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Timing of the reproductive cycle of waved whelk, *Buccinum undatum*, on the U.S. Mid-Atlantic Bight

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Abstract

Development of the unmanaged waved whelk (*Buccinum undatum*) fishery on the Mid-Atlantic continental shelf of the United States has initiated investigation into fisheries-related biological and population attributes of the species in this region. Maturation and reproduction timing vary by location for this species and are likely linked to bottom water temperature. This study examined the seasonal fluctuations in relevant body metrics and gonadosomatic index in relation to bottom temperature to assess the timing of the reproductive cycle of the *B. undatum* population in the southern-most extent of this species' range in the Atlantic. To characterize variation over the maturation schedule, nine locations in the Mid-Atlantic Bight (MAB) were sampled five times between January 2017 and September 2017. Maturity was assessed macroscopically, with morphological methods, and via gonadosomatic indices. Male behavioral maturity estimates, based on a penis length to shell length index (PL₅₀), were compared to estimates made using other methods for assessing maturity to test the efficacy of this commonly used ratio. Mature whelk were found in all months and peak reproductive activity was observed in spring and early summer. This timing suggests that ideal sampling to visually identify maturity to estimate size of maturity would be late winter or early spring. Unique oceanographic dynamics in the MAB, such as strong seasonal stratification results in large changes in annual bottom temperature which appears to be closely linked to the reproductive cycle in this region. Our data suggest that *B. undatum* in the MAB experience spawning and development at ~7–8 °C; temperatures warmer than Canadian populations and cooler than some UK conspecifics. To our knowledge, this is the first study to document the annual reproductive cycle of waved whelk in the United States.

Keywords: *Buccinum undatum*, Reproduction, Maturity estimates, Fisheries, Temperature, Gonadosomatic index

Introduction

The waved or common whelk (*Buccinum undatum*) is a cold-water subtidal marine gastropod, distributed through the North Atlantic and adjoining seas. Throughout its distribution, it is commercially important and has been harvested in Europe and Canada for both bait and human consumption for decades [1–4]. New fisheries for this species have recently been developed in several

countries, including the United States [5, 6], specifically the Mid-Atlantic region of the Northeast U.S. Shelf (NE Shelf). As is now well documented, assessing and monitoring waved whelk has proven to be difficult due to spatially variable life-history parameters [3, 5, 7–9] and its ability to form localized subpopulations [10–13], both of which make this species vulnerable to overexploitation if fishery managers assume equivalency across the range of the animal [3, 5, 7–9]. To inform future management in the Mid-Atlantic region of the US, it is critical that appropriate data is collected during early fisheries development to understand population structure and spatially variable biology [14].

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Buccinum undatum is gonochoric, its reproductive cycle has been well documented across most of its range with considerable variability in spawning timing [2, 15–18]. Whelk display distinct breeding periods with clear seasonal development of the gonads, the onset of spawning is signaled by a noticeable increase in gonad size [9]. Females aggregate during spawning and lay small spherical egg capsules that are deposited on hard surfaces such as rock or shell [15]. Larval development occurs inside the egg capsules and depending on location and temperature, egg masses take between 10 weeks to 9 months to develop into crawl-away juveniles [15, 17, 19].

Whelk gonads undergo seasonal reproductive cycles [16, 17] which have proven to be useful indicators to determine reproductive timing through the species' range. Studies in the eastern Atlantic have shown that at the southern extent of whelk distribution, egg-laying primarily occurs through the fall and winter months when water temperatures are trending downward to their annual minimum ($\sim 4\text{--}10\text{ }^{\circ}\text{C}$) [2, 9, 17, 20]. Whelk populations from west Iceland and Sweden, the northern end of the species distribution, follow a similar pattern as European populations with egg-laying occurring from fall to winter [21–23]. In contrast, in the upper northwest Atlantic, Gulf of St. Lawrence, Canada, egg-laying was observed in spring and summer directly after annual minimum bottom temperatures gradually increased to $\sim 2\text{--}3\text{ }^{\circ}\text{C}$ [15].

Across the distribution of *B. undatum*, a broad thermal range is experienced by different populations with annual temperatures ranging from below $0\text{ }^{\circ}\text{C}$ to above $22\text{ }^{\circ}\text{C}$ [19]. Egg-laying and development do not occur over this entire temperature range and have been observed to be limited to temperatures between 2 and $10\text{ }^{\circ}\text{C}$ [20] with thermal reproductive tolerance varying between populations. This variation in development timing has been linked to differences in temperature during development, where small increases in temperature, specifically at the lower end of the thermal range, result in shorter periods of development timing [19]. Juvenile whelk in the UK emerge from their egg capsules 3 to 5 months after egg-laying, while in Canada this takes place after 5 to 8 months [15, 17]. Martel et al. [15, 16] suggest that overall variation in timing of the reproductive cycle in *B. undatum* between European waters and those of Eastern Canada may be due to water temperatures, with European recorded winter water temperatures higher than the average summer temperature reported in the Gulf of St. Lawrence. However, Laptikhovsky [24] suggested the switch in reproductive timing in the northwest Atlantic may be an adaptation to protect newly emerged juveniles from seasonal predatory pressure from their major

predator, *Leptasterias polaris*, which is non-existent in European waters.

Seasonal patterns in gonad condition can be identified by fluctuations in gonadosomatic indices (GSI), gonad indices, and macroscopic assessments [9, 16–18, 21]. For males, behavioral maturity, the ratio of penis length to shell length, has been used regularly to confirm male maturity [3, 5, 25, 26], yet recent work has questioned the validity of this maturity classification method due to incorrect assessment of visually immature animals [9, 21]. To examine the efficacy of penis length as an indicator of male maturity, iterative search procedure have been used to examine this morphological relationship [9, 21, 27, 28]. The seasonality variation in gonad condition results in fluctuations in maturity estimates throughout the year. Both Hollyman [21] and Haig et al. [9] highlight the need for sampling and maturity assessments to occur before the spawning season, when individuals display maximum gonad differentiation, as these maturity estimates may be used to inform fisheries management regulations, and if estimates are misspecified due to inappropriate sampling timing, a population could be inadequately protected.

