–	–
	Gompertz	559	3347.9	55.0	0.966	4.79	72.3	–	–	0.59	1.92
Male	**VBGF**	135	844.9		0.931	5.37	87.6	−0.17	0.22	–	–
	Gompertz	135	857.3	12.4	0.925	5.62	71.5	–	–	0.55	1.66
Female	**VBGF**	191	1228.8		0.903	5.91	104.0	−0.18	0.16	–	–
	Gompertz	191	1240.2	11.4	0.897	6.09	79.2	–	–	0.44	2.01

Fig. 2. Length-at-age of *Buccinum undatum* for males (dark grey) and females (light grey) using observed and back-calculated data with VBGF estimates and associated 95% confidence intervals. Size at first maturity for males (dark grey) and females (light grey) from the region have been overlaid (Borsetti et al., 2020).

Table 2

Parameter estimates for both the von Bertalanffy (VBGF) and Gompertz growth function for all individuals (including laboratory-hatched juveniles; n = 233), males, and females. Parameters include - L_∞ is asymptotic length parameter in mm, t_0 is the theoretical age (years) at which length is zero, k is the growth rate parameter in yr^{-1} for the VBGF, gi is the instantaneous growth rate at the inflection point and t_i is the age (years) at the inflection point for the Gompertz model. 95% upper and lower confidence intervals included.

Sex	Model	Parameters	Estimates	95% LCI	95% UCI
Sexes combined	VBGF	L_∞	94.43	88.8	100.07
		k	0.20	0.18	0.22
		t_0	−0.009	−0.04	0.03
	Gompertz	L_∞	72.29	70.53	74.06
		g_i	0.59	0.56	0.62
		t_i	1.92	1.85	2.00
Male	VBGF	L_∞	87.59	77.91	97.27
		k	0.22	0.18	0.27
		t_0	−0.17	−0.31	−0.03
	Gompertz	L_∞	71.55	67.66	75.44
		g_i	0.55	0.48	0.63
		t_i	1.66	1.49	1.83
Female	VBGF	L_∞	104.03	89.77	118.30
		k	0.16	0.12	0.20
		t_0	−0.18	−0.37	−0.01
	Gompertz	L_∞	79.23	74.36	84.10
		g_i	0.44	0.38	0.50
		t_i	2.01	1.83	2.19

3.5. Biochronology modeling

3.5.1. Intrinsic sources of growth variation and random factors

Statolith ring increments were measured on 316 whelk, resulting in 1145 increments in total. Statolith diameter was significantly correlated to TSL for both sexes (Fig. S3) confirming that these hard structures are suitable proxies of somatic growth of *B. undatum* in this region.

The best random effect structure for average individual growth was the most complex and included random *age* slopes for *year* and *individual whelk ID* (Table S1), indicating that the growth:age relationship varied among individuals, and the growth:year relationship varied among years. Using this random effect structure, the best intrinsic fixed effect model includes *age* and *AAC* (Table S2). *Age* was the best predictor of growth and its fixed effect explained a large portion of the variance in the growth increment dataset with increment width declining with increasing age (Fig. 4). Inclusion of the *AAC* term in the model indicates that there is evidence for biases in age-selectivity in the sample. Individual growth was negatively related to *AAC* and declined with *age*. *B. undatum* displayed annual variation in growth over the sampling period with the lowest growth in 2011 and highest growth in 2018 (Fig. 5). The average AAC of whelk was 4.8 years old and the increased uncertainty in growth estimates from 2009 through 2013 is related to the smaller sample size of older individuals in this dataset.

