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Research Article

The Reproductive Biology of the Softshell Clam, *Mya arenaria*, in Ireland, and the Possible Impacts of Climate Variability

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Little is known about the biology of the softshell clam in Europe, despite it being identified as a potential species to culture for food in the future. Monthly samples of the softshell clam, *Mya arenaria*, were collected intertidally from Co. Wexford, Ireland, over a period of sixteen months. The mean weight of sampled individuals was 74 ± 4.9 g and mean length was 8.2 ± 0.2 cm. Histological examination revealed a female-to-male ratio of 1 : 1.15. In 2010, *M. arenaria* at this site matured over the summer months, with both sexes either ripe or spawning by August. A single spawning event was recorded in 2010, completed by November. Two unusually cold winters, followed by a warmer-than-average spring, appear to have affected *M. arenaria* gametogenesis in this area, potentially affecting the time of spawning, fertilisation success, and recruitment of this species. No hermaphrodites were observed in the samples collected, nor were any pathogens observed. Timing of development and spawning is compared with the coasts of eastern North America and with other European coasts.

1. Introduction

The softshell clam, *Mya arenaria,* is widely distributed in coastal and intertidal soft substrates in boreal waters and is often a dominant species in benthic communities [1]. *Mya arenaria* currently occupies a wide geographical range in the northern hemisphere, on the east and west coasts of North America, where it is commercially important for fisheries and aquaculture [2, 3]. In 2008 alone, the National Marine Fisheries Service of USA reported approximately 1.73 million kg of *M. arenaria* harvested, worth in excess of €16 million [4].

The present European distribution of *M. arenaria* ranges from Northern Norway to Portugal, including the Black Sea [5–7], with recent reports of its introduction to the Mediterranean Sea [4]. *Mya arenaria* is rarely collected for food or bait in European waters, but it is an ecologically important food source for fish such as plaice (*Pleuronectes platessa*) and flounder (*Platichtys flesus*) [6], shrimp, sandworms, crabs, and wading birds such as oystercatchers (*Haematopus ostralegus*) and curlew (*Numenius arquata*) [8]. Due to the softshell clams' ability to survive and reproduce in a variety of differing areas such as mud and gravel, it could be an ideal species to culture in European waters in the future. *Mya arenaria* are widespread around all Irish and British coasts [9, 10], but little information is currently available on reproductive biology in these areas.

Previous work in the United States has revealed that the sexes of *M. arenaria* are usually separate, with a sex ratio of 50 : 50 [11, 12]. On eastern North American coasts *M. arenaria* usually begins spawning in May or June and can continue for two to three months. Though most sampled populations of *M. arenaria* spawn once a year [13], there have been examples of two spawning periods occurring, in spring and autumn [12, 14]. In European waters single spawning events have been recorded in the Black Sea [15], the Wadden Sea [16, 17], the west coast of Sweden [18], and on the east coast of Denmark [19], while biannual spawning events were observed in Oslofjord, Norway [20], and the south coast of England [21]. To date, details of the reproductive cycle of *M. arenaria* in the Irish Sea have not been recorded.

Environmental conditions such as water temperature, food availability, and the presence of pollution have been shown to affect gametogenesis and spawning of *M. arenaria* [12, 22], and the increase or decrease in sea surface temperature (SST) can affect the distribution and abundance of some bivalve species [23]. There have been records of spawning at different temperatures across the native range of *M. arenaria*, from 4°C to 25°C [14, 24]. In the Celtic/Biscay shelf, sea water temperatures are predicted to increase between 1.5 and 5°C over the next 100 years [25], with global temperature hypothesized to increase 1.8 to 4°C by the end of the 21st century [26]. However, the rate of change of temperature is highly variable spatially [27], with extreme episodes of unusual temperatures occurring in some areas. Some studies are indicating that annual seawater temperatures may rise in European, including Irish, waters in the future [28, 29], while the winter of 2009-2010 in Ireland was the coldest in 50 years, with December 2010 being the coldest on record [30].

This study was undertaken due to the lack of knowledge of the reproductive biology of *Mya arenaria* in Irish waters, and their potential as a future commercial food species. The potential effects of climate change on this species can be investigated in the short term (the effect of cold winters) and provide a baseline for longer term climate change studies in European waters. The aims of the current paper were to investigate, using histological analysis, the annual reproductive cycle of *M. arenaria* in Ireland under natural conditions, in an area close to the centre of the introduced European range and to determine whether there are differences in the reproductive cycle between that recorded in the Irish Sea and other European sites and whether patterns are similar to those observed in the native range in eastern North America.