The description of annual reproductive timing has yet to be performed on southern populations on the NE shelf, along the Mid-Atlantic Bight (MAB), particularly in waters of New Jersey where fishery development is occurring. Recent expansion of the unmanaged waved whelk fishery on the Mid-Atlantic continental shelf has initiated investigation into fisheries-related biological and population attributes of the species in this unique region. This region experiences intense stratification as surface water temperatures rise in response to surface heating while deeper waters are influenced by cold waters from the north [29]. Stratification begins in the spring, and by early summer forms one of the world's sharpest thermoclines with temperatures range from $\sim 30^{\circ}$ to $8\text{ }^{\circ}\text{C}$ in just a few meters [30]. A band of cold bottom water extends over this region and persists until early fall when the passage of storms reduces the stratification [31–37]. Additionally, this region along the NE shelf has experienced the largest change in thermal conditions observed in temperate waters off North America [38–40]. Studies show that invertebrate communities of the NE shelf are likely vulnerable to the effects of climate change. Particularly sensitive are those animals like the waved whelk that are less mobile, dependent upon calcium carbonate shells, and associated with specific habitats [41, 42].

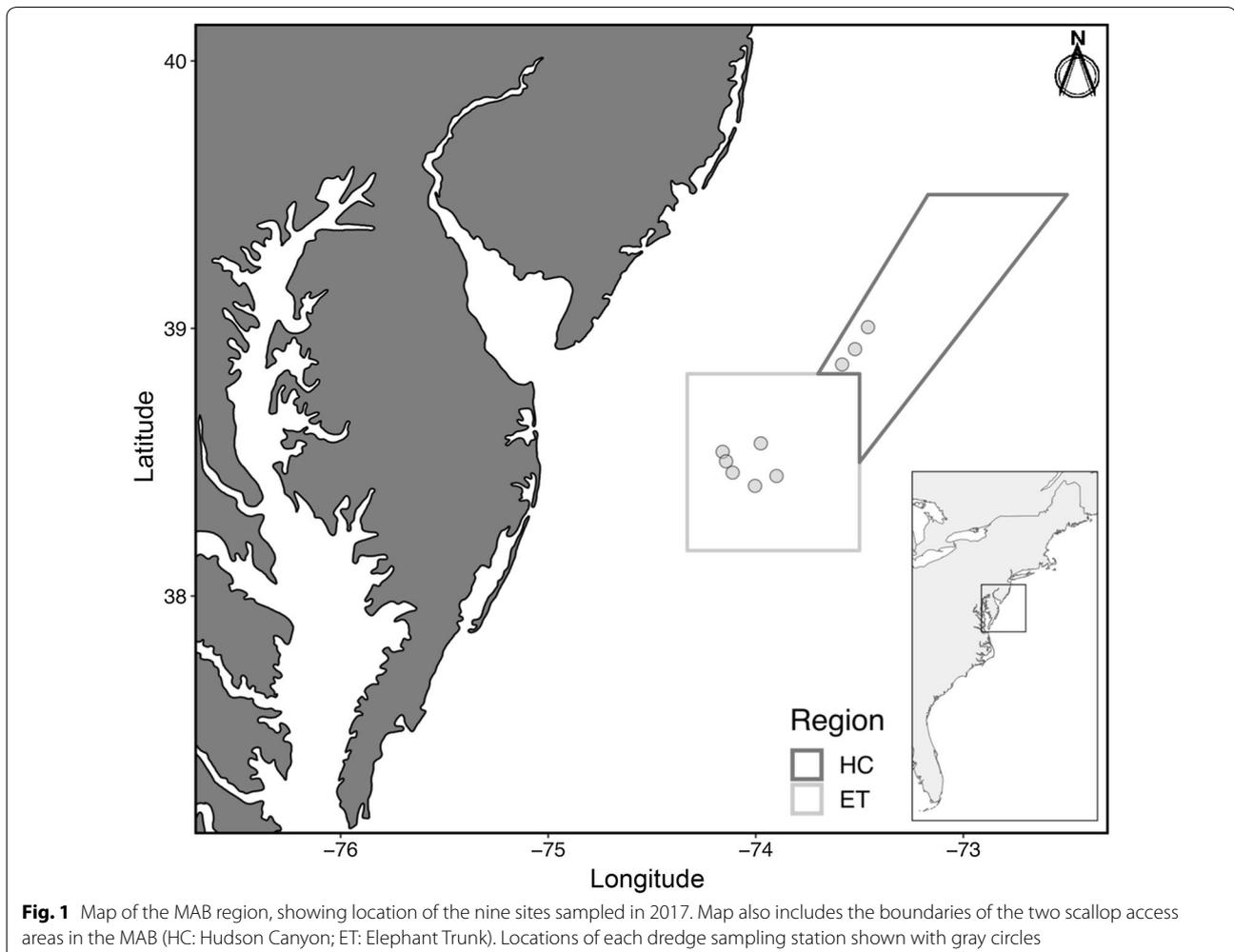
Due to stratification and a seasonally persistent band of cold bottom water (cold pool) in the MAB, large fluctuations in annual bottom temperature may result in unique reproductive timing for *B. undatum*. Systematic observations of the timing of reproductive events in the Mid-Atlantic region would provide

a better understanding of whelk population dynamics. In addition to understanding the relationship between temperature and reproductive timing, it is important to comprehend the reproductive cycles of exploited stocks, such as waved whelk, as it has significant implications for this species' vulnerability to exploitation. This study tests the validity of multiple metrics for estimating male maturity and examines fluctuations in various body metrics and GSI in relation to observed and modelling bottom temperature. The collected information allows determination of the annual pattern of reproductive events and suggests recommended timing for sampling whelk in the MAB to most accurately estimate maturity. Finally, this study culminates with a description of the reproductive cycle of *B. undatum* for the southern-most population in the range of this species in the Northwest Atlantic Ocean. To our knowledge, this is the first study to document the annual reproductive cycle of waved whelk in the Mid-Atlantic.

Methods

Sample collection

Samples were collected in the MAB in partnership with Virginia Institute of Marine Science (VIMS) sea scallop targeted fishery sampling. Sampling occurred at the same nine stations approximately every 2 months from January 2017 through September 2017 onboard commercial scallop vessels (Fig. 1). These sampling events targeted Atlantic sea scallops (*Placopecten magellanicus*), although *B. undatum* were incidentally caught. Borsetti et al. [5] show that whelk and sea scallops commonly co-occur throughout the domain of this region. At each station, a dredge with a 2.4 m wide frame equipped with 5.1 cm rings, 10.2 cm twine top, and a 3.8 cm mesh liner was towed for 15 min at a speed of approximately 3.8–4.0 knots [43, 44]. No estimate of whelk catch efficiency for this survey gear is available; however, Borsetti et al. [5] calculated an average abundance for this region of 0.0012 whelk/m². Whelk collected by dredge ranged from 21.9 to 87 mm total shell length (TSL). Distance towed, depth,



and bottom water temperature were recorded at each station. At each sampling station, all whelk were retained, labelled with station information, and frozen for subsequent analysis.

