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The spawning of king scallop, *Pecten maximus*, in Welsh waters – A preliminary study

PRIFYSGOL BANGOR UNIVERSITY

Harriet Salomonsen, Gwladys Lambert, Lee G. Murray & Michel J. Kaiser

School of Ocean Sciences, College of Natural Sciences, Bangor University

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INTRODUCTION

The *Pecten maximus* fishery

Over 90% of the Welsh fishing fleet consists of vessels under 10m (MMO 2011). They are generally not nomadic and therefore rely heavily on local stocks. *Pecten maximus* (King scallop) are the most valuable species landed in Wales with a value of £7.6 million landed in 2012 (MMO 2013). The sustainable management of the scallop stocks is vital to ensure the future of this important industry for the Welsh economy. Protecting the spawning stock biomass as well as settlement habitats is essential to improve productivity and conserve scallop stocks (Beukers-Stewart *et al.* 2005). Knowledge of reproduction and spawning is key to understanding the recruitment and population dynamics of marine species. However, this knowledge is limited for the scallop stocks in Welsh waters.

Reproduction of *Pecten maximus*

P. maximus are hermaphrodite (i.e. containing both sperm and eggs) broadcast spawners (i.e. releasing gametes into the water column). At two years old they are reproductively mature. Gametogenesis (i.e. the formation of reproductive products) occurs regularly though out an adult scallop's life and involves various stages of development (Barber & Blake 2006). These produce macroscopic changes to the gonad which allow the maturity stage to be determined visually with relative certainty (Mason 1958). The different stages are: 0- immature (virgin), 1- developing (virgin), 2 – differentiated (obvious male and female parts), 3 – recovering (after spawning), 4 – filling, 5 – half full 6 – full and 7 - spent. The timing and duration of the reproductive cycle is affected by both internal (i.e. genetic) and external (i.e. environmental) factors. When spawning occurs the sperm and eggs are released sequentially into the water column usually within hours of each other. This does not occur in a particular order (Mason 1958). Here fertilisation takes place around 24 hours after spawning (Pennec *et al.* 2003) Mason (1958) observed *P. maximus* spawning on several occasions. The gametes are passed out first into the mantle cavity, and then emitted in a cloud through the exhalent opening in the shell. The eggs settle downwards and the sperm disperse into the water column. Releasing sperm and eggs separately, combined with the

different behaviour of the gametes in the water column, increases the chance that these sessile organisms breed with other individuals rather than self-fertilising. This is important since self-fertilisation has been shown to decrease the number of larvae produced, increase larval mortality, and reduce growth rates (Beaumont & Budd, 1983). The resulting larvae remain in the water column for 23-41 days before settling on the seabed (Cragg, 1980). As a result they are affected by the wind and tide driven currents that can transport them several kilometres from adult beds (e.g. Wilson, 1987) or cause them to remain near the spawning site (e.g. Heipel *et al.* 1998). Using a model based on the hydrodynamics of the Irish Sea and the behavioural ecology of *P. maximus* larvae, we have begun to investigate the potential for dispersal of scallop larvae from adult beds. The model relies on a set of important input parameters such as spawning time and location and fecundity (i.e. number of eggs produced by an individual).

Spawning times

The majority of *P. maximus* populations in Europe are documented to have continuous low level spawning throughout spring and summer (April – September) with filled gonads found throughout the year (Barber and Blake 2006). This is interspersed with peaks of synchronous spawning episodes to ensure successful fertilisation. The frequency, timing and duration of these events varies by geographic region, sometimes at very small spatial scales. Past studies have shown that in Holyhead spawning had two peaks one in spring and one early summer, followed by rapid recovery with the gonads remaining full for the rest of the year (Baird, 1966). In Ireland the first spawning event was a month later (May) in Kilkieran Bay in the north than in Birterbury Bay (April) in the south (Wilson, 1987). In the Isle of Man significant spatial variation in maturation rates was found (Lo, 2009). In Norway a distinct difference was found between scallops from Northern locations and those from the South (Magnesen & Christophersen, 2008). In the north scallops rebuilt gonads directly after spawning (as is common for most studied populations) whereas in the south scallops rebuilt gonads the following spring. This has only been recorded for one other population of *P. maximus*, in St Brieuc Bay in France (Paulet *et al.*1988).

There is much debate whether spawning times are linked solely to environmental factors or also genetic differences between stocks. There have been several studies such

as those in the Bay of Saint-Brieuc that have tried to elucidate this (e.g.Mackie & Ansell, 1993; Cochard & Devauchelle, 1993;Wilding *et al.* 1997). A restocking programme in this bay in France provided an opportunity to look at differences between local stocks and those transplanted here under the same environmental conditions. The Bay of Saint-Brieuc scallops' reproductive cycle was very different to those in the Bay of Brest, which are geographically close, and to the scallops transplanted from Scotland. The failure of scallops to develop the same reproductive cycle under the same environmental conditions implied genetics may have a major role in determining spawning times (Mackie & Ansell, 1993). However, there were also differences seen between the transplanted Scottish scallops in relation to their native stocks. This suggests environmental factors must have had some impact. Furthermore St Brieuc scallops transplanted to Quiberon Bay, France, synchronised their gonad development with the local population (Latrouite & Claude, 1979). The reproductive cycle can be viewed as a genetically controlled response to the environment (Sastry, 1979).