2. Materials and Methods

2.1. Study Site. Bannow Bay, Co. Wexford is an estuary on the southeast coast of Ireland, located at the interface between the Celtic and Irish Seas (52°27′ N 006°47′ W). It covers an area of *ca* 1050 ha, is 8 km long and between 1 and 3 km wide [31]. The intertidal habitat consists of mud and sand flats, and approximately 75% of the bay is uncovered at average low tide. The tidal range at Bannow Bay is 0.6 to 3.8 metres. There is oyster cultivation on the eastern side of the estuary, and the surrounding land mainly supports dairy and arable farming.

2.2. Sampling. Softshell clam, *M. arenaria,* specimens ($n \approx 30$) were collected by digging in the lower intertidal (52°13′ 33 N 006°47′51 W) each month from March 2010 to June 2011, generally during the first week of each month in low Spring tides. Specimens were located in the muddy sediment by identifying the characteristic "key-hole" shaped opening left by the siphons. Digging beside these siphon holes allowed for the collection of individuals without breaking the brittle shells. *Mya arenaria* were usually found at a depth of 30 cm, though could be as deep as 40 cm during the colder months. The first 30 siphon holes identified were dug out and the individuals collected below these apertures were used. Most key-hole shaped openings were produced by larger individuals, and very few small *M. arenaria* were encountered while digging. Density estimates were not obtained as the substrate containing *M. arenaria*, consisting of mud and gravel, was not suitable for collecting density data. *Mya arenaria* were transported to a cold room (4°C) within four hours of collection and left overnight for dissection the next morning. Each clam was numbered and the total wet weight (g), shell length from anterior to posterior end (cm), and width from dorsal side to ventral side (cm) of each individual were recorded. No sample could be taken in December 2010 due to severe weather conditions preventing travel to the sampling area.

A continuous temperature monitor, the Stowaway Tidbit Weatherproof & Waterproof Temperature Logger, was deployed underwater 10 m from the *M. arenaria* collection site in Bannow Bay from June 2010. The monitor recorded ambient temperature at 16 minute intervals, and the monthly mean was calculated from this date to the end of the study. Data were obtained from the monitor using an Optic base Station/Coupler Kit and BoxCar Pro 4.3 Starter Kit Software. As temperature for the site was only available from June 2010, air temperature data from January 2008 to July 2011 was also obtained from Met Eireann for Johnston Castle, which is approximately 20 km from Bannow Bay.

2.3. Histological Techniques. The soft tissue of each clam was dissected within 24 hours of collection from the fresh individuals. Two cuts through the body of the animal provided a transverse section of the visceral mass, which contained the gonad, renal gland and digestive tract, and sections of the gill and mantle. The tissue was fixed in Davidson's solution for 48 hours and stored at 4°C. Slides were prepared using standard histological techniques, where tissues were dehydrated in alcohol, cleared in xylene, embedded in paraffin wax, sectioned at 7 μm, and stained with Harris' hematoxylin and eosin before being mounted on clean standard microscope slides [32]. The prepared microscope slides were examined using 10x, 20x, and 40x magnification, to determine sex and stage of reproductive development. Individuals were also screened for the presence of any parasites and abnormal conditions or pathologies.

2.4. Staging of Gonadal Development. Clam reproductive maturity was categorised into five stages using the maturity scale described by Brousseau [12], whereby maturity stages were designated as "indifferent, developing, ripe, spawning, and spent." When more than one developmental stage was present in a single individual, the maturity was scored based on the most prevalent stage.

The indifferent stage of female *Mya arenaria* is identified when the distinctive female inclusions are visible in the follicle cells and extremely small primary oocytes are present in the alveolar membrane. The developing stage is recognised by an increase in the number and the size of oocytes. A central lumen is present in each follicle, into which protrude the stalked oocytes. In the ripe female there are many mature, spherical oocytes which appear to be free within the follicular lumen. In the spawned stage, the mature oocytes are gradually discharged. Emptying follicles and the cessation of oogenesis in all follicles is characteristic of this stage. In the spent stage, unspent oocytes in the early phases of cytolysis are present. These appear in the lumen as large, darkly staining bodies with obscure nuclei. Follicle cells begin to reinvade the follicles from the basal membrane.