Temperature

Observed

A Star-Oddi tilt sensor (a device that records time, angle of inclination, temperature, depth) was mounted to the dredge frame and was used to determine dredge bottom contact time. A shipboard GPS unit logged vessel location every 2 s and was used to estimate the activity of the sampling gear in time and space [43]. For the purposes of this analysis, temperature measurements from the sensor were integrated to the GPS data and only measurements taken when the dredge was in contact with the seafloor were retained. For each sampling trip, bottom temperatures across all 9 sampling sites were pooled to calculate an average bottom temperature for a given sampling event. The observed bottom water temperatures were compared to model-generated temperatures (described in the following section) to characterize the thermal conditions experienced by whelk in this region.

Modelled

A 35-year (1980–2015) hindcast of ocean temperature is available as output from the Regional Ocean Modeling System (ROMS) model [45]. This modelling temperature time series was bias-corrected using observed bottom water temperatures [46] measured during the National Marine Fisheries Service/Northeast Fisheries Science Center assessment surveys, conducted mainly in spring, summer, and fall of each year. These fisheries surveys, typically occur during the annual minimum and maximum bottom temperatures. Bias correction substantively improved the fit of ROMS model temperature output relative to observations. The bias-corrected hindcast temperature time series provided continuous oceanographic conditions that were used to resolve seasonal minimum and maximum bottom temperatures over the study area.

These simulated data formed the basis for the generation of a 10-year, monthly climatology from 2005 to 2015 for the southern MAB region. This climatology was then used to examine the relationship between temperature and the reproductive cycle of whelk in the MAB.

Maturity

Whelk retained during dredge surveys were thawed before processing. Each specimen was extracted following methods detailed in Borsetti et al. [5]. Sex was recorded for each individual and was determined by the presence or absence of a penis. Whelk display distinct seasonal breeding periods and therefore gonads of mature whelk are variable throughout the year. The first measure of maturity, a macroscopic assessment of gonadal maturity, was used to determine functional maturity [9, 27, 47]. A maturity stage; immature, developing, or mature (Table 1), was assigned based on development of the gonad [9, 47, 48]. From the macroscopic assessment of maturity, each whelk was assigned a binary factor of functional maturity (mature/developing = 1; immature = 0).

Monthly population estimates of functional maturity were calculated using a logistic regression model and defined as the size at which 50% of the population is mature (L_{50}) [49, 50]. Whelk with an atypical gonad as a result of parasite infestation were excluded from the analysis of size of sexual maturity [51]. More information about size of maturity calculation can be found in Borsetti et al. [5]. Maturity curves were fit using a base R code (adapted from Harry [52]), which is available online and has also been utilized in a number of studies for this species (i.e. [5, 9, 21, 53]). Confidence intervals were added by bootstrapping the generalized linear model (10,000 runs). Significance was tested by comparing the amount of deviance explained relative to the null model using Chi squared tests. Monthly L_{50} estimates were then compared to a previously predicted size of maturity estimate from the same region [5].

Table 1 Maturity stage assessment definitions for male and female whelk using visual assessment methods. Modified from Haig et al. [9]

Stage	Male	Female	Mature
Immature (I)	No obvious differentiation between digestive gland and gonad (testis). Vas deferens invisible	No obvious differentiation between digestive gland and gonad (ovary)	0
Developing (II)	Some visible differentiation between the anterior edge of digestive gland and gonad (testis), possibly a visible vas deferens	Some visible differentiation between the anterior edge of digestive gland and gonad (ovary), possibly a visible pallial oviduct	1
Mature (III)	Full differentiation between digestive gland and gonad (testis) obvious, visible vas deferens in males	Fully differentiation between digestive gland and gonad (ovary), visible enlarged pallial oviduct	1

Similarly, males were given a binary factor of behavioral maturity to indicate maturity stage based on a penis length to shell length index (PL_{50}). Males with a penis length greater than or equal to half of their shell length ($PL: SL$) were considered behaviorally mature [3, 4, 54]. To examine the efficacy of penis length as an indicator of male maturity, an iterative search procedure was used to examine this morphological relationship using the following linear model:

$$SL = PL * I(x < c) + x * I(x > c)$$

where * is the main effects and interactions for both variable. This model searches for deviations from the linear model and estimates an inflection (or breakpoint) (c) between shell length (SL) and penis length (PL) by finding a point where the residual standard error is minimized [9, 55]. Inflection points were calculated for each sampling event and for data aggregated from all MAB samples and indicate the fluctuations in male behavioral maturity estimates throughout the year.

Fluctuations in female GSI, the ratio between the gonadal weight and the total eviscerated weight, were examined to identify peak periods of gonad development. The gonadal weight comprised of the ovary and pallial oviduct (composed of the seminal receptacle, albumen gland, capsule gland, and bursa) which were dissected and a combined weight was recorded [3]. The eviscerated weight, total weight minus the gonad and variable digestive gland, was also recorded [16]. Fluctuations in female GSI for developing, mature, and both developing and mature were examined and compared using a repeated measures ANOVA and a Tukey's post hoc test.

Additionally, similar to other studies, the relationship between the mature female gonad (pallial oviduct and ovary) and digestive gland were examined [16, 18]. To streamline sample processing, the pallial oviduct and ovary (POO) weights were combined during dissection. This combined weight was used because studies have shown that weight of these two female structures had the same trend throughout the reproductive season [16, 18]. The average POO and digestive gland were compared for mature females over the sampling period. Seasonal changes in the size of the female gonad and digestive gland were compared using a repeated measures ANOVA and a Tukey's post hoc test.

Results

Sample Collection

A total of 602 whelk were caught over five sampling trips from January 2017 to September 2017. During

Table 2 Sample dates and total catch composition separated by sex

Sample date	Males	Females	Observed temperature	Modelled temperature
January 2017	32	49	10.2	10.4
March 2017	118	138	8.1	6.4
May 2017	63	89	7.0	9.2
July 2017	13	24	–	8.7
September 2017	34	42	9.4	12.1

Bottom temperature from observed bottom temperatures (dredge sensor) and modelled hindcast temperatures. Dashes indicate that data was not available

each sampling trip, the number of whelk collected varied by month and sex (Table 2).