Welsh stocks

Studies of *P. maximus* in the Irish Sea have collected data on reproduction at single points in time, allowing only for spatial comparisons across Wales not temporal (e.g. Lo, 2009; Lambert, *et al.* 2014). To determine when spawning events occur in Welsh waters, scallop gonad condition must be monitored on a regular basis and over a continuous period of time to try to time the transition of the gonad status between stage 6 and 7, i.e. from full of reproductive products to empty. The aim of this study was to develop a method of collecting this data, with a view to examining spatial and temporal variation in spawning times and fecundity, and the environmental and genetic drivers behind this.

Determining spawning patterns will serve to enhance our connectivity model. Results from our genetic studies suggest there is connectivity between scallop beds over large spatial scales as well as beds with low connectivity. It is these more isolated populations that are at risk of over exploitation if the stocks were managed as a single unit as they have limited recruitment from neighbouring populations. Further genetic samples were collected during this study to build on these investigations of genetic and oceanographic connectivity.

The closed season for King scallop fishing in Wales runs from the 1st May until the 31st October and as a result obtaining regular samples from the scallop fishing fleet in summer is not feasible. Therefore this study also assessed the feasibility of using a single dredge towed from a whelk/pot fishing vessel as a means of obtaining samples.

There were three aims of this study:

1. Design a methodology for summer sampling,
2. Investigate spawning times,
3. Collect genetic samples to add to our studies on stock connectivity.

METHODS

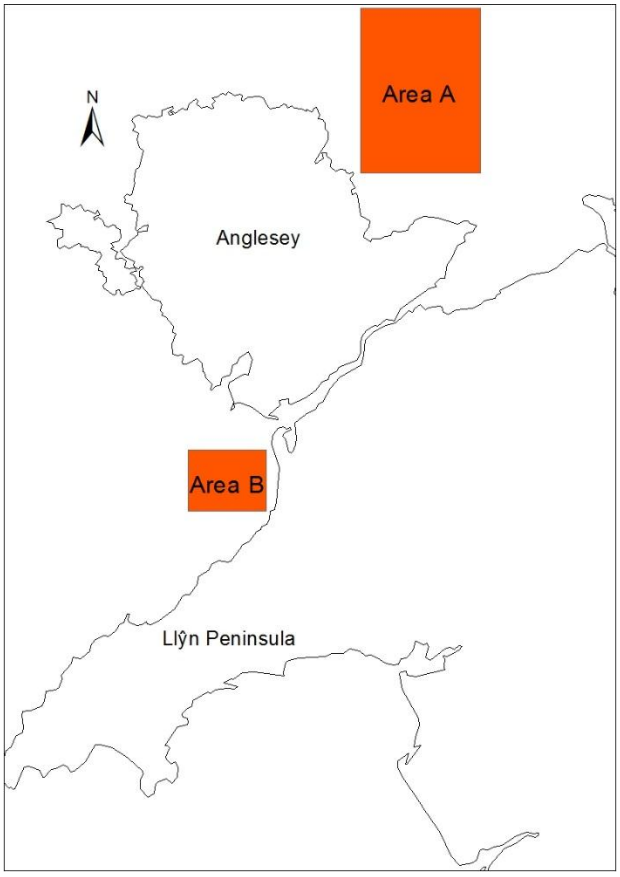

Figure 1: Map of sampling locations

Samples of scallops were collected by fishermen from May until the start of November 2014 to cover the known spawning period for *P. maximus*. Two sampling locations were chosen, one off the North coast of Anglesey (site A) and the other in Caernarfon Bay (site B) (Figure 1). A sample size of between 20 and 50 scallops of 95mm upwards per week per location was requested. These samples were collected by fishermen as bycatch from their summer fishing or by using a single dredge towed behind their vessel.

Site A scallop samples were collected from Holyhead and stored on ice, allowing them to be processed fresh. Site B scallops were frozen and then collected and processed at a later date.

Laboratory Protocol

The following laboratory protocol was established to ensure consistency with the scallop processing.

1. Scallops were washed to remove silt, sand and pebbles caught inside. The outside of the shells were cleaned to remove any large epifauna (such as barnacles and hydroids) growing on them that could have affected the total weight.
2. Scallops were drained and blotted with blue roll to remove excess water. The total wet weight was then recorded.
3. Scallops were shucked and the individual wet weight of the adductor muscle, gonad and all remaining soft tissues recorded. The soft tissues included the sinuous part attached to the adductor muscle. The weight of the gonad was used to calculate the gonad index (GI) (see below).
4. The height and width of the scallop shell was recorded and they were aged using the growth rings on the flat shell (Figure 2). The flat shell was labelled and kept for future reference.

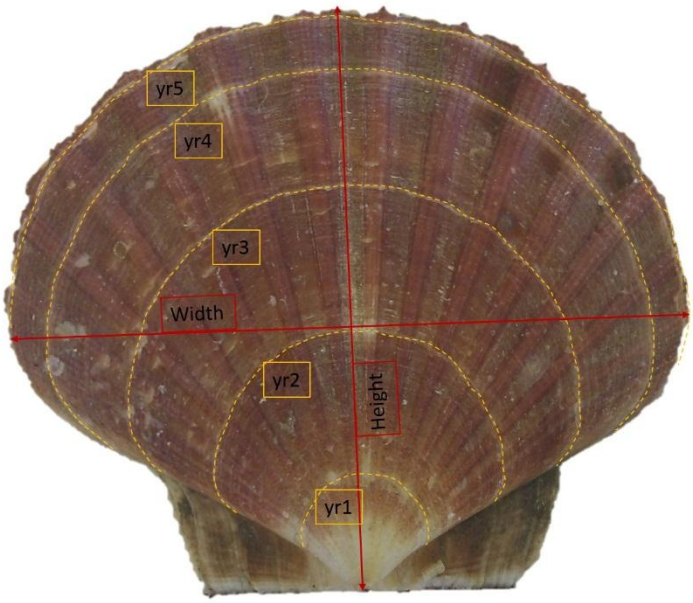

Figure 2: Measuring and ageing using the flat shell. The yellow lines show the annual growth rings counted to find the age of the scallop. The red lines show where the width and height measurements were taken.