3.5.2. Extrinsic source of growth variation: temperature

Between 2009 and 2018, bottom water temperatures spanned a range of 19.3 °C (2.6–21.9 °C; Fig. S2). The inclusion of bottom temperature improved the optimal model. Average bottom temperature was
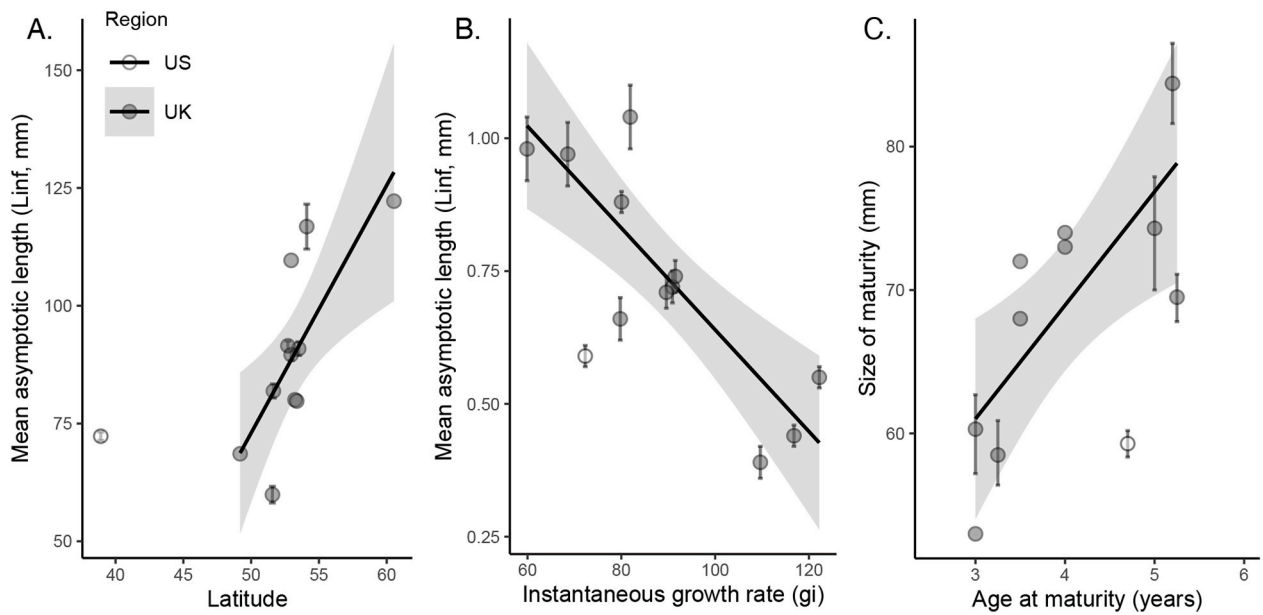
Fig. 3. Comparison of Gompertz growth coefficients from populations assessed using statolith obtained from published literature [U.K., grey (Hollyman 2017; Hollyman et al., 2018b; Emmerson et al., 2020); U.S., white (this study; Borsetti et al., 2020)] A. Trend in mean asymptotic length (L_∞, mm) by latitude. Error bars represent standard errors. If exact latitudes not available, approximate location based on study details. B. Trend in instantaneous growth rate (gi) by mean asymptotic length (L_∞, mm). Error bars represent standard errors. C. Trend in size of maturity with 95% confidence intervals and approximate age-at-maturity.
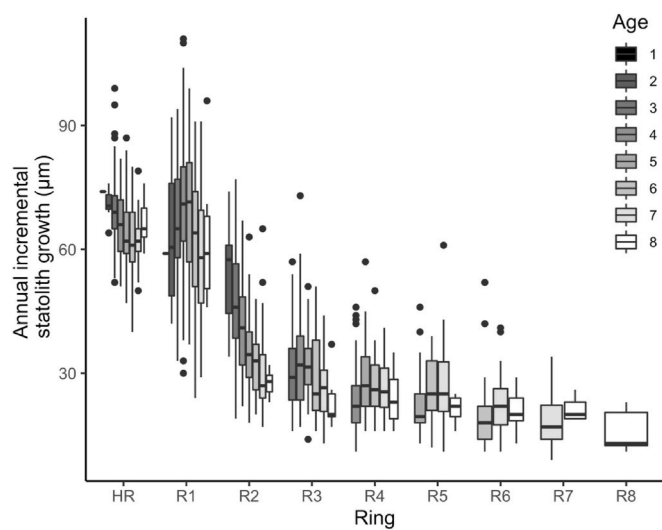
Fig. 4. Boxplot displaying the incremental growth for each statolith ring grouped by age of the whelk. Rings include hatching ring (HR) each subsequent ring is labeled chronologically (i.e. R1; first ring after HR). The central line in each boxplot indicates the median value. Top and bottom edges of the box indicate the 25th and 75th percentile, the whiskers extend 1.5 times the interquartile range beyond the edge of the box. Points above and below the whiskers indicate outliers.

the best explanatory bottom temperature covariate (Table 3). Increasing bottom temperature throughout the year had a positive effect on growth (Fig. 6a)

However, when certain seasonal bottom temperatures were added to the optimal model they were also supported (ΔAICc<2; Table S3). Inclusion of the interaction between whelk age and summer bottom temperatures resulted in an age-dependent growth response to temperature where the positive impact of warmer summers on growth became negligible around age 5. Beyond these intermediate ages, warming summer bottom temperatures had a negative impact on growth (Fig. 6b;
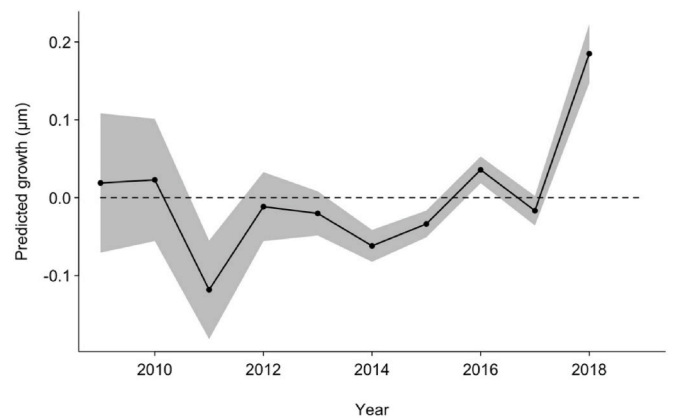

Fig. 5. Variation in predicted annual growth accounting for intrinsic effects of waved whelk, represented by year random effect. Standard errors are shown as grey band.

Table 3
Parameter estimates (with SE), 95% confidence intervals and test statistic (t) from the best-fit model of waved whelk (*Buccinum undatum*) annual growth.