Temperature

Observed

Monthly average bottom temperatures ranged from a minimum of 7 °C in May 2017 (Table 2) to a maximum of 16.6 °C in November of 2016 (Fig. 2a), representing a seasonal change of almost 10 °C through the year (Table 2). The temperature sensor was not mounted to the dredge during the month of July and therefore no bottom temperatures are available for that sampling date.

Modelled

The average monthly temperature from the model generated 10-year hindcast climatology ranged from a minimum of 6.4 °C in March 2017 (Table 2) to a maximum of 15.8 °C in November 2016 (Fig. 2a). Both observed and modelled bottom temperatures depict similar annual trends in temperature. Temperature minimums are observed in the spring (March–May) and temperature maximums in the fall and winter months (October–December) (Fig. 2a). Similarities among observed and modelling bottom temperatures suggest that this study occurred during a year in which bottom temperatures were within the expected temperature range for the MAB region.

Maturity

The proportion of whelk in each reproductive stage varied over time. Mature whelk were found during each sampling with the highest percentage in May for males and September for females (Fig. 2b, d). There was a large increase in the proportion of immature males and females in the month of March.

The estimated functional L_{50} , based on macroscopic assessments, varied for each month sampled due to the seasonality of the whelk breeding cycle which results in

(See figure on next page.)

Fig. 2 **a** Average bottom temperature (black line) with 95% confidence interval (grey band) calculated from 10-year hindcast climatology and average bottom temperature (black diamond) with standard deviation calculated from observed data from each site sampled (white circle) **b** Proportion of males in each maturity stage (Immature: light gray; Developing: gray; Mature: black). **c** Comparison of three different male maturity metrics (IP: inflection point, black; L_{50} based on visual assessment of gonads with 95% confidence interval, grey; PL_{50} shell length: penis length 95% confidence interval, white). **d** Proportion of females in each maturity stage (Immature: light gray; Developing: gray; Mature: black). **e** Female GSI separated by qualitatively assigned maturity stage (Developing: white; Mature: gray; Developing and mature: black) for each month sampled with 95% confidence interval

fluctuations in gonad development. Maturity at length curves for each month sampled were all significant when tested against the null model (Fig. 3). Gradual slopes for each of the maturity curves indicate maturation occurs over a range of lengths even within a sample. In all months sampled females consistently had a larger L_{50} than males. Functional estimates of maturity range from 57.1–64.2 mm for females and 54.6–62.5 mm for males. The female population level L_{50} is at its largest in January (64.2 mm) and decreases slightly during the expected egg-laying period (March, 60.9 mm and May, 63.1 mm). By September, after egg-laying is expected to have occurred, the observed L_{50} is at its smallest (57.1 mm). Male population level L_{50} follows an inverse trend to that of females. In January, the males have the lowest observed L_{50} (54.6 mm) which steadily increases through the spring and fall and peaks in September (62.5 mm). Overall L_{50} estimates for all months sampled is 56.9 mm for males and 61.6 mm for females.

Iterative searches found the inflection in the PL: SL relationship to be highest in January (65.3 mm), steadily decrease during spring and summer (March—58.3 mm, May—54.1 mm), and starting to build again by fall (61.6 mm) (Fig. 4). The inflection points closely resemble the behavioral PL_{50} estimates and follows a similar trend (Fig. 2c). PL_{50} slightly overestimates maturity; however, some of these overestimates still fall within the 95% CI of behavioral maturity. The PL_{50} and inflection point calculated for January are highly similar but disagree with the functional maturity estimate by approximately 10 mm. Due to small sample size, the iterative search procedure was unable to be completed for July.

Female GSI varied over the sampling period, particularly among mature females. Mature female average GSI was largest in January and decreased in size significantly by May ($p=0.05$), indicating spawning had occurred (Fig. 2e, gray points). For developing females there was an increasing trend in GSI throughout the year, peaking in September. When mature and developing females are pooled, differences between months are no longer significant.

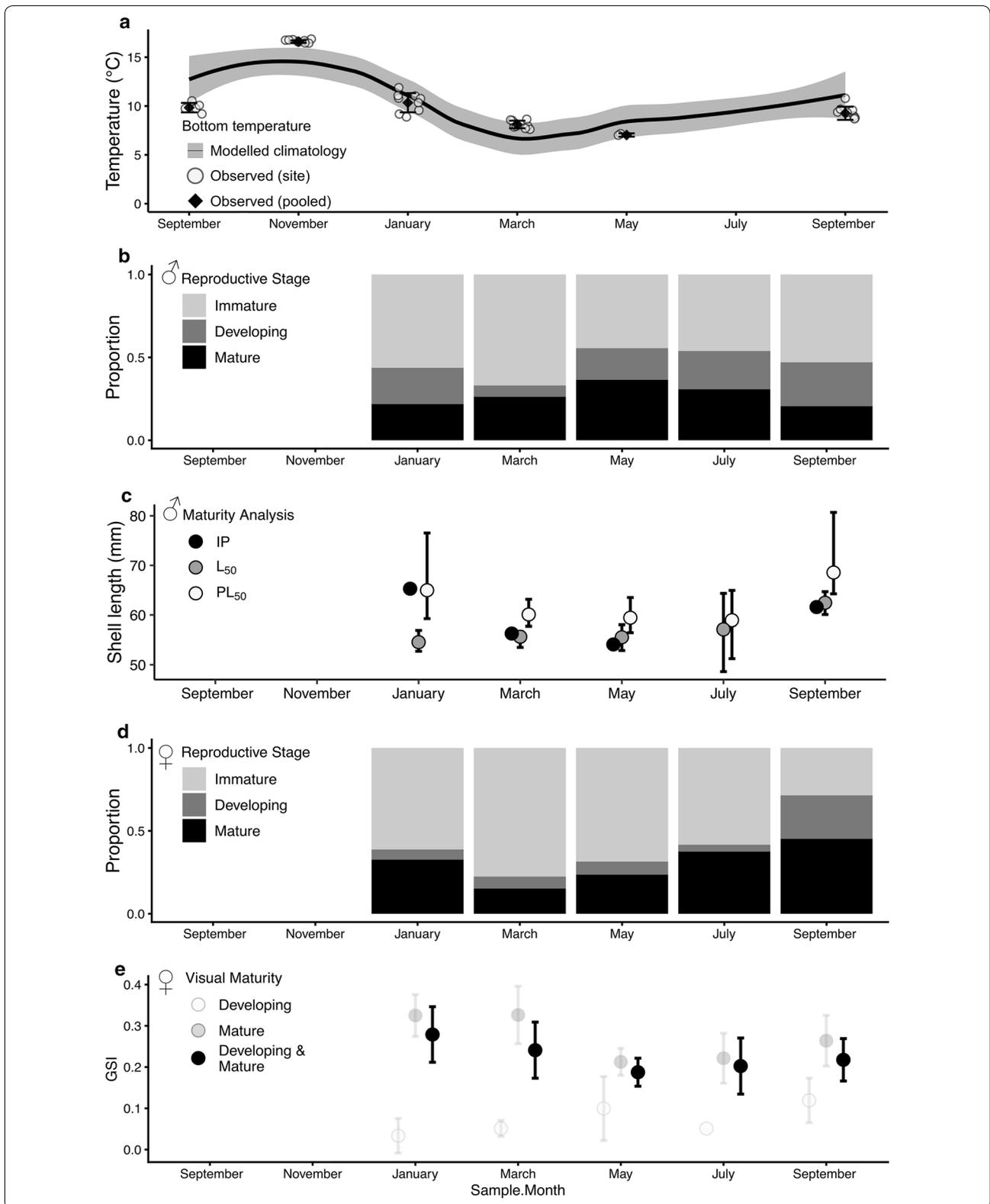
For mature female whelk, there is a clear inverse seasonal pattern between the weight of the female gonad (POO) and digestive gland (Fig. 5). Sampling began in