5. A 5mm sample of the mantle tissue was taken from each scallop. This was placed in a 2 ml tube with 70% Ethanol (ETOH) and stored for genetic analysis.
6. The gonads were photographed and assigned a maturity stage, as described in Mason (1958).
7. The gonads were split such that the testes (white tissue) and ovary (orange tissue) could be weighed separately. These weights were necessary for future fecundity analysis. The male part was weighed with the foot removed.
8. The mature gonads (stage 5/6) were kept for further processing for histological and egg quality analysis (see below).

Gonad index

The gonad index was calculated using the following equation. This is way of measuring sexual maturity, by calculating the gonad mass as a proportion of the total body mass. This was calculated using wet weights as previous research has shown there to be no significant difference in the gonad index derived from either wet or dry weight (Lo, 2009).

$$\text{Gonad index} = \frac{\text{Fresh weight of gonad}}{\text{Shell weight}} \times 100$$

Processing for histology and egg quality

Samples of the ovary were taken to look at the fecundity and egg quality of scallops in different age/size categories. Since it was unknown how homogenous the ovary was it was split into three roughly equal sections. This allowed for samples to be taken from the tip, the middle, and the end of the ovary adjoining the testes thereby accounting for any variation in egg quality or development within the ovary. Due to the curved shape of the gonad the incisions were made radiating from a central dorsal point. This was the point where the ovary and testes join.

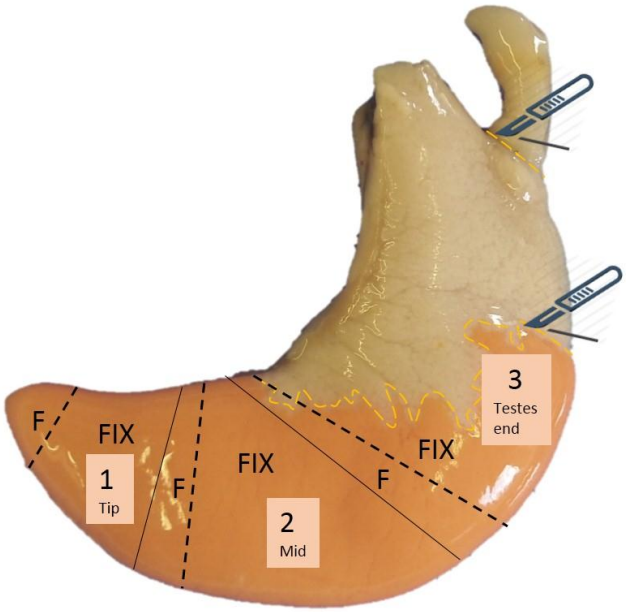

Figure 3: Where the sections of the gonad were cut. F – Freeze; FIX – to be fixed in Davidson's solution.

Each of these three sections (tip, mid and testes end) were then further divided (Figure 3). A small (approx. 5mm wide) slice was cut from each piece and placed in a labelled 1 ml Eppendorf tube (Figure 3 section labelled 'F'). These were stored in a -20°C freezer for future elemental composition analysis. This uses a CHN analyser to determine the Carbon, Hydrogen and Nitrogen content of the tissue which is needed for assessing quality.

The remaining tissue (Figure 3 section labelled 'Fix') from each section was placed in a labelled histology macro cassette. They were fixed for 48 h at 4°C in Davidson's solution before being rinsed in distilled water and then stored at 4°C in 70% ETOH for future histological analysis. By examining thin slices of the gonad it will be possible to look at egg size, density and development and estimate fecundity.

RESULTS

A total of 132 scallops were obtained from fishers in Caernarfon Bay and 588 from a fisher off the north coast of Anglesey between 8th May and 3rd November 2014. These had shell widths from 95 to 194 mm and were aged 2 to 11 years old.

Sampling methodology

Scallops from Area A were collected using queen scallop dredges as bycatch from a fisherman's queen scallop fishing activity. Scallops from Area B were collected by two fishermen using different methods. One fishermen collected scallops as bycatch from otter trawling, the other used a single scallop dredge towed behind his vessel during his whelk fishing activity.

Weekly sampling using queen scallop dredges proved to be the most successful way of obtaining regular samples of an appropriate size. Apart from three occasions, samples of over 20 scallops were obtained weekly from the fisherman in Area A.

In Area B samples were obtained for 3 weeks in both May and June and 1 week in July and August but sample sizes were only over 20 on two occasions. The sizes of the samples collected as bycatch from fishing using an otter trawl were small (under 10 scallops in 5 out of 6 samples). Although used weekly the single dredge only caught effectively (i.e. over 20 scallops) once each month. Feedback from the fisherman suggested the dredge was too light to fish in anything but the calmest conditions with low tidal flow.