Parameter	Estimate	SE	95% LCI	95% UCI	t
Intrinsic factors					
Intercept	3.54	0.01	3.52	3.56	322.61
Age-at-capture	- 0.15	0.03	- 0.21	- 0.09	- 4.56
Age	- 0.68	0.05	- 0.78	- 0.58	- 13.67
Extrinsic factor					
Average BT	0.05	0.02	0.02	0.09	2.87

Table S4). When examining statolith incremental growth across the range of summer bottom temperatures, year 1 statoliths increased by 14.37 μm, whereas year 8 statoliths decreased by 0.73 μm (Fig. 6b). There was also support for models which included spring bottom temperature (rising temperatures having a positive effect on growth) and winter (rising temperatures having a negative effect on growth) (ΔAICc<2; Table S3).
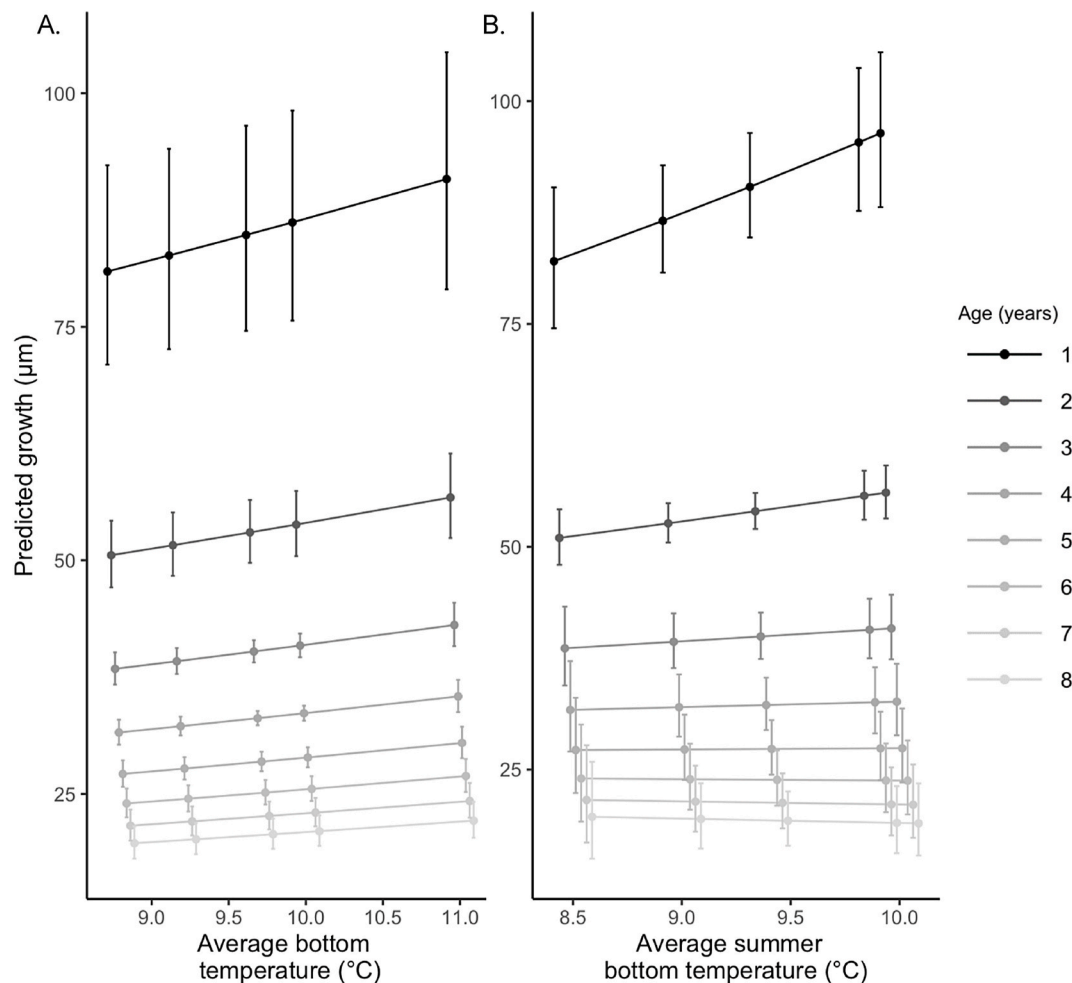
Fig. 6. Predicted differences in statolith growth by age (year) of waved whelk and associated 95% confidence intervals under different average bottom temperatures (C). A. Predicted statolith growth in increasing average bottom temperature over the year (January–December) B. Predicted statolith growth in increasing average summer bottom temperature (June–August).

4. Discussion

Using a combination of established methods, an age-at-length relationship was created for the unfished waved whelk population in the Mid-Atlantic Bight. Growth curve parameters of *B. undatum* varied between males and females. Sexual dimorphism is similarly observed in size of sexual maturity (L_{50}) and length frequencies, with females having a larger L_{50} and median length than males in three regions in the U.S. (Borsetti et al, 2018, 2020). Other assessed populations observed males with larger L_∞ values than females; however, these populations experience much higher fishing pressure (i.e. Hollyman 2017; Hollyman et al., 2018b). Long-standing fishing pressure experienced in other populations, such as the U.K., may have selectively removed larger females resulting in a shift in L_∞ towards smaller females. However, if large, old individuals were underrepresented in these samples this could result in an underestimation of L_∞ (Taylor et al., 2005).