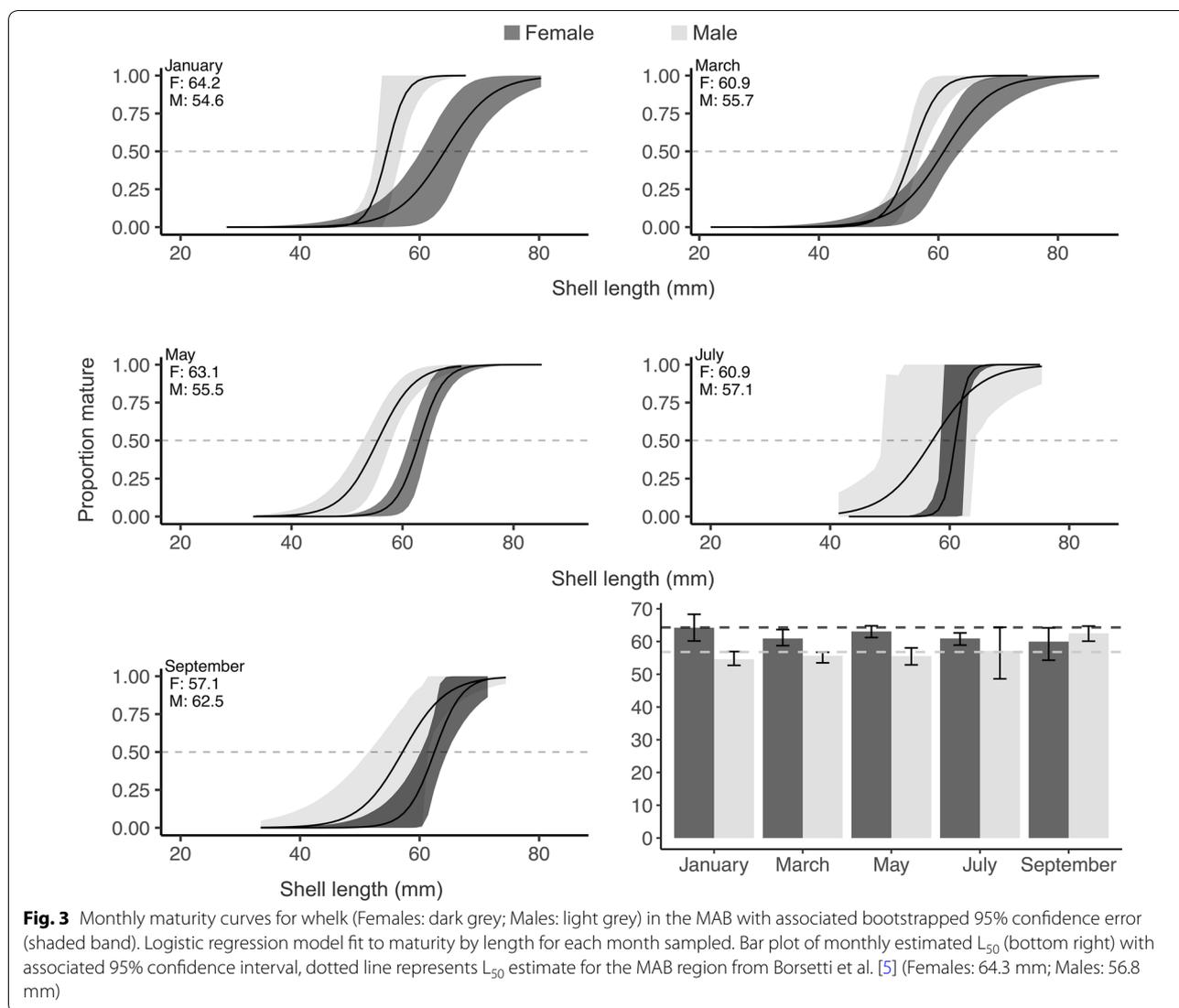
winter with the female POO larger than the digestive gland. By spring the difference in size between these structures decreased. In early summer, the female gonad is significantly reduced in size ($p=0.02$) and is now smaller than the digestive gland, this trend is observed throughout summer sampling. There is a significant reduction in average size of the female gonad when comparing samples from January to May ($p=0.05$). The digestive gland reaches its peak size in late summer. By fall, both the female gonad and digestive gland has decreased in size, resulting in the two structures being comparable weights. No relationship exists between the female gonad (POO) and digestive gland for both immature and developing females.