Area A – North of Anglesey

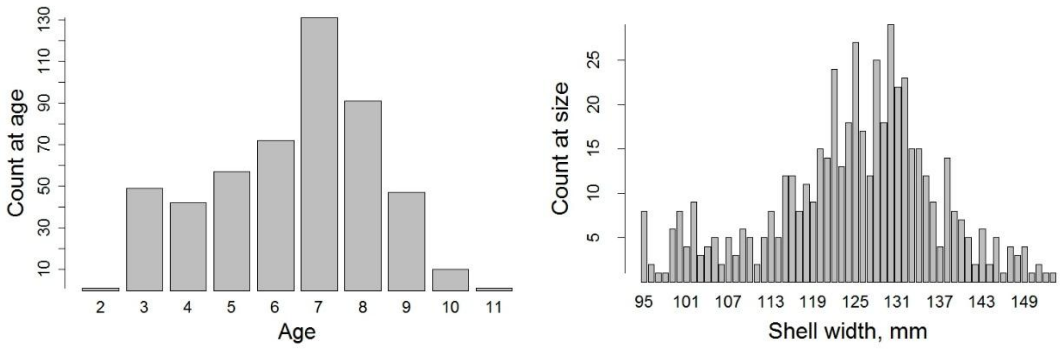

Figure 4: (left) the number of scallop in each age class in area A; (right) the number of scallops found at each shell width in area A.

Scallops from site A were collected weekly from 8th May until 3rd November. There was a gap in July/August (10th July-4th August) when there was no fishing as the boat was undergoing its annual maintenance. These samples were collected as bycatch by a fisherman using queen scallop dredges. Scallops in the age group 6-8 were the most frequently found in area A. The largest scallop collected was 152mm (shell width) and aged 11, and the youngest was aged 2 and 101mm (Figure 4).

Spawning times

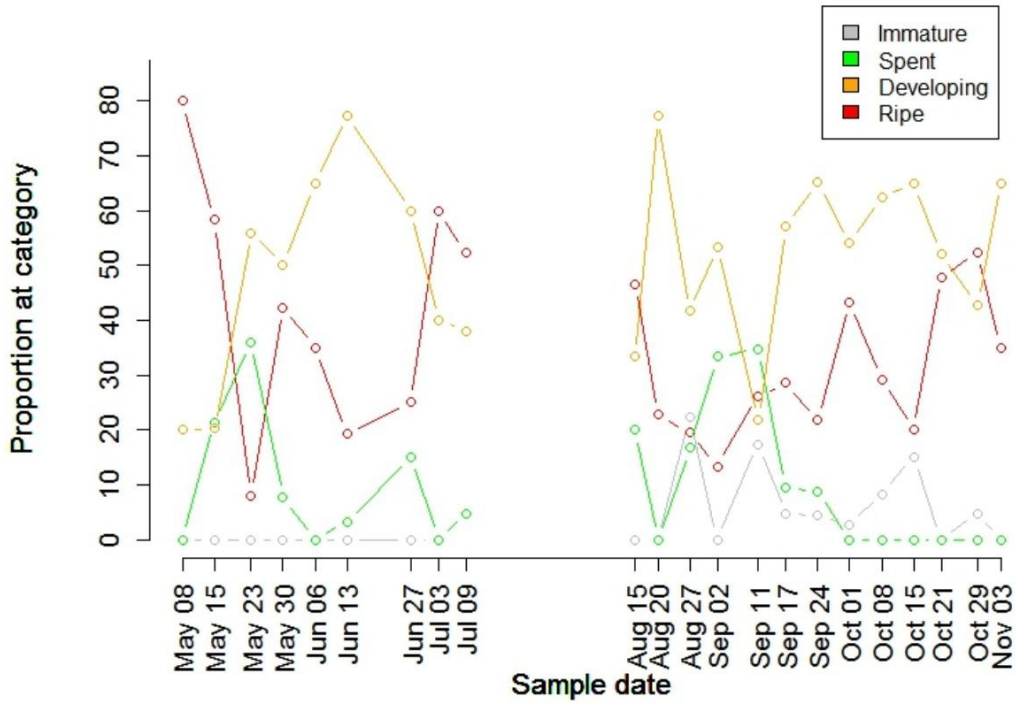

Figure 5: The proportion of King scallops found at each of 4 stages of maturity between May and November in area A.

The maturity stages assigned using Mason (1958) were grouped into four categories: immature (stages 1 and 2), developing (stages 3 and 4), ripe (stages 5 and 6) and spent (stage 7). Spawning follows a general pattern of increasing numbers of scallops with 'developing' gonads, followed by peaks in the number with 'ripe', and a simultaneous drop in the number with 'developing' with an increase in 'spent' gonads (Figure 5).

In the first sample processed from the 8th May all scallops were mature, 80% with ripe gonads and 20% with developing. This was followed by a decrease in the number of scallops with ripe gonads to 8% by the 23rd May, the remaining scallops were either spent (36%) or developing (56%). Before the gap in sampling there are two smaller spawning peaks observed (42% 30th May and 60% 3rd July). There are more scallops in the developing phase in the first of these, but by 3rd July the majority of scallops are ready to spawn.

The results show that there are major peaks in spawning but that trickle spawning seems to be continuous until the end of September. At this time no scallops are found with spent gonads; the majority are either developing or ripe, suggesting that they have entered a resting and rebuilding period. It is unfortunate that we have no data between 9th July and 15th August as it is possible there was another major spawning event like that seen at the start of May.