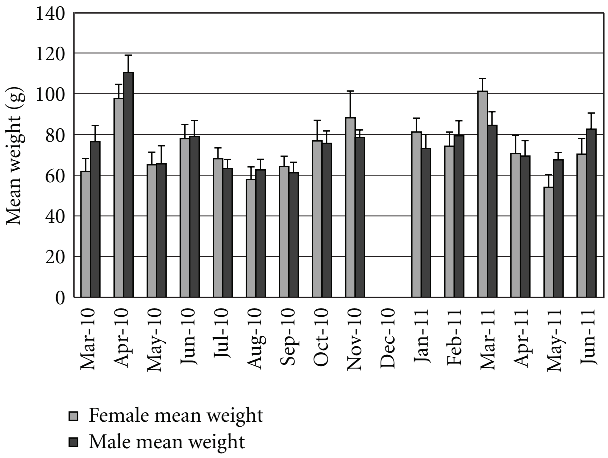
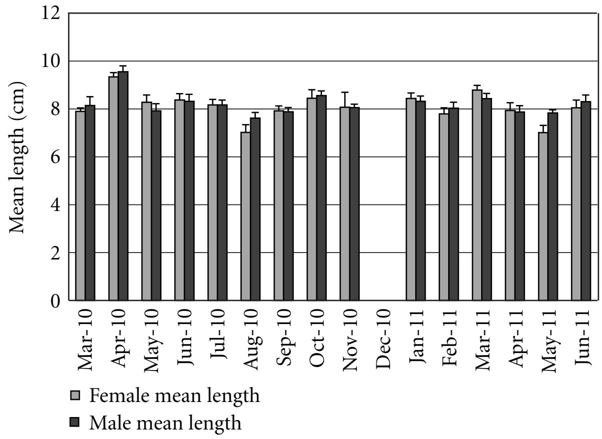


Figure 1: Mean weight (±S.D.) of female and male *Mya arenaria* sampled at Bannow Bay from March 2010 to June 2011.



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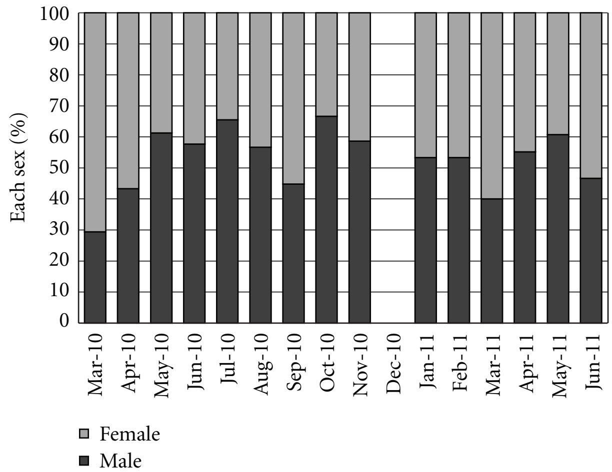

Figure 3: Sex ratio of *Mya arenaria* sampled at Bannow Bay over study period.

During the indifferent stage of male *Mya arenaria* the follicles contain the aberrant forms, multinucleated non-pycnotic cysts and pycnotic cells. The basal membrane and follicle cells are the dominant structural elements, with a few primary spermatocytes or spermatogonia visible at the periphery of the lumen. In the developing stage, the maturation and proliferation of the spermatocytes takes place. In the ripe male clam the follicle is filled with dense radiating bands of spermatozoa, the tails of which project into the central lumen. In the spawned stage the follicle is characterised by fewer spermatozoa than the ripe clam. A few spermatozoa remain in the radiating bands but the rows of follicle cells gradually increase to replace the spawned spermatozoa. In the spent male, the follicles are almost completely filled with follicle cells and the reduced lumen contains a few sex cells [12].

3. Results

3.1. Measurements. Of the 432 individuals collected over 16 months from March 2010 to June 2011, the average weight of all individuals was 74 g ± 4.9 g (Figure 1) with the lightest individual collected weighing 3.1 g, and the heaviest 200 g. Over the months sampled, mean monthly values ranged from 60.5 g ± 4 g to 103 g ± 5.4 g. The average length of all *M. arenaria* collected was 8.2 cm ± 0.2 cm (Figure 2). Individuals collected ranged from 2.6 to 11.6 cm in length, with the mean monthly lengths ranging from 7.4 cm ± 0.1 cm to 9.4 cm ± 0.1 cm. Due to the nature of collection, only softshell clams with visible siphon holes were collected. Very few spat were observed at this area while sampling. All lengths and weights of *Mya arenaria* were observed in various stages of gametogenesis apart from males under 5.9 cm (Figures 5, 6, 8, and 9).

The average weight and length of female individuals were 74 g ± 3.5 g and 8.1 cm ± 0.2 cm, respectively, while the average weights and lengths of male individuals were 75 g ± 3.2 g and 8.2 cm ± 0.1 cm. On average, female individuals were both lighter and shorter than male *M. arenaria*, though this was not statistically significant when using a t-test ($t = 0.53$, $df = 28$, $P > 0.1$). Only measurements of undamaged shells were included in the results.