Discussion

The reproductive cycle of *B. undatum* in the Mid-Atlantic Bight observed from January 2017 through September 2017 suggests that the principal egg-laying period in this portion of its range is March through May. This period coincides with minimum bottom temperatures in the MAB suggesting that temperature may be driving reproductive timing in this region. This reproductive timeframe is supported by both a morphometric indicator of male maturity and GSI for mature females, which sharply and significantly decreased between March and May, suggesting that egg-laying occurred. Eggs have been observed in benthic samples during the summer months, May through August (pers. obs.), supporting this suggested reproductive timing window. The relationship between the two body-component indices (POO & digestive gland) demonstrates that mature female gonad mass is reduced by March indicating that some of the population has already spawned and begun to lay eggs.

Determination of sexual stages in this study are based on multiple approaches: macroscopic assessment of gonad, dissection and weighing of gonad, and comparison of penis length [8, 9, 18, 48]. Methods for this study were selected because they were more time-efficient and allowed for larger sample sizes, even though they lack some of the precision of other methods (i.e. histological observations). The functional L_{50} varied by sample for both sexes, yet females consistently had larger maturity estimates in all months. Previous maturity estimates in





this region used different methods, however, past estimates only slightly overestimate maturity [5] (Fig. 3). In comparison, estimates made in this study may be more conservative due to the inclusion of developing whelk in the mature category (Table 2). Despite differences in methodology, females consistently had larger size of maturity estimates [5]. This trend is not consistent in all assessed populations, some studies have found no differences in size of maturity between sexes [26], while others in heavily fished regions have found males consistently maturing at larger sizes than females [9, 21]. Female L_{50} increased in January prior to spawning. Similarly, during January and March female whelk had higher GSI values. The L_{50} value progressively decreased throughout the sampling period. Similar seasonal changes in maturity have been observed in Wales [9, 21] indicating that increases in L_{50} coincide with peaks in the seasonal

breeding cycle. Male functional maturity based on macroscopic assessment revealed an inverse L_{50} trend when compared to females. The L_{50} value progressively increased throughout the sampling period, reaching a maximum in September. Suggesting an inverse relationship between male testis development and ovary development in females. This unusual pattern, first described by Martel et al. [16], was attributed to male's long-term ability to store sperm. Trends in increasing male testis index in both *Buccinum undatum* [16] and *Buccinum isaotakii* [56] have been directly correlated with increases in water temperature which was associated with the advancement in spermatogenesis. In this study, the greatest proportion of mature male whelk samples were found in the warmest months, January and September.

Estimates of maturity based on both the iterative search procedure and the male behavioral assessment for all

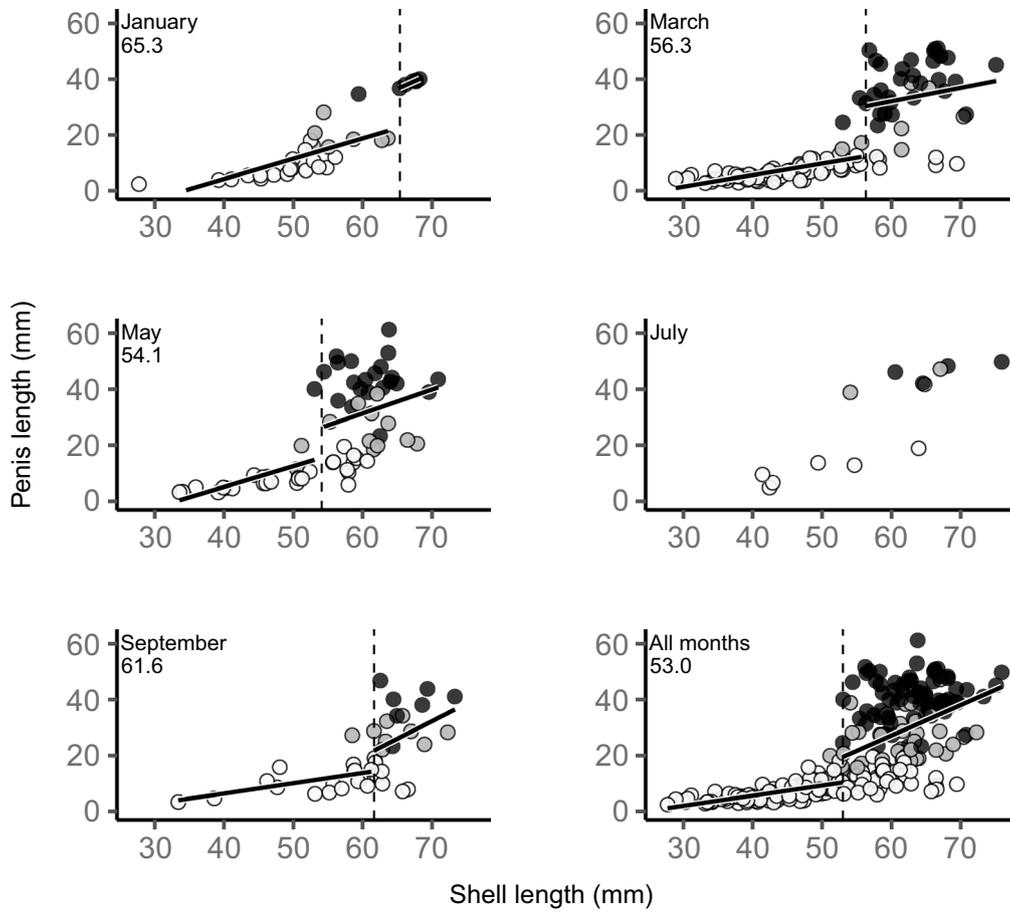


Fig. 4 Inflection point for each month sampled and all months combined indicating allometric growth patterns based on the variance between iterative tests on linear models of penis length (mm) and total shell length (mm) for males. The dotted black line indicates the value for each month with the lowest standard error. Maturity stage, based on macroscopic examination of the gonad are indicated by the color of the points (Immature: white; Developing: gray; Mature: black)