Gonad index

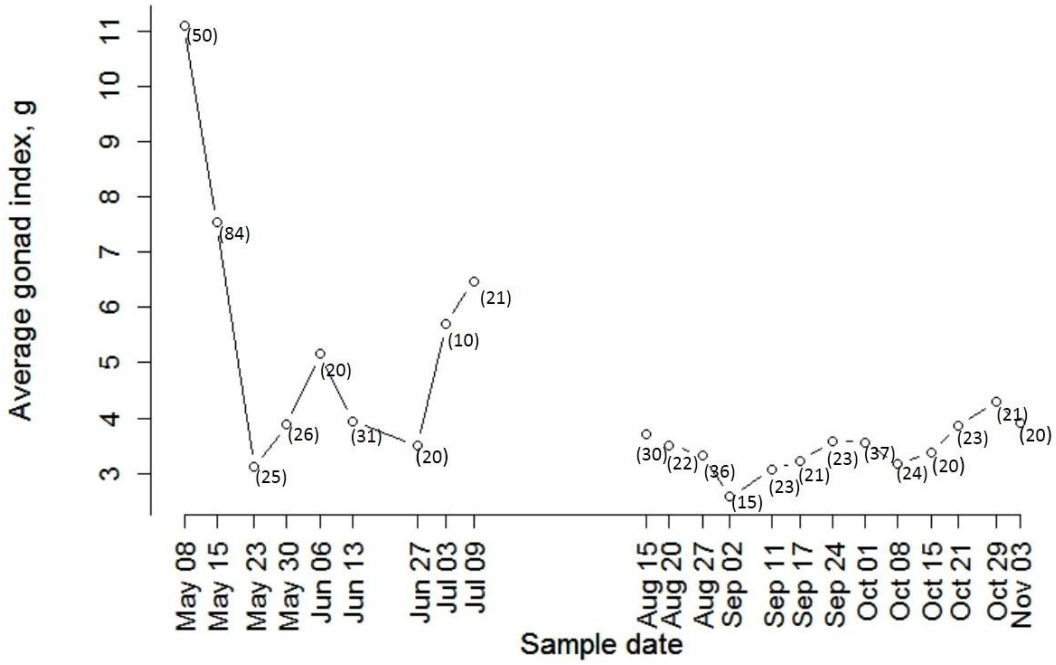

Figure 6: The average gonad index found between May and November in area A, also showing the sample sizes for each date.

The gonad index follows a similar pattern to that seen with the spawning times, validating visual grading as a means of assessing maturity. The GI shows a substantial decrease between 8th May and 23rd May followed by a gradual rise by the time of the break in sampling. From August until the end of sampling it remains low but gradually increasing as the gonads rebuild (Figure 6).

Area B – Caernarfon Bay

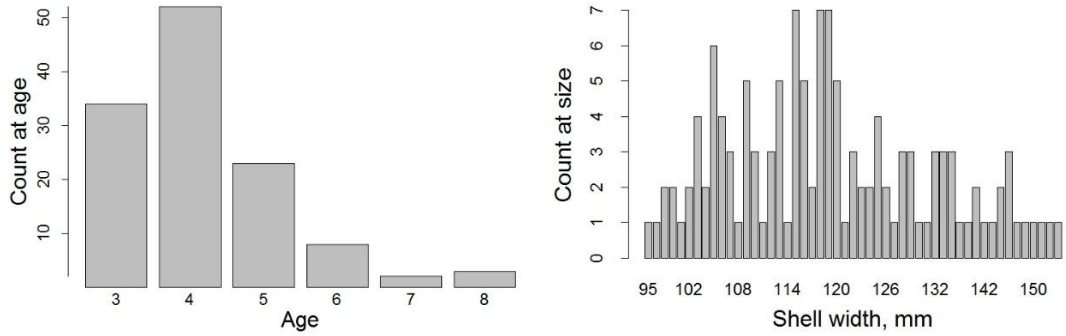

Figure 7: (left) the number of scallop in each age class in area B; (right) the number of scallop found at each shell width in area B.

Samples from site B were collected by fishermen using a single dredge towed behind their vessel as well as some from bycatch. Samples were received in 3 weeks in May and 3 weeks in June and once each in July and August. Scallops in the age group 3-5 were the most frequently found in area B. The largest scallop collected had a shell width of 149mm and was aged 8, the youngest was aged 3 and 108mm (Figure 7).

Spawning times

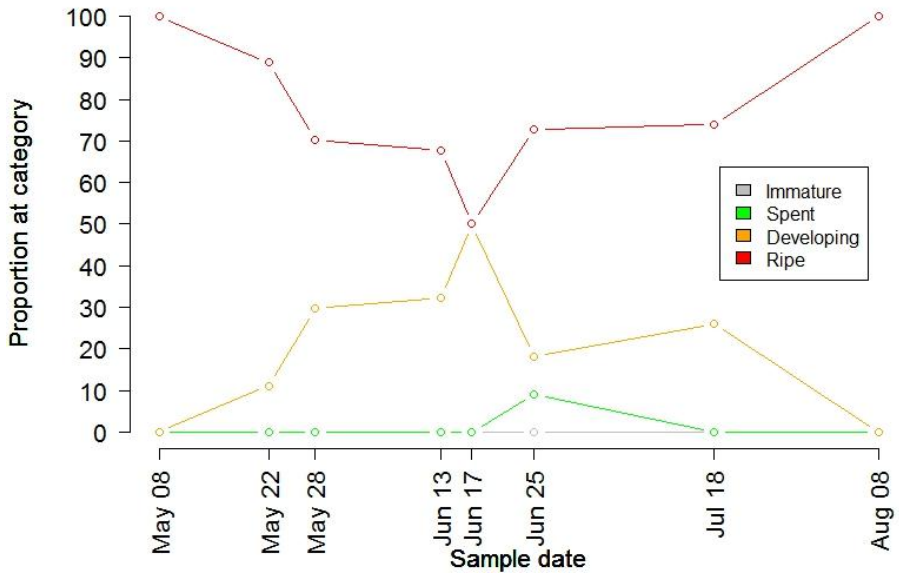

Figure 8: The proportion of King scallops found at each of 4 stages of maturity between May and November in area B. This is shown for each sample date.