In this study, the VBGF performed better than the Gompertz growth curve when fitting size-at-age. However, Hollyman et al. (2018b) found that the Gompertz growth equation fitted much better to data from study sites in the U.K. Additionally, based on these findings, Emmerson et al. (2020) also used the Gompertz growth equation to model whelk growth in the Irish Sea. The Gompertz growth equation has been used to model growth in several other marine gastropods which exhibit sigmoidal or slow initial growth (see examples in Hollyman et al., 2018b). On the opposite, the VBGF reflects rapid initial growth followed by gradually slower growth rates as individuals get larger. Past studies have modelled

B. undatum growth with the VBGF (i.e. Hancock 1963; Santarelli and Gros 1985; Fahy et al., 1995; Kideys 1996; Shelmerdine et al., 2007; Heude-Berthelin et al., 2011; Lawler 2014). It was hypothesized that these studies, which lacked data on juveniles, made it difficult to adequately fit the lower end of the sigmoid Gompertz growth curve (Hollyman, 2017; Hollyman et al., 2018b).

A possible explanation for the variation in performance of the models could be linked to distinct variability in life history strategies due to environmental differences experienced by the U.S. and U.K. populations of *B. undatum*. This species is a cold-water spawner and at the southern ends of its distributional range, development predominantly occurs when water temperatures are at their coolest (Smith and Thatje, 2013). Whelk in the MAB likely lay their eggs in the spring and early summer, when temperatures are at their minimum (~7–8 °C), hatching in late summer and fall when bottom temperatures are increasing eventually reaching their annual maximum around November (Borsetti et al., 2020). Juvenile whelk are exposed to warming water, which encourages rapid early growth, and are not subjected to cooling temperatures which may slow growth for approximately 5–6 months post-hatching. Populations in the U.K. deposit eggs during autumn and winter months, after bottom temperature maxima as water temperatures drop (~4–10 °C) (Smith et al., 2013), hatching around January – approximately 2 months prior to minimum annual temperatures (Hollyman, 2017). This shortened window of warm bottom water could result in depressed early growth, resulting in a sigmoidal growth curve. Hollyman (2017) hypothesized that the slow initial growth was likely linked to time of

hatching corresponding to coldest seawater temperatures during the annual seasonal cycle in the Menai Strait. Laptikhovsky (2014) suggested that the difference in reproductive timing between the northeastern Atlantic (France to Iceland) and the northwest Atlantic (Gulf of St. Lawrence) was due to differences in predation pressure, with winter hatching in Canadian populations occurring when there is reduced pressure from a major predator of the waved whelk, the starfish *Leptasterias polaris*, which is absent in European waters.

The overall trend of earlier age-at-maturity estimates observed in the exploited U.K. population compared to the unexploited U.S. populations could be due to fishing pressure. Exploitation of late-maturing populations can induce shifts towards smaller maturation sizes and younger ages, which may depress stock productivity (i.e. Law and Grey 1989; Rowell 1992; Roff 2002; Gårdmark et al., 2003; Ernande et al., 2004). Fishing, specifically size-selective exploitation for larger individuals, can result in uneven pressure on mature individuals in targeted populations which in turn can select for accelerated life histories, such as earlier maturation (Baulier et al., 2006; Dunlop et al., 2009). It is well established that the minimum conservation reference size (45 mm TSL) adopted in most European countries is inadequately protecting populations with L_{50} that exceeds this landing restriction, as it allows for fishers to target immature animals (Fahy et al., 2000; Heude-Berthelin et al., 2011; Shelmerdine et al., 2007). Fisheries-induced changes in life history traits, such as maturation, appear to be slow to reverse when fishing pressure decreases, which could be potentially due to reduced genetic variation in exploited populations (Pinsky and Palumbi, 2013). Further work should be done to directly examine the impact of different levels of exploitation in these populations now that growth parameters are available from an unexploited stock.

Age of the individuals explained a substantial amount of the variation in annual growth and reflects the commonly observed pattern of decline in age-dependent growth. The significance of *individual whelk ID* and *year* term indicates high interindividual and interannual variation in growth and differences in increment:age and increment:year relationship among whelks. The importance of the *AAC* as an explanatory growth term can indicate the presence of age-bias in the sample data (Morrongiello et al., 2015), though the magnitude of this effect was low. Samples were predominantly medium-sized individuals, with very large old adults and small juveniles (<20 mm) less well represented in this dataset (Borsetti et al, 2018, 2020), slightly hampering the ability to examine growth phenotypes at both extremes (Morrongiello et al., 2012). Regardless, this study demonstrated that a sclerochronological approach provides insight into whelk growth at all life stages without the need for tagging experiments, difficult in the natural environment, and unrealistic under laboratory conditions.