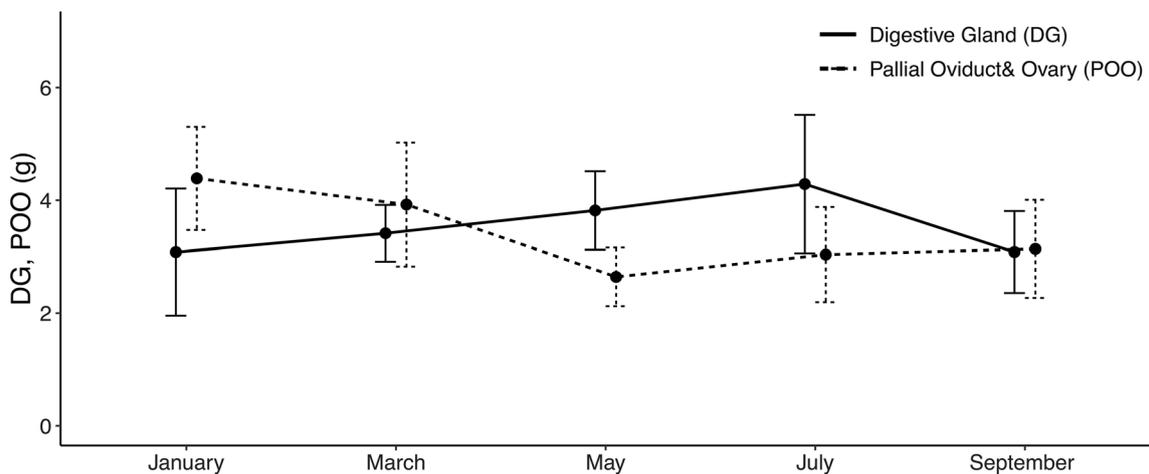


Fig. 5 Average seasonal variation in the weight (grams) of mature female body-component indices of the digestive gland (DG) (solid line) pallial oviduct and ovary (POO) (dotted line) and associated 95% confidence interval

months were similar; however, the PL_{50} estimates slightly overestimate maturity. Conversely, the winter functional maturity (L_{50}) appears to be an underestimate perhaps because the L_{50} curve is based more on developing rather than mature whelk. Despite these differences, behavioral maturity (the penis length to shell length ratio) is a viable method of determining maturity in males in this region, particularly, when gonad differentiation is indistinguishable (i.e. directly after spawning when gonads are spent) [9, 57]. Some studies have found the maturity estimates made using PL_{50} closely resemble those made using L_{50} [26], yet others have found that PL_{50} slightly [21] or considerably [9] overestimates maturity.

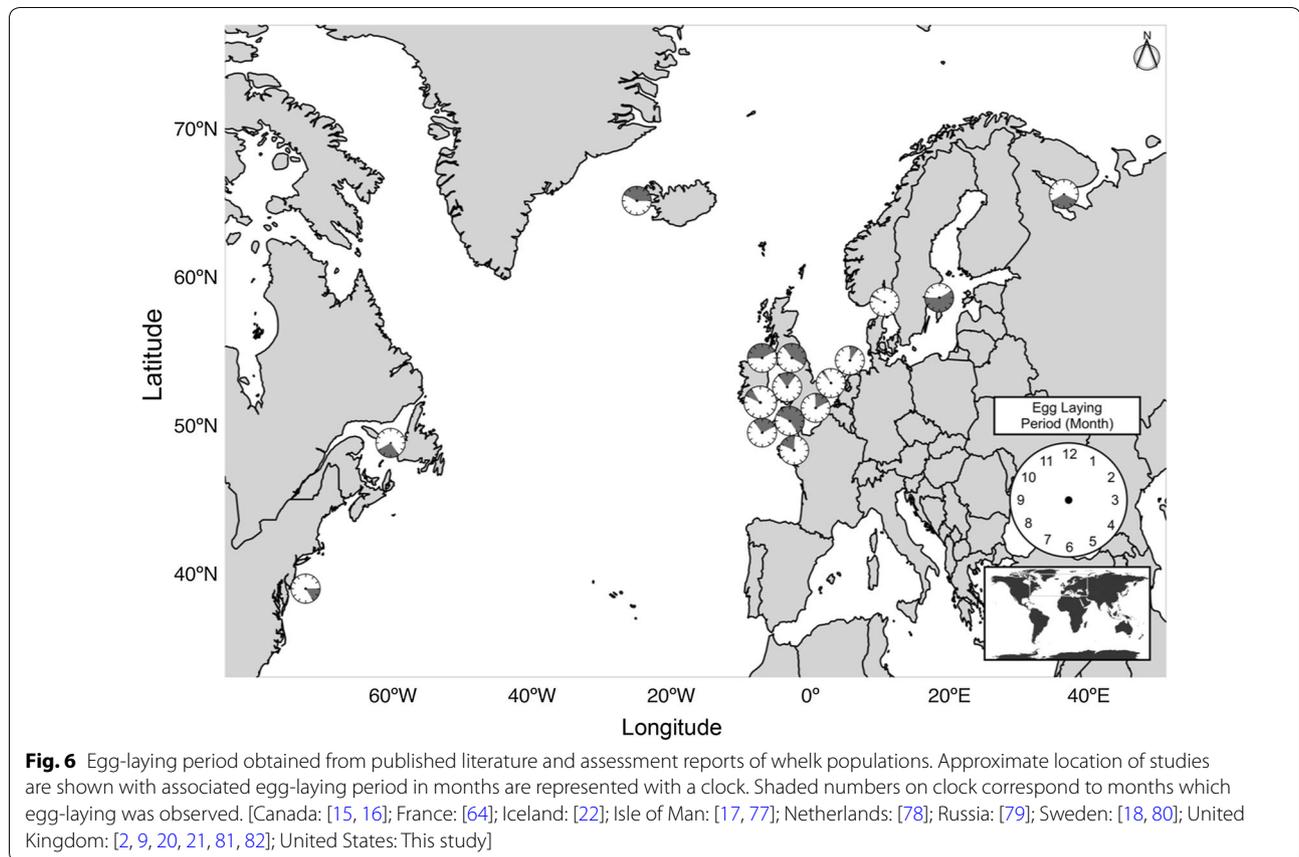
Seasonal fluctuations in L_{50} have implications on future fisheries management for this species. Minimum landing size, a common fisheries management approach, can be informed by estimated size of sexual maturity. If misspecified, a population could be inadequately protected if L_{50} is underestimated due to the timing of sampling. Future assessments of the size of sexual maturity should aim to include this seasonal consideration into study design to ensure proper assessment of maturity. Seasonal variation in maturity observed in this and other studies suggest that assigning maturity is more difficult outside of annual reproductive periods [9]. Because of this species' distinct reproductive seasonality, gonads are not equally apparent throughout the year. An ideal time to visually assess gonads is prior to the spawning season when there is the greatest differentiation between the ovary and associated digestive gland. This study suggests that the ideal time is during late winter or early spring in the MAB. If assessing size of maturity during other seasons, it may be useful to incorporate other indicators of maturity to confirm maturity. Replication of this study is recommended to fill sampling gaps during unsampled months and years with bottom temperature anomalies to examine if seasonal patterns are consistent.