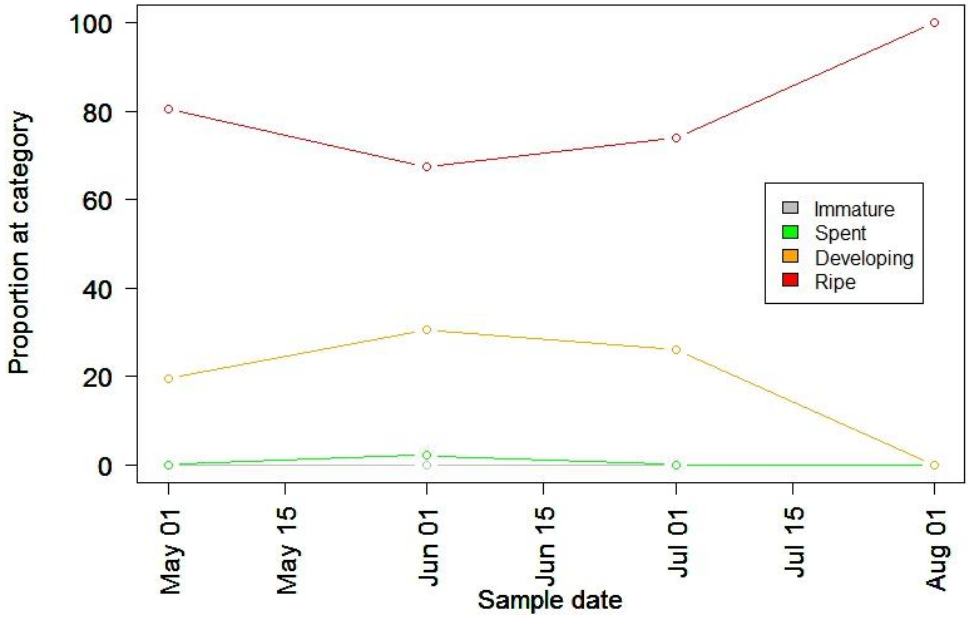

Figure 9: The proportion of King scallops found at each of 4 stages of maturity between May and mid-August in area B. This shows the samples pooled by month.

At the start of the sampling period all of the scallops were mature. This was followed by a decrease in June and a rise in July. Very few (9% in June) were found with spent gonads. The general pattern follows that as the number of scallops with ripe gonads decreases the number with developing gonads increases (Figure 8). The increase in the number of scallops with ripe gonads seen by August is unreliable as it is based on a sample size of 9, which is too few. The data was pooled to give appropriate sample sizes, but as a result the spawning patterns cannot be observed (Figure 9). The results highlight the importance of regular sampling at short (weekly) intervals, with good sample sizes.

Gonad index

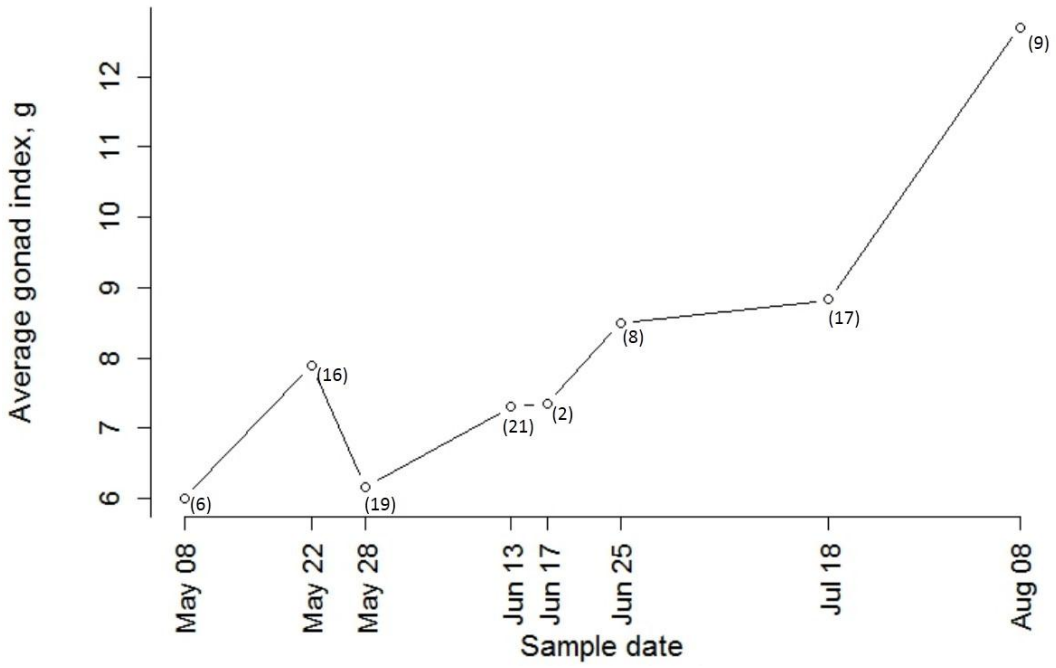

Figure 10: The average gonad index found between May and mid-August in area B, also showing the sample sizes for each date.