3.2. Histology

3.2.1. Sex Ratio. Of the softshell clams examined, 199 (46%) were female, 229 (53%) were male, and four (1%) were immature or the sex could not be determined (Figure 3). A Chi-squared (χ^2) was used to analyse sex ratios. The overall female:male sex ratio of 1 : 1.15 did not show a significant divergence from a 50 : 50 ratio ($\chi^2 = 2.57$, $df = 1$, $P > 0.05$). Within months, it was revealed that there was no statistically significant divergence from the 50 : 50 ratio of sexes ($\chi^2 = 0.133$, $df = 1$, $P > 0.05$ to $\chi^2 = 2.882$, $df = 1$, $P > 0.05$), though the closest to showing a significant divergence was the October 2010 sample, with 10 female and 20 male *M. arenaria* ($\chi^2 = 3.333$, $df = 1$, $P > 0.05$).

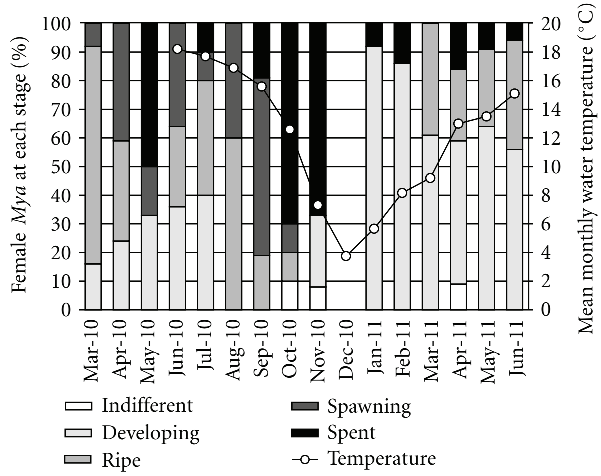

Figure 4: Stages of gametogenesis observed in female clams over the study period.

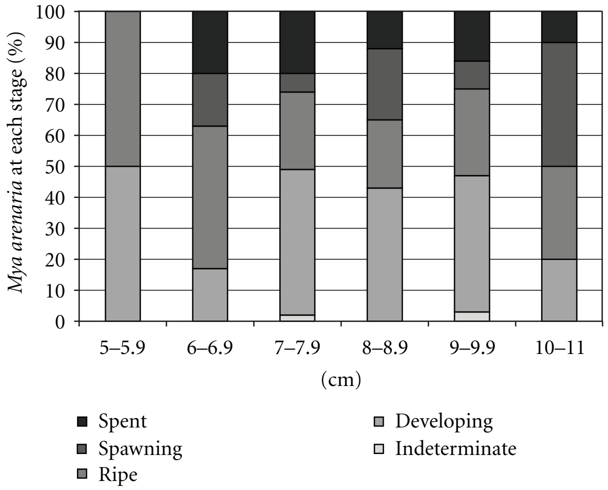

Figure 5: Relationship between female *Mya arenaria* length and stage of gametogenesis.

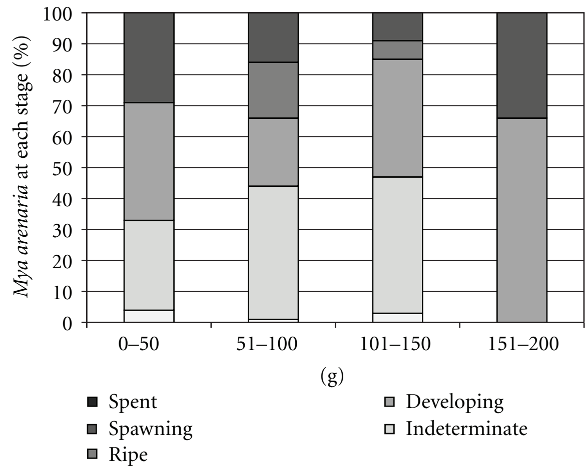

Figure 6: Relationship between female *Mya arenaria* weight and stage of gametogenesis.

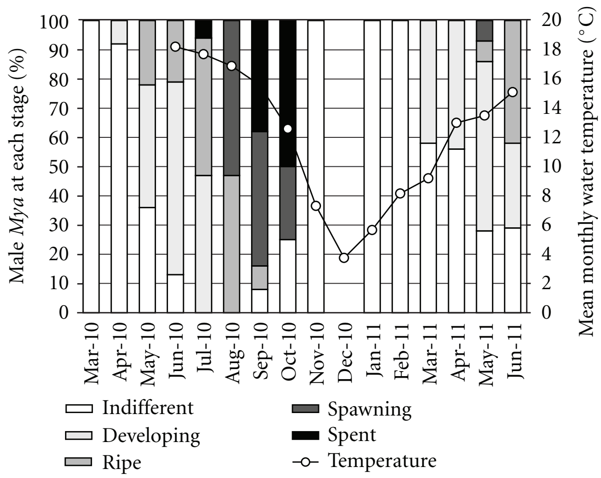

Figure 7: Stages of gametogenesis observed in male clams over the study period.