Results herein demonstrate that whelk growth fluctuates through time, with higher annual bottom temperatures having a positive effect on whelk of all ages. Initial increases in temperature can be beneficial for some species allowing for improved energy and therefore increased growth (Takasuka and Aoki, 2006). However, temperatures exceeding the species-specific thermal optimum can be deleterious to growth (Wang and Overgaard, 2007). Whelk in this region display plasticity in their ability to cope with a broad range of temperatures. With bottom temperatures expected to continue to rise, it is unknown if growth will continue to be positively impacted due to increasing bottom temperature. There has been an observed warming in the Northwest Atlantic (NWA) Ocean (Collins et al., 2013) and recently these trends have been revisited suggesting that warming over the NWA continental shelf may be greater and faster than those previously projected (Saba et al., 2016). Warming on a scale of 3–4 °C has been shown to cause extreme impacts on the ecosystem, especially on commercially important fisheries (Jossi and Benway, 2003; Narváez et al., 2015).

Seasonally, increasing summer temperatures have an age-dependent impact with warming temperatures positively impacting young whelk and negatively impacting older whelk growth. Similarly, Emmerson et al. (2020) found that warmer bottom temperature, which may limit

potential maximum size of whelk, can accelerate the growth rate during early life-stages. This may be due to the trade-off between growth and reproduction for mature whelk, resulting in a decrease in the duration of the growing season with age (Lankford et al., 2001; Stearns, 1992). Further relationships were found between growth and seasonal temperature variations, the positive effect of increased bottom temperature in spring and summer could be responsible for the extended growing season in years with warm bottom water. Higher summer temperatures provide larger time-windows for growth, facilitating increased growth in early life stages supporting the difference in fit of growth curves between the Mid-Atlantic populations and those assessed in the U.K. Temperatures in all seasons fall within the theoretical optimum temperature range (approximately 8–18 °C) proposed for *B. undatum* growth (Hollyman 2017). Bottom temperatures in the MAB are warmest during winter months and these warm temperatures experienced by this population could be expected to negatively affect whelk growth.

This study estimates growth parameters for an unexploited whelk population which follows a different growth pattern than previously studies populations of *B. undatum*. Through the novel application of mixed-effects models, this study accounted for biological and environmental influences on whelk growth. Further, the results herein demonstrate that in absence of fishing pressure, whelk growth fluctuates in time; with MAB whelk population growth positively correlating with increasing annual bottom temperature over a 10-year period (between 2009 and 2018). Further comparison of the biological characteristics of the unexploited MAB waved whelk stock to stocks elsewhere in the North Atlantic Ocean that have experienced fishing pressure for multiple decades can help illuminate the nature of fisheries influences on growth and maturation.

CRediT authorship contribution statement

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107255.

Funding

References

Barrow, J., Ford, J., Day, R., Morrongiello, J., 2018. Environmental drivers of growth and predicted effects of climate change on a commercially important fish, *Platycephalus laevigatus*. Mar. Ecol. Prog. Ser 598, 201–212. https://doi.org/10.3354/meps12234.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48.

Baulier, L., Heino, M., Lilly, G., Dieckmann, U., 2006. Body condition and evolution of maturation of Atlantic cod in Newfoundland. ICES CM 2006/H:19.

Begg, G.A., Hare, J.A., Sheehan, D.D., 1999. The role of life history parameters as indicators of stock structure. Fish. Res. 43, 141–163.

Borsetti, S., Munroe, D., Rudders, D., Chang, J.H., 2020. Timing of the reproductive cycle of waved whelk, *Buccinum undatum*, on the U. S. Mid - Atlantic Bight. Helgol. Mar. Res. 74 (5) https://doi.org/10.1186/s10152-020-00537-6.

Borsetti, S., Munroe, D., Rudders, D.B., Dobson, C., Bochenek, E.A., 2018. Spatial variation in life history characteristics of waved whelk (*Buccinum undatum* L.) on the U.S. Mid-Atlantic continental shelf. Fish. Res. 198, 129–137. https://doi.org/10.1016/j.fishres.2017.10.006.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York, USA.

Cailliet, G.M., Goldman, K.J., 2004. Age determination and validation in chondrichthyan fishes. In: Carrier, J., Musick, J.A., H, M. (Eds.), Biology of Sharks and Their Relatives. CRC Press, San Diego, CA, pp. 399–439.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59, 197–242. https://doi.org/10.1006/jfbi.2001.1668.

Castelao, R., Glenn, S., Schofield, O., Chant, R., Wilkin, J., Kohut, J., 2008. Seasonal evolution of hydrographic fields in the central Middle Atlantic Bight from glider observations. Geophys. Res. Lett. 35, L03617.

Chatzinikolaou, E., Richardson, C., 2007. Evaluating growth and age of netted whelk *Nassarius reticulatus* (Gastropoda : Nassariidae) using statolith growth rings. Mar. Ecol. Prog. Ser 342, 163–176. https://doi.org/10.3354/meps342163.

Chen, Z., Curchitser, E., Chant, R., Kang, D., 2018. Seasonal variability of the cold pool over the mid-atlantic Bight continental shelf. J. Geophys. Res.: Oceans 123, 8203–8226.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A. J., Wehner, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Doschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 1029–1136.

Dunlop, E.S., Heino, M., Dieckmann, U.L.F., 2009. Eco-genetic modeling of contemporary life-history evolution. Ecol. Appl. 19, 1815–1834. https://doi.org/10.1890/08-1404.1.