The gonad index does not follow a similar pattern to the spawning results when plotted by date illustrating the unreliability of these data (Figure 10). There is a small peak in GI on 22nd May and an increase by 25th June which roughly follows spawning results when plotted monthly. Here in May and at the start of July (end of June) there is a rise

in the proportion of scallops with ripe gonads. The results again illustrate the impact of low samples numbers.

Genetic samples

Table 1 above shows the number of samples obtained for genetics at each age class. The aim is for roughly 100 per age group for the genetic studies in the future.

Age	2	3	4	5	6	7	8	9	10
Count	1	48	42	54	72	130	87	45	9

Table 1: The number of genetic samples taken for each age class in area A.

DISCUSSION

The results from Area A indicate that *P. maximus* exhibits continuous spawning from May until September with peak spawning events within this time period. In future studies starting sampling earlier would be recommended as the results indicate spawning had occurred just as we began our sample collection. The qualitative visual grading system used to assess maturity was validated by findings from the quantitative GI suggesting this is a reliable method of visually determining the maturity of scallops. These findings are similar to those of Mason (1958) who looked at *P. maximus* from the Isle of Man (IOM) and found them to have at least two main spawning events; however, the timings differed, with IOM *P. maximus* having a second major spawning event in the autumn. The results are also in agreement with studies of other populations of *P. maximus* in Europe (Duinker & Nylund, 2002a; Paulet *et al*., 1988; Wilson, 1987). In the future it would be interesting to look at the environmental drivers behind these events such as water temperature, and nutrient and phytoplankton levels.

The age structure appeared different in the two areas, but with too few samples in Area B a robust comparison could not be made. These preliminary results suggest that younger scallops are more common in Area B (most frequent age category seen 3-5) than Area A (6-8). The annual stock assessments we have carried out provide more

detailed information on spatial differences in scallop size/age structure across Wales for three consecutive years (Lambert *et al*. 2015).

The difference in the quality of the data obtained from Area A and Area B proved a good assessment of the appropriate methodology to use in the future for a study of this kind. Weekly sampling is necessary to visualise the fluctuations in maturity and capture smaller spawning events. However, this is dependent on large enough sample sizes (minimum 20 scallops). In this study the most successful way of obtaining samples of this size was as bycatch from queen scallop fishing. However, this does limit sampling to areas where this activity is happening. As a future consideration, adapting the single dredge to improve its efficiency could be another option. When this caught successfully sample sizes were sufficient (n = 25, 25 and 27) in one or two passes.

The scallop gonad samples that were collected from the mature (stage 5/6) scallops will be analysed in the future to look at egg quality and fecundity. For the samples to be viable it was found that fresh samples were needed. Freezing affects the structure of the tissue with the potential for rupturing the eggs stored inside and altering the Carbon and Nitrogen content of the tissue which is needed for assessing quality. In this study fresh scallop samples were collected from Area A and stored in ice until processing. Logistically this was not feasible from Area B. These scallops were frozen and then processed when time allowed. This is fine for assessing maturity stages when looking at spawning times but not for further reproductive investigations. This is an important consideration when planning future work to look at spatial differences in egg quality or fecundity.

In the future histological analysis will be conducted on the stored samples of mature scallop ovary from Area A. Thin slices of the ovary are taken and set on slides. These are looked at under the microscope and the eggs (oocytes) counted allowing us to estimate the fecundity at age/size of the scallops. This cellular detail will enable the percentage of mature oocytes within an ovary to be estimated, providing us with a more detailed estimate of fecundity as only mature oocytes will produce larvae (Dorange & Pennec, 1989). Dorange & Pennec (1989) found that atresic (degenerated) oocytes can represent up to 40% of the total number in a mature gonad. This is an important fact to take into consideration. Although egg number could be exponentially linked with age

(Langton *et al.* 1987) these eggs may not all be viable. It would be interesting to see if the number of degenerated eggs increases with age to investigate the impact of age on fecundity. The histology will also allow us to accurately validate the maturity staging.

A CHN analyser will be used to carry out elemental analysis on the ovary samples stored at -20C which gives us information on the quality of the eggs produced. It has been found that egg quality is linked to quantity (Pennec *et al.* 1998). The results of this combined with the histology will enable us to see at what age/size *P. maximus* are most reproductively fit. It is not known whether they have a peak in fitness and senesce as they age, or whether they continue to produce large quantities of healthy eggs as they grow. It is important to understand this for management of the species. For example, if there is a peak in reproduction at a certain age then these scallops will need more protection as the key spawning stock. This could be in the form of a legal landing size limit reflective of this age/size group or the suggestion of areas to protect them as a priority where they occur. This knowledge will give us insight into whether it is more beneficial to protect younger, faster growing scallops, or whether there is benefit in protecting the larger, older scallops which may prove a more important spawning stock, for example.