3.2.2. Sexual Cycle

Female. During the course of the study, all five of the stages of gametogenesis described by Brousseau [12] were observed. In 2010, the sampled female *M. arenaria* showed a less defined cycle than the male individuals, with development, ripening and spawning taking place from March to October (Figure 4). Fifty percent of individuals were spent in May 2010, following a large number (76%) ripe in March, and 41% spawning in April. The percentage of females developing rose from March to July 2010, with all individuals either ripe or spawning by August 2010 (Figure 4). The majority of spawning individuals were present in September (62%), with all spawning completed by November 2010. October and November samples contained the highest percentage of spent females, at 70% and 67%, respectively, with some indifferent individuals also present (10%).

In 2011 most females were developing over the winter months of January and February (~90%), with some spent individuals present (~10%). Female *M. arenaria* began ripening in March 2011, similar to 2010, but at a much lower percentage (39%). The majority of individuals (~60%) were developing from March to June 2011, with some at the ripe stage (~30%) but none were spawning, in contrast to the same period in 2010. There were spent females present in April, May, and June of 2011, and individuals of indifferent stage present in April (9%).

Male. In the collected samples, all male *M. arenaria* were indifferent in March 2010 (100%), which steadily decreased until June (13%) (Figure 7). Development of the male gonads began to take place in April (8%) and spawning was observed for the final time in October 2010. The number of developing individuals rose to 66% in June and 47% in July 2010. Ripe individuals were first present in May (22%), and by August all males were either ripe (47%) or spawning

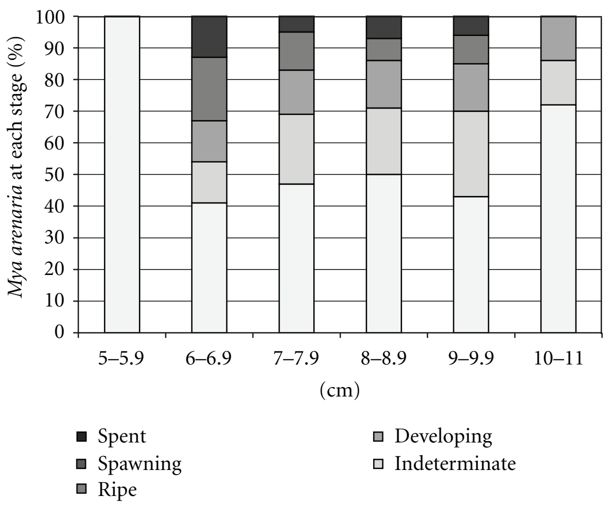

Figure 8: Relationship between male *Mya arenaria* length and stage of gametogenesis.

(53%). Spawning was completed by November 2010, with the majority of individuals spent in September (38%) and October (50%) samples. All males collected from November 2010 to February 2011 were in the resting indifferent stage, with development beginning earlier in March 2011, as compared to the previous year, when developing individuals were not detected until April. Ripe individuals were present in May 2011, similar to the previous year, though some spawning individuals were present in this month, compared to a lack of spawning individuals until August in 2010. There were a higher number of indifferent individuals present in June 2011 (29%) as opposed to June 2010 (13%).

The smallest reproducing female and males sampled were 5.1 cm (17.8 g) and 6.1 cm (29.0 g), respectively. The only immature clam collected was 2.6 cm in length, and 3.1 g in weight.

3.2.3. Disease. Screening of the histological sections of the visceral mass, gill, and mantle of sampled *Mya arenaria* revealed no parasites or pathological indications of disease, such as hematopoietic neoplasia, in any of the individuals sampled in Bannow Bay over the study period.

Table 1: The mean, minimum, and maximum monthly water temperatures and degree days per month, recorded by a continuous temperature monitor in Bannow Bay from June 2010 to June 2011.

Month	Mean temperature	Minimum temperature	Maximum temperature	Degree days/month
Jun-10	18.21	10.34	27.97	546.3
Jul-10	17.7	13.51	27.31	548.7
Aug-10	16.89	9.48	26.32	523.59
Sep-10	15.59	8.62	24.06	467.7
Oct-10	12.59	5.73	18.21	390.29
Nov-10	7.31	−1.35	16.43	219.3
Dec-10	3.75	−1.66	8.33	116.25
Jan-11	5.66	−0.44	9.48	175.46
Feb-11	8.16	4.6	11.8	228.48
Mar-11	9.2	4.9	16	285.2
Apr-11	13	8	22.2	403
May-11	13.5	8.6	20.6	418.5
Jun-11	15.1	10.3	26.4	453