Emmerson, J.A., Hollyman, P.R., Bloor, I.S.M., Jenkins, S.R., 2020. Effect of temperature on the growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis within the Irish Sea. Fish. Res. 223, 105437. https://doi.org/10.1016/j.fishres.2019.105437.

Ernande, B., Dieckmann, U., Heino, M., 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proc. R. Soc. B 271, 315–423.

Fahy, E., Grogan, S., Byrne, J., Carroll, J., 2006. Some thick shelled whelk Buccinum undatum characteristics and fisheries in Ireland. Irish Fish. Bull. No. 25. Fisheries Science Services, Marine Institute, Co., Galway, pp. 1–16.

Fahy, E., Masterson, E., Swords, D., 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, 6. Irish Fisheries Investigations, Marine Fisheries Services Division, Dublin 15, pp. 1–67.

Fahy, E., Yalloway, G., Gleeson, P., 1995. Appraisal of the whelk *Buccinum undatum* fishery of the Southern Irish Sea with proposals for a management strategy. Irish Fish. Investig. Ser. B (Marine) 42, 1–26.

Ferreira, T., Rasband, W., 2012. ImageJ User Guide 1.46r. ImageJ/Fiji 1.46.

Food and Agriculture Organization of the United Nations (Fao), 2017. Species Fact Sheets: Buccinum undatum. http://www.fao.org/figis/geoserver/factsheets/species.html.

Fox, J., 2003. Effect displays in R or generalised linear models. J. Stat. Software 8 (15), 1–27.

Friedland, K.D., Morse, R.E., Manning, J.P., Melrose, D.C., Miles, T., Goode, A.G., Brady, D.C., Kohut, J.T., Powell, E.N., 2020. Trends and change points in surface and bottom thermal environments of the US Northeast Continental Shelf Ecosystem. Fish. Oceanogr 29 (5), 1–19. https://doi.org/10.1111/fog.12485.

Gaichas, S.K., Link, J.S., Hare, J.A., 2014. A risk-based approach to evaluating northeast US fish community vulnerability to climate change. ICES J. Mar. Sci. 71, 2323–2342. https://doi.org/10.1093/icesjms/fsu048.

Gårdmark, A., Dieckmann, U., Lundberg, P., 2003. Life-history evolution in harvested populations: the role of natural predation. Evol. Ecol. 5, 239–257.

Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new method of determining the value of life contingencies. Philos. Trans. R. Soc. 115, 513–585.

Griffiths, S.P., Fry, G.C., Manson, F., Lou, D., 2010. Age and growth of longtail tuna (*Thunnus tonggol*) in tropical and temperate waters of the central Indo-Pacific. ICES J. Mar. Sci. 67, 125–134.

Hancock, D.A., 1963. Marking experiments with the commercial whelk (*Buccinum undatum*). Spec. Publ. Int. Comm. NW. Atl. Fish. 176–187.

Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M.A., Scott, J.D., Alade, L., Bell, R.J., Chute, A.S., Curti, K.L., Curtis, T.H., Kircheis, D., Kocik, J.F., Lucey, S.M., McCandless, C.T., Milke, L.M., Richardson, D. E., Robillard, E., Walsh, H.J., McManus, M.C., Marancik, K.E., Griswold, C.A., 2016. A vulnerability assessment of fish and invertebrates to climate change on the Northeast U.S. continental shelf. PloS One 11, 1–30. https://doi.org/10.1371/journal.pone.0146756.

Heude-Berthelin, C., Hégron-Macé, L., Legrand, V., Jouaux, A., Adeline, B., Mathieu, M., Kellner, K., 2011. Growth and reproduction of the common whelk *Buccinum undatum* in west Cotentin (Channel), France. Aquat. Living Resour 24, 317–327. https://doi.org/10.1051/alr/2011048.

Hilborn, R., Walters, C.J., 1992. Quantitative fisheries stock assessment: Choices. Dynamics and Uncertainty Chapman & Hall, New York, NY.

Hollyman, P.R., Chenery, S.R.N., Leng, M.J., Laptikhovsky, V.V., Colvin, C.N., Richardson, C.A., 2018a. Age and growth rate estimations of the commercially fished gastropod *Buccinum undatum*. ICES J. Mar. Sci. 75, 2129–2144. https://doi.org/10.1093/icesjms/fsy100.

Hollyman, P.R., Laptikhovsky, V.V., Richardson, C., 2018b. Techniques for estimating the age and growth of Molluscs : Gastropoda. J. Shellfish Res. 37, 773–782. https://doi.org/10.2983/035.037.0408.

Hollyman, P.R., Leng, M.J., Richardson, C., 2018c. Statoliths of the whelk *Buccinum undatum*: a novel age determination tool. Mar. Ecol. Prog. Ser 598, 261–272. https://doi.org/10.3354/meps12119.

Hollyman, P.R., 2017. Age, Growth and Reproductive Assessment of the Whelk, *Buccinum undatum*, in Coastal Shelf Seas. Doctoral Dissertation. Bangor University, Menai Bridge, Anglesey, U.K, School of Ocean Sciences.