Several gastropods reduce feeding during their breeding season, this includes several whelk species, *Nucella (Thais) lapillus* [58], *Nucella lamellosa* [59, 60], and *Buccinum undatum* [2, 16, 61]. During the warm winter months this population appears to be building gonad which coincided with reduced feeding activity and thus a smaller digestive gland. Experimental fishing with baited pots in early December of the previous year in the MAB, a period when bottom temperatures were relatively warm (~15 °C), resulted in extremely low catch (unpublished data, pers. obs.), which may support this hypothesis of reduced feeding during early winter months. Similarly, studies in Ireland show a decrease in catch through the summer months when feeding is at its lowest and temperatures were at their highest [62, 63]. The inverse cycle observed for mature females between the digestive gland

and gonad agrees with other studies [16, 18] and further confirms that feeding activity is reduced during the reproductive season. After the primary egg-laying period, which occurs between March and May, the female gonad start to slowly develop again and are similarly sized to the digestive gland by September, suggesting that there was little rest period before renewed ovarian development.

Some studies examining reproductive cycles of this species have used baited pots for sample collection (i.e. [9, 18, 64]). Santarelli and Gros [4] indirectly indicate a link between the reduced feeding and onset of reproduction in the French fishery based on catch per unit effort, which severely decreased from August through October. Other studies have also suggested that whelk are less attracted to baited pots during reproduction [65, 66] which may bias samples collected during this time to non-reproductive members of the population. Feeding activity and catchability in waved whelk may change with reproductive state [65] such that catch from baited pots may result in a biased sample that fails to include maturing females that are building gonad. Dredge catches may provide a better representation of the population [5] and likewise the reproductive cycle over the annual period.

Waved whelk are a boreal species, its temperature tolerance does not favor an energetically costly reproductive period over the summer in Europe [16]. Studies have described populations at the southern end, mainly the UK, of this species' distribution as fall/winter spawners, with eggs being laid as water temperatures cool and reach their annual minima. Populations previously studied in the northwest Atlantic inhabit colder waters and lay eggs spring and summer as water temperatures warm from annual minima [16, 17, 67] (Fig. 6). Whelk in Breiðafjörður (Iceland) had a similar reproductive season to that of Europe (October–March) but seawater temperature (0–5 °C) during this time were more similar to those experienced by whelk in the Gulf of St. Lawrence [22, 23]. This suggests that the seasonality of European whelk may be linked to timing of juvenile hatching to allow rapid growth during times when abundant food reserves are present. The population examined in this study represents the southern-most for *B. undatum* in the northwest Atlantic [5]. Our results suggest that in the MAB egg-laying occurs during the spring and early summer (March–May) slightly earlier than conspecifics to the north. The MAB population is more similar to those in the UK which lay their eggs when the bottom water temperature is at a minimum, rather than during rising temperatures (i.e. Canada). Given the findings from this work, it appears that whelk in the MAB experience spawning and development at warmer temperatures (~7–8 °C) than Canadian populations and cooler than some UK populations. Hatching juveniles likely emerge



during warm fall temperatures—a similar pattern to those in the UK, but with an inverse season. The MAB, with its unique bottom temperature dynamics as a result of strong stratification and a sustained cold pool, could be creating an annual reproductive period that appears offset compared to *B. undatum* populations previously examined elsewhere.

The Northeast U.S. Shelf Ecosystem is one of the most rapidly warming marine systems in the world with a sea surface temperature trend (from 2004 to 2012) of increasing ~ 0.2 °C a year [68]. Should this trend continue, these temperatures may fall outside of the thermal tolerance for waved whelk and could have a significant impact on survival and development. Studies have shown that warming conditions can lead to lower recruitment, deleterious physiological effects, suboptimal growth, impacts on development and reduction in survival which can affect fisheries productivity in the future [69–71]. There is growing evidence that both interannual and decadal shifts, either poleward or to deeper water, have caused a redistribution of marine organisms which partly associated with thermal habitat preference and changing temperature [72–76]. When testing the thermal tolerance of *B. undatum* to examine the possible impact of

climate warming on range shift, Smith et al. [19] found that during the early ontogeny, whelk possess thermal resilience to ocean warming; however, it comes at the cost of a reduced number of offspring. Successful development was greatest within their natural developmental temperature range (6–10 °C) but was observed up 18 °C, rates of development increased with temperatures yet the proportion of each egg mass developing successfully decreased [19]. This developmental plasticity with increasing temperature suggests that *B. undatum* may possess thermal flexibility to ocean warming, but this resilience comes with fewer offspring which can negatively impact population size at the southern species distribution, such as the MAB. Should ocean warming continue, *B. undatum* and other cold-water species may be forced to migrate, if possible, seeking deeper and colder waters which are more optimal for physiology [23] which could negatively impact the economic viability of this emerging fishery.

Conclusions

Given the expansive distribution of *B. undatum* and its commercial importance, it is critical to fully understand reproductive development in this species. In the

Mid-Atlantic waters of the U.S. this species is largely unexploited; however, growing interest in developing a commercial fishery lends importance to understanding population dynamics. While reproductive dynamics in this species fluctuate globally, our results suggest early spring as an appropriate time to assess size of sexual maturity in the MAB. Understanding the reproductive cycle and its relationship with bottom water temperature allows forecasting sampling windows and collection of appropriate population data; however, additional studies would allow for an understanding of interannual variability. Moving forward, investigators should focus on *B. undatum* population growth, connectivity, and ecosystem interaction, all of which, are essential to fully understanding this species in the U.S. waters.

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Authors' contributions

This study is part of the Ph.D. of SB, who collected the samples, performed data analyses, interpreted the results, and wrote the manuscript. DM participated in fieldwork, helped with the writing of the manuscript, and supervised SB work during her Ph.D. JHC provided bias-corrected modelling temperature data of bottom water temperatures from the Regional Ocean Modeling System (ROMS) model and offered valuable review of this manuscript. DR hosted SB on sampling trips, assisted with sample collection, and offered valuable review of this manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article. Datasets are available from the corresponding author on request.

Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with animals which require institutional animal care and use committee (IACUC) review or approval. This article does not contain any studies with human participants performed by any of the authors.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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