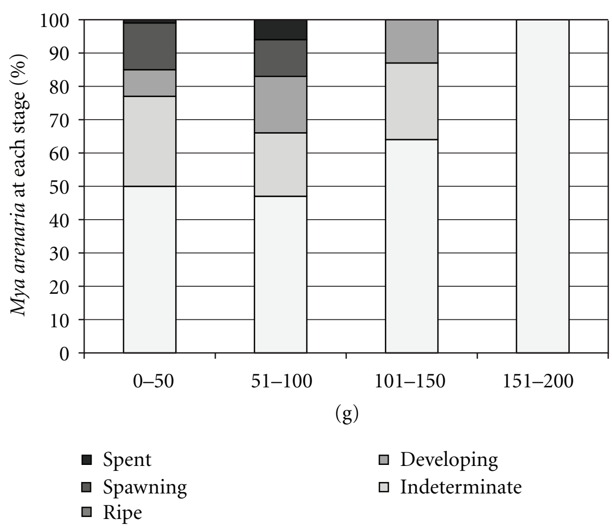

Figure 9: Relationship between male *Mya arenaria* weight and stage of gametogenesis.

3.3. Temperature. The mean monthly temperature recorded by the Stowaway Tidbit Temperature Logger, underwater, at Bannow Bay was highest in June 2010 at 18°C and decreased each subsequent month to 3°C in December 2010 (Table 1). The highest recorded temperature points in 2010 were 27.97°C on June 26th and 27.31°C on July 12th, and the lowest was −1.66°C on December 24th and 25th. The lowest water temperature recorded in 2011 was recorded at −0.44°C on 29th January. Mean monthly water temperatures rose from 5.66°C in January 2011 to 15.1°C in June, peaking at 26.4°C on 3rd June 2011 (Table 1).

Air temperature readings at Johnstown Castle from January 2008 to July 2011 showed a decrease in the monthly minimum temperatures recorded during the winter months, from 4.4°C in January 2008 to 2.3°C in January 2009, and −0.15°C in December 2010. The mean monthly winter temperatures also showed a decrease during this time, from 6.9°C in January 2008 to 4.9°C in January 2009, and 2.2°C in December 2010 (Figure 10).

In 2008 the mean monthly air temperatures at Johnstown Castle rose from 6.9°C and 6.5°C in January and February, respectively, to 15.4°C in July and August, peaking at 18.5°C in July 2008. Mean monthly air temperatures fell to 4.9°C in January 2009, and increased to 15.2°C in August, with the maximum temperature of 2009 recorded at 18°C in August. In 2010 the mean monthly air temperature of 3.5°C was recorded in January, rising to 16.5°C in July, and peaking at 19.2°C. In 2011 the mean monthly air temperatures at Johnstown Castle were 1.7°C warmer, on average, from January to June, than the same months in 2010. The

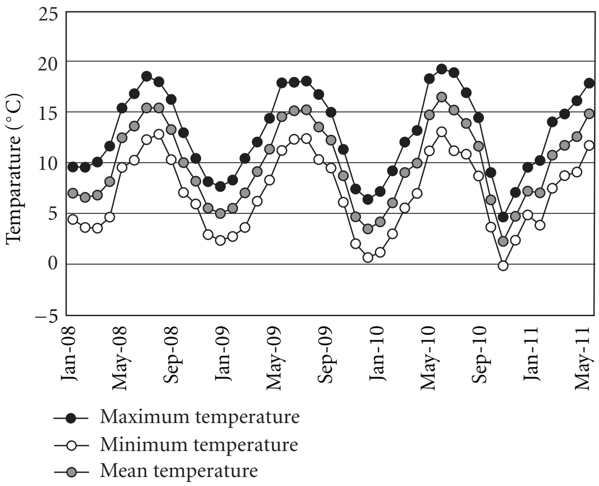

Figure 10: Air temperature reading for Johnstown Castle, January 2008 to July 2011, showing mean, maximum, and minimum temperature for each month.

maximum temperature recorded in 2011 up to the end of the field trial was 17.8°C in July (Figure 10).

4. Discussion

Of the sampled *Mya arenaria*, the average length of all individuals was 8.17 ± 0.18 cm, with the shortest measuring 2.6 cm and the longest 11.5 cm. Previous studies in North American [33] and European [20] waters have revealed maximum lengths of individuals between 10 and 17 cm [34, 35]. Past work has revealed that softshell clams smaller than 2 cm in length are usually immature, with indistinguishable gonads [12, 24]. First reproduction usually occurs at a size of 2–5 cm in length [6, 36] which, depending on environmental conditions, can mean the individual is anything from 1 to 4 years of age [6]. Newell and Hidu [11] suggested that the size of the individual is more important than age when it comes to the initiation of a spawning event. Data collected in the present study correlate with this, in that the smallest reproducing female and male were 5.1 and 6.1 cm, respectively. The sex of the smallest clam sampled (2.6 cm) was not discernible as the clam was immature.