Hollyman, P.R., Chenery, S.R.N., Eimf, Ignatyev, A., Laptikhovsky, V.V., Richardson, C.A., 2019. Micro-scale geochemical and crystallographic analysis of *Buccinum undatum* statoliths supports an annual periodicity of growth ring deposition. Chem. Geol. 526, 153–164. https://doi.org/10.1016/j.chemgeo.2017.09.034.

Hollyman, P.R., Leng, M.J., Chenery, S.R.N., Sloane, H.J., Richardson, C.A., 2020. Calibration of shell δ^{18}O from the common whelk *Buccinum undatum* highlights potential for palaeoenvironmental reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 560. https://doi.org/10.1016/j.palaeo.2020.109995, 109995.

Izzo, C., Doubleday, Z.A., Grammer, G.L., Thomas, C., Delean, S., Ferguson, G.J., Gillanders, B.M., 2016. Multi-species response to rapid environmental change in a large estuary system: a biochronological approach. Ecol. Indicat. 69, 739–748.

Izzo, C., Gillanders, B.M., 2020. Port jackson shark growth is sensitive to temperature change. Front. Mar. Sci. 7, 1–7. https://doi.org/10.3389/fmars.2020.00240.

Jensen, O., Branch, T., Hilborn, R., 2012. Marine fisheries as ecological experiments. Theor. Ecol. 5, 3–22. https://doi.org/10.1007/s12080-011-0146-9.

Jossi, J.W., Benway, R.L., 2003. Variability of temperature and salinity in the Middle Atlantic Bight and Gulf of Maine based on data collected as part of the MARMAP ships of opportunity Program, 1978-2001. NOAA Technical Memorandum NMFS-NE-172 1–92.

Kenchington, E., Glass, A., 1998. Local adaptation and sexual dimorphism in the waved whelk (*Buccinum undatum*) in atlantic Nova scotia with applications to fisheries management. Can. Tech. Rep. Fish. Aquat. Sci. No. 2237 iv+43pp.

Kideys, A.E., 1996. Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off douglas, Isle of Man. Helgol. Meeresunters. 50, 353–368. https://doi.org/10.1007/BF02367109.

Kideys, A.E., Nash, R.D.M., Hartnoll, R.G., 1993. Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. J. Mar. Biol. Assoc. U. K. 73, 391–403. https://doi.org/10.1017/S002531540003294X.

Kimura, D.K., 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77, 765–776.

Lankford, T.E., Billerbeck, J.M., Conover, D.O., 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vunerability to predation in *Menidia menidia*. Evolution (N. Y) 55, 1873–1881.

Laptikhovsky, V.V., 2014. Does starfish predation determine spawning seasonality in the whelk *Buccinum undatum* in the Gulf of St Lawrence? J. Molluscan Stud 80, 219–221. https://doi.org/10.1093/mollus/eyu010.

Law, R., Grey, D.R., 1989. Evolution of yields from population with age-specific cropping. Evol. Ecol. 3, 343–359.

Lawler, A., 2014. Determination of the Size of Maturity of the Whelk *Buccinum undatum* in English Waters.

Levin, J., Arango, H.G., Laughlin, B., Wilkin, J., Moore, A.M., 2019. The impact of remote sensing observations on cross-shelf transport estimates from 4D-var analyses of the Mid-Atlantic Bight. Adv. Sp. Res. https://doi.org/10.1016/j.asr.2019.09.012.

Magnúsdóttir, H., 2010. The Common Whelk (*Buccinum undatum* L.): Life History Traits and Population Structure. University of Iceland. MSc Thesis. Faculty of Life and Environmental Sciences, University of Iceland, Reykjavik.

Magnusdottir, H., Palsson, S., Westfall, K.M., Jonsson, Z.O., Goodall, J., Ornolfsdottir, E. B., 2019. Revised phylogeography of the common whelk *Buccinum undatum* (Gastropoda: Buccinidae) across the north atlantic. Biol. J. Linn. Soc. 127, 890–899. https://doi.org/10.1093/biolinnean/blz060.

Mariani, S., Peijnenburg, K.T.C.A., Weetman, D., 2012. Independence of neutral and adaptive divergence in a low dispersal marine mollusc. Mar. Ecol. Prog. Ser 446, 173–187. https://doi.org/10.3354/meps09507.

Martel, A., Larrivée, D.H., Klein, K.R., Himmelman, J.H., 1986. Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. Mar. Biol. 92, 211–221. https://doi.org/10.1007/BF00392838.

Matta, M.E., Rand, K.M., Arrington, M.B., Black, B.A., 2020. Competition-driven growth of Atka mackerel in the Aleutian Islands ecosystem revealed by an otolith

biochronology. Estuar. Coast Shelf Sci. 240 https://doi.org/10.1016/j.ecss.2020.106775, 106775.

Mazerolle, M.J., 2015. AICcmodavg: Model Selection and Multimodel Inference Bases on (Q)AIC(c). R package version 2.0-3, Available online: https://cran.r-project.org/package=AICcmodavg.

MMO, 2019. UK Sea Fisheries Statistics 2018. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/920110/UK_sea_fisheries_statistics_2018_002.pdf.

Morrongiello, J.R., Thresher, R.E., Hobbs, N.T., 2015. A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. Ecol. Monogr 85, 93–115. https://doi.org/10.1890/13-2355.1.