As a preliminary investigation this study has enabled us to find an appropriate methodology to look at the spawning time of scallops. The results focussed on one location in Welsh waters and in the future we would like to expand this to look at regional differences in the timing of spawning and fecundity with age. Results from our genetic analysis have found stocks in Cardigan Bay to be genetically distinct from other local scallop beds (Hold *et al.* In prep.). This is supported by findings from our oceanographic modelling suggesting they are a self-recruiting stock, or with limited recruitment from elsewhere. If this is true then the reproductive behaviour could also be unique, as found in other isolated stocks (e.g. Mackie & Ansell, 1993). Again this information is important for management plans. For example, the appropriate timing of closed seasons to protect scallops during spawning may differ between regions. Furthermore, if there is limited connectivity with other stocks, these would be less resilient to fishing pressures and careful management would be needed to prevent stock collapse if these local stocks were depleted.

The extra genetic samples collected during this study will enable more detailed genetic analysis to be continued. Looking at the effect of age on fecundity and spatial differences in spawning in the future, together with this genetic data will elucidate the level of connectivity of Welsh scallop stocks. It will allow us to answer questions such as when and where are larvae released, are there self-recruiting areas and are Welsh scallops one stock or several? This information is essential for future sustainable management of the *P. maximus* fishery.

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REFERENCES

Barber, B.J. and N.J. Blake, 2006. Reproductive physiology. Pages 357-416 in, Scallops: Biology, Ecology and Aquaculture, Second Edition, S.E. Shumway and G.J. Parsons, eds. Elsevier Science Publishers.

Baird, R. H. (1966). Notes on an escallop (*Pecten* maximus). *Journal of the Marine Biological Association of the United Kingdom*, 33–47.

Beaumont, A. R., & Budd, M. D. (1983). Effects of self-fertilisation and other factors on the early development of the scallop Pecten maximus. *Marine Biology*, *76*(3), 285–289.

Beukers-Stewart, B. D., Vause, B. J., Mosley, M. W. J., Rossetti, H. L., & Brand, A. R. (2005). Benefits of closed area protection for a population of scallops. *Marine Ecology Progress Series*, *298*, 189–204.

Cochard, J. C., & Devauchelle, N. (1993). Spawning, fecundity and larval survival and growth in relation to controlled conditioning in native and transplanted populations of *Pecten maximus* (L): Evidence for the existence of separate stocks. *Journal of Experimental Marine Biology and Ecology*, *169*, 41–56.

Cragg, S. M. (1980). Swimming behaviour of the larvae of *Pecten maximus* (L.) (Bivalvia). *Journal of the Marine Biological Association of the United Kingdom*, *60*(03), 551.

Dorange, G., & Pennec, M. L. (1989). Ultrastructural study of oogenisis and oocytic degeneration in *Pecten maximus* from the Bay of St. Brieuc. *Marine Biology*, *348*, 339–348.

Duinker, A., & Nylund, A. (2002). *Processes related to reproduction in great scallops (P. maximus)*. University of Bergen, Norway.

Heipel, D. A., Bishop, J. D. ., Brand, A. R., & Thorpe, J. P. (1998). Population genetic differentiation of the great scallop *Pecten maximus* in western Britain investigated by randomly amplified polymorphic DNA. *Marine Ecology Progress Series*, *162*, 163–171.

Lambert, G. ., Murray, L. G., Hinz, H., & Kaiser, M. J. (2015). Status of scallop populations in Welsh waters – Results of 3 years of research surveys 2012 - 2014 –. *Bangor University, Fisheries and Conservation Science Report*, (41), 61.

Langton, R.W., Robinson, W.E., Schick, D. (1987). Fecundity and reproductive effort of sea scallops *Placopecten magellanicus* from the Gulf of Maine. *Marine Ecology Progress Series*, *37*, 19–25.

Lo, M. C. (2009). Spatial variation in king scallop *Pecten maximus* maturation state around Isle of Man. Bangor, Wales.

Mackie, L. a., & Ansell, A. D. (1993). Differences in reproductive ecology in natural and transplanted populations of *Pecten maximus*: evidence for the existence of separate stocks. *Journal of Experimental Marine Biology and Ecology*, *169*(1), 57–75.

Magnesen, T., & Christophersen, G. (2008). Reproductive cycle and conditioning of translocated scallops (*Pecten maximus*) from five broodstock populations in Norway. *Aquaculture*, *285*(1-4), 109–116.

Mason, J. (1958). The Breeding of The Scallop, *Pecten maximus* in Manx waters. *Journal of Experimental Marine Biology and Ecology*, 653–671.

Paulet, Y, M., Lucas, A., & Gerard, A. (1988). Reproduction and larval development in two *Pecten maximus* populations from Brittany. *Journal of Experimental Marine Biology and Ecology*, *119*, 145–156.

Pennec, M. L. E., Robert, R., & Miguel, A. (1998). The importance of gonadal development on larval production in pectinids. *Journal of Shellfish Research*, *17*(1), 1992–1996.

Pennec, M. l., Paugam, A., & Pennec, G. l. (2003). Review article The pelagic life of the pectinid *Pecten maximus* — a review. *ICES Journal of Marine Science*, *3139*(02), 211–223.

Wilding, C. S., Beaumont, a R., & Latchford, J. W. (1997). Mitochondrial DNA variation in the scallop Pecten maximus (L.) assessed by a PCR-RFLP method. *Heredity*, *79 (Pt 2)*(August 1996), 178–189.

Wilson, J. H. (1987). Spawning of *Pecten maximus* (Pectinidae) and the artificial collection of juveniles in two bays in the west of Ireland. *Aquaculture*, *61*(2), 99–111.

Websites

MMO (2013) Uk Sea Fisheries Annual Statistics Report 2013. Available at: www.gov.uk/government/statistical-data-sets/uk-sea-fisheries-annual-statistics-report-2013 [Accessed May 25, 2015]