The overall female:male sex ratio of 1 : 1.15 in the present study did not show a significant divergence from the 50 : 50 ratio previously described in Denmark [19] and Oslofjord, Norway [20], and on north American coasts in Massachusetts and Connecticut [12, 24], in Maryland [37], and in Washington [32]. There was no evidence of hermaphroditism or protandry in the present study, in keeping with recordings of low incidences of hermaphroditism in past studies [19, 24, 38]. All stages of gametogenic development of *M. arenaria* previously described by Brousseau [12] were observed over the period of sampling. *Mya arenaria* matured over the summer months of 2010, with both sexes either ripe or spawning by August, similar in timing to the spawning period recorded in New England [13], in Massachusetts, USA [39, 40], in Denmark [41], and in the Dutch Wadden Sea [17].

Previous studies of *M. arenaria* in both North America and continental Europe have shown that softshell clams can spawn either once or twice during one year, with the majority of spawning taking place during June, July, and August [6, 12, 35]. The data from the present study demonstrated that male *Mya arenaria* of Bannow Bay had one spawning period at the end of summer 2010. These data are in keeping with previous observations in the north east Atlantic in the Black Sea [15], on the west coast of Sweden [18], on the east coast of Denmark [19], and in the Wadden Sea [16, 17]. The female *M. arenaria* of Bannow Bay show a less tightly defined spawning period than the males, with spawning individuals recorded from March to October, and peaks in spawning taking place in April, June, and August/September 2010. However, all female individuals were either ripe or spawning in August 2010, with a large percentage in these stages in September, and most individuals spent in October and November. Based on the data collected at Bannow Bay, Ireland, and previous research across the North Atlantic, it would seem that the reproductive cycle of *Mya arenaria* is affected by more than just latitudinal distribution of individuals [12, 42].

In eastern Atlantic waters the majority of spawning periods have been recorded in the summer months of May and June (Table 2). Where *M. arenaria* were recorded as spawning biannually, in Oslofjord, Norway, and S. E. England, the second spawning took place in or around September. In 2010, the present study revealed spawning at a similar time of March to July for female softshell clams, and August to October for both female and male clams (Table 3). The less tightly defined spawning period of female *M. arenaria* compared to male individuals has not been recorded previously in European waters, and was not repeated in 2011, when no spawning had taken place in female *M. arenaria* by June, when the field study concluded.

Environmental conditions including food availability and temperature have been shown to affect gametogenesis and spawning of *M. arenaria* [24]. It is currently unknown whether a "critical" water temperature is more important at a certain point in gonadal development, to progress maturation, or to begin the spawning event itself [24, 43], though Belding [40] concluded that the degree of maturation of *M. arenaria* is dependent on the number of days the water temperature remains in the desired range for gamete formation. It is generally considered that spawning of *M. arenaria* begins when water temperature rises to 10°C [4, 44], though this can depend on the area, as a spawning peak was recorded at 4–6°C in Massachusetts [24] while Belding [40] reported a spawning peak at 22°C in the same area. When *M. arenaria* are forced to spawn in culture, water temperature needs to reach 22 to 24°C before spawning begins [45]. The male *M. arenaria* of this study began spawning in August 2010, which had an average daily water temperature of 16.9°C. However, the two preceding months of June and July had average daily water temperatures of 18.2 and 17.7°C, respectively, with 22°C and 24°C first recorded in late May 2010. The majority of spawning of female *M. arenaria* also took place in August and September 2010, with a small group spawning

Table 2: The timing of spawning seasons, by latitude, of European *Mya arenaria* reported in the literature.

Area	Latitude	Tidal level	Spawning	Month	Authors
Oslofjord, Norway	59°91′N 10°37′ E	Intertidal	Biannual	June and September	Winther and Gray, 1985 [20]
West coast of Sweden	57°37′ N 35°51′ E	Intertidal	Annual	June/July	Möller and Rosenberg, 1983 [18]
Wadden Sea	55°00′ N 6°7′ W	Intertidal	Annual	May/June	Günther, 1992 [16]
Dutch Wadden Sea	55°00′ N 6°7′ W	Subtidal and Intertidal	Annual	July–November	Cardoso et al., 2009 [17]
Denmark	55°55′ N 12°0′ E	Subtidal	Annual	May/June	Munch-Petersen, 1973 [19]
S.E. Ireland	52°13′ N 06°47′ W	Intertidal	Annual	August/September	Current paper
S.E. England	50°37′ N 4°25′ W	Intertidal	Biannual	March and late Summer	Warwick and Price, 1975 [21]
Black Sea	42°30′ N 35°00′ E	N/A	Annual	Late May	Began, 1979 [15]

Table 3: The number of female and male *Mya arenaria* individuals present each month, in the five stages of gametogenesis.

	Indeterminate		Developing		Ripe		Spawning		Spent	
	F	M	F	M	F	M	F	M	F	M
Mar-10		5	2		9		1			
Apr-10		12	4	1	6		7			
May-10		7	4	8		4	2		6	
Jun-10		2	4	10	3	4	4			
Jul-10			4	9	4	9	1		1	1
Aug-10					9	8	4	9		
Sep-10		1			3	1	10	6	3	5
Oct-10	1	5			1		1	5	7	10
Nov-10	1	17	3						8	
Jan-11		16	13						1	
Feb-11		16	12						2	
Mar-11		7	11	5	7					
Apr-11	1	9	6	7	3				2	
May-11		5	7	10	3	1		1	1	
Jun-11		4	9	4	6	6			1	

in May. In 2011, water temperatures first rose to 10°C in the last week of February, and male development began in early March. Female development was in progress during the winter months, but ripe individuals were first detected in March 2011. The critical spawning temperature of 22°C was first recorded in 2011 on 2nd June. The critical upper temperature of 28°C [4, 6] was never reached in the waters of Bannow Bay in 2010, though a peak of 27°C was recorded in July 2010 for a short period of time.

The winters of 2009/2010 and 2010/2011 were exceptionally cold in Ireland, with air temperatures decreasing to −17°C in Northern areas in January 2011 [30]. Air temperature data, collected at Johnstown Castle (20 km from Bannow Bay) for the period January 2008 to July 2011, reveal that the lowest recorded temperatures dropped each winter from 3°C in March 2008, to 2.34°C in January 2009, 0.65°C in January 2011, and to −0.2°C in December 2010 (Figure 10). Unusually cold intervals similar to this have lead to mass mortalities of bivalve species, and contraction of species range in the past [46]. A disparity in gametogenic development timing between the sexes may be a critical factor reducing recruitment in the species, as it results in less overlap of months where both sexes are spawning simultaneously. In 2010, female and male *M. arenaria* of Bannow Bay were spawning synchronously in the months of August, September, and October, while the gametes released by female individuals from March to July 2010 would have remained unfertilised.

Following the period of cold winters, air temperature readings from Johnstown Castle reveal monthly mean temperatures were greater in 2011 compared to 2010, from January to May (Figure 10). In the present study, the effects of two unusually cold winters, followed by a warmer than average spring, would seem to have affected the timing of development in *M. arenaria* individuals in 2011, compared to 2010. In the males of the species, the variable temperatures appear to have advanced the progression of gonad development, with 42 and 44% of males developing in March and April 2011, though none or few individuals were developing in the same months in the previous year. Ripe males were first recorded in May of each year, with spawning taking place in 2010 in August, though spawning was observed as early as May in 2011. In contrast, the development of female *M. arenaria* would seem to have been inhibited in 2011, with the majority of individuals still developing in March, compared to the majority of females already being ripe in March 2010. Also, though spawning individuals were present from March in 2010, by June 2011 only ripe individuals were still present in the sample, with many (56%) still developing. Overall, the cold winters followed by a warmer than average spring appeared to have accelerated gametogenesis in males in 2011, compared to 2010, and had the opposite effect in female *Mya arenaria*. This asynchronous spawning may be a critical factor reducing recruitment in the species if climatic variability continues and male and female *Mya arenaria* continue to spawn at different times.

No disease or pathogens have been observed in the Irish Sea *M. arenaria*, despite the fact that other bivalves such as *Cerastoderma edule* collected monthly in the same area have revealed a heavy prevalence of trematodes, neoplasia and *Nematopsis* spp. (Morgan, pers comm). To date, only low levels of disease or pathogens has been reported in Mya arenaria on European shores [47], despite a number of diseases and parasites being present in the *M. arenaria* populations of North America, particularly hematopoietic neoplasia, which was not observed in this study [48–53]. This could be due to a lower density of these animals, than in the intensively cultured areas of North America [54].

In summary, the *Mya arenaria* of Bannow Bay of south east Ireland matured over the summer months of 2010, with both sexes either ripe or spawning by August in a single spawning episode, and all spawning being completed by November. Gametogenic development of female *M. arenaria* would seem to be inhibited in 2011, compared to 2010, while development of male clams has been advanced. Progression of developmental stages suggests that a discrepancy between the sexes spawning events could occur, affecting recruitment in Bannow Bay *M. arenaria*.

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