Morrongiello, J.R., Thresher, R.E., Smith, D.C., 2012. Aquatic biochronologies and climate change. Nat. Clim. Change 2, 849–857. https://doi.org/10.1038/nclimate1616.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed effects models. Methods Ecol. Evol. 4, 133–142.

Narváez, D.A., Munroe, D.M., Hofmann, E.E., Klinck, J.M., Powell, E.N., Mann, R., Curchitser, E., 2015. Long-term dynamics in Atlantic surfclam (*Spisula solidissima*) populations: the role of bottom water temperature. J. Mar. Syst. 141, 136–148. https://doi.org/10.1016/j.jmarsys.2014.08.007.

Nasution, S., Roberts, D., Farnsworth, K., Parker, G.A., Elwood, R.W., 2010. Maternal effects on offspring size and packaging constraints in whelk. J. Zool. 281, 112–117. https://doi.org/10.1111/j.1469-7998.2009.00681.x.

Ogle, D.H., 2019. FSA: Fisheries Stock Analysis. R package version 0.8.12.

Ogle, D.H., 2016. Introductory Fisheries Analysis with R. CDC Press, Boca Raton, FL.

Pinsky, M.L., Palumbi, S.R., 2013. Meta-analysis reveals lower genetic diversity in overfished populations. Mol. Ecol. 23, 29–39.

R Core Team, 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Richardson, C., Saurel, C., Barroso, C., Thain, J., 2005. Evaluation of the age of the red whelk *Neptunea antiqua* using statoliths, opercula and element ratios in the shell. J. Exp. Mar. Biol. Ecol. 325, 55–64.

Rodhouse, P.G., Hatfield, E.M.C., 1990. Age determination in squid using statolith growth increments. Fish. Res. 8, 323–334.

Roff, C.A., 2002. Life History Evolution. Sinauer Associates, Sunderland, MA.

Roman, S.A., Rudders, D.B., 2019. Selectivity of Two Commercial Dredges Fished in the Northwest Atlantic Sea Scallop Fishery. J. Shellfish Res 38, 573. https://doi.org/10.2983/035.038.0308.

Rowell, C.A., 1992. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In: Stokes, T.K., McGlade, J., Law, R. (Eds.), The Exploitation of Evolving Resources. Springer-Verlag, Berlin, pp. 44–61.

Saba, V.S., Griffies, S.M., Anderson, W.G., Winton, M., Alexander, M.A., Delworth, T.L., Hare, J.A., Harrison, M.J., Rosati, A., Vecchi, G.A., Zhang, R., 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. J. Geophys. Res. Ocean 121 (1), 118–132. https://doi.org/10.1002/2015JC011346.

Santarelli, L., Gros, P., 1985. Age and growth of the whelk *Buccinum undatum* L. (Gastropoda: prosobranchia) using stable isotopes of the shell and operculum striae. Oceanol. Acta 8, 221–229.

Shelmerdine, R.L., Adamson, J., Laurenson, C.H., 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. Fish. Res. 86, 201–206. https://doi.org/10.1016/j.fishres.2007.06.005.

Smith, K.E., Thatje, S., 2013. Nurse egg consumption and intracapsular development in the common whelk *Buccinum undatum* (Linnaeus 1758). Helgol. Mar. Res. 67, 109–120. https://doi.org/10.1007/s10152-012-0308-1.

Smith, K.E., Thatje, S., Hauto, 2013. Thermal tolerance during early ontogeny in the common whelk *Buccinum undatum* (Linnaeus 1785): bioenergetics, nurse egg partitioning and developmental success. J. Sea Res. 79, 32–39.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Takasuka, A., Aoki, I., 2006. Environmental determinants of growth rates for larval Japanese anchovy *Engraulis japonicus* in different waters. Fish. Oceanogr. 15, 139–149.

Taylor, N.G., Walters, C.J., Martell, S.J.D., 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Can. J. Fish. Aquat. Sci. 62, 215–223.

Thomas, M.L.H., Himmelman, J.H., 1988. Influence of predation on shell morphology of *Buccinum undatum* L. on Atlantic coast of Canada. J. Exp. Mar. Biol. Ecol. 115, 221–236. https://doi.org/10.1016/0022-0981(88)90156-6.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10, 181–213.

Wang, T., Overgaard, J., 2007. The heartbreak of adapting to global warming. Science 315 (5808), 7461–7465.

Weisberg, S., Spangler, G., Richmond, L.S., 2010. Mixed effects models for fish growth. Can. J. Fish. Aquat. Sci. 67, 269–277.

Wilkin, J., Levin, J., Lopez, A., Hunter, E., Zavala-Garay, J., Arango, H., 2018. A coastal ocean forecast system for the U.S. Mid-Atlantic Bight and Gulf of Maine. In: Chassignet, E., Pascual, A., Tintoré, J., Verron, J. (Eds.), New Frontiers in Operational Oceanography. GODAE OceanView, pp. 593–624. https://doi.org/10.17125/gov2018.ch21.

Wittman, T., Izzo, C., Doubleday, Z.A., McKenzie, J., Delean, S., Gillanders, B.M., 2016. Reconstructing climate–growth relations from the teeth of a marine mammal. Mar. Biol. 163, 1–11.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY.