



Spatial variation in the gonad condition of the scallop *Pecten maximus* L.



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SPATIAL VARIATION IN THE GONAD CONDITION OF THE SCALLOP *PECTEN MAXIMUS* L.

ABSTRACT

Small spatial scale variation in the gonad conditioning and the onset of spawning of *Pecten maximus* was inferred from interviews with scallop fishers and subsequently verified by empirical observations. The potential drivers (environmental and fishing) of these spatial patterns were then investigated using a generalised additive modelling approach. In general the fishers' observations were accurate and validated by the current study. Statistically significant differences in the gonad condition of scallops over small spatial scales (< 5 km) were found but these spatial patterns varied temporally over 13 months. The within site variation in gonad condition was also high, indicating a "bet hedging" reproductive strategy. Long term drivers of gonad weight were identified as average annual chlorophyll a concentration, scallop density, stratification index and shell size. The rate of change in temperature over the month prior to sampling was identified as the short term driver of gonad wet weight associated with the autumn spawning event. The GAM explained 42.8% of the deviance in gonad weight. An increase in shell length from 100mm to 110mm equated to an increase of approximately 20% in gonad weight. In the IOM protecting scallops from fishing mortality until 110mm (age 4) compared to 100mm (age 3) may lead to an overall increase in lifetime reproductive output of 3.4x. The "bet hedging" reproductive strategy can decrease the chance of fertilisation especially at low the densities found on commercial scallop grounds and therefore areas protected from fishing, where scallop densities can increase may help to buffer against reproductive failure and the allee effect.

INTRODUCTION

Local Ecological Knowledge (LEK) or Traditional Ecological Knowledge (TEK) has increasingly been used in ecology, conservation and fisheries management. Examples include estimates of abundance (Anadón *et al.* 2009), ecology and reproduction in fish (Silvano and Begossi 2005), essential fish habitat (Hilborn *et al.* 2004), tidal and lunar movements and aggregations of fish (see Johannes, Freeman, & Hamilton (2008)) and the location and depletion of spawning aggregations of Grouper (Serranidae) (Johannes *et al.* 1999; Hamilton *et al.* 2005). The use of LEK can also help to focus scientific effort to the appropriate sampling locations and seasons, and thereby improve efficiency (Davis, Hanson, Watts, & MacPherson, 2004; Johannes *et al.*, 2008), avoid missing important biological and ecological changes (Johannes *et al.* 2008) and help develop hypotheses.

The king scallop, *Pecten maximus* is a functional hermaphrodite of commercial importance, found in European waters from Norway to Spain with landings of approximately 60,000 tonnes in 2009 (FAO 2012). Scallops are the third most valuable fishery in the UK (MMO 2012) of which the main commercial species is *P. maximus*. In the Isle of Man *P. maximus* accounts for over 65% of all fishery income (Beukers-Stewart *et al.* 2003). Previous work has demonstrated considerable variability in the timing and synchronisation of spawning over large spatial scales (100s of kms) (Mason 1958; Paulet *et al.* 1988; Cochard and Devauchelle 1993; Mackie and Ansell 1993). Although one might expect less variation in reproductive schedules at smaller scales, fishers will often target a particular scallop ground with good quality roe until the scallops spawn and then move on to another ground just tens of kms away which are yet to spawn (Fishers, IOM, Pers. Comm.). The higher market value of good quality roe ensures that fishers are sensitive to the gonad maturation state and therefore their knowledge on reproductive schedules could be valuable for scallop and fisheries biologists. If reproductive variation is present on such a small spatial scale this provides challenges for effective management of the stock and understanding this variation and the parameters driving it is essential and periods of spatially favoured fishing at a time of gonad ripening could also make the fishery more susceptible to collapse.

P. maximus first show signs of gametogenic maturation in the second year of growth (Mason 1958; Devauchelle and Mingant 1991), although an adult pattern of spawning

may not develop until their fourth year of growth (Mason 1958). *P. maximus* is reported to exhibit several patterns of spawning: continual partial spawning from spring until early autumn; bimodal peaks in spawning (spring and autumn) or a single synchronised spawning event (Mason 1958; Paulet *et al.* 1988; Pazos *et al.* 1996). These strategies seem to be genetically mediated (Cochard & Devauchelle 1993, Mackie & Ansell 1993) although environmental conditions appear to alter the timing and onset of maturity and spawning (Magnesen and Christophersen 2008). Understanding reproduction in *P. maximus* is important for a number of reasons. Market value increases with high quality roe attached hence the timing of harvesting affects the profitability of the fishery. Variation in reproductive schedules, driven by climatic variation and hydrographic conditions, can affect the consistency of recruitment (Orensanz *et al.* 2006). Therefore management of recruitment-limited fisheries, such as the Isle of Man king scallop (Beukers-Stewart *et al.* 2003), requires in-depth knowledge of factors that influence reproductive ecology.

Explanatory variables for the onset of spawning

Changes in water temperature or temperature threshold are potential triggers for the onset of gonad maturation and spawning in different Pectinid species (Paulet *et al.* 1988; Pazos *et al.* 1996). In many populations, spawning coincides with different temperatures and with both rising temperatures in the spring and falling temperatures in the autumn (Mason 1958; Pazos *et al.* 1996). Hence, it is probable that change in temperature *per se*, rather than absolute temperature is a key factor in the onset of the rate of spawning.

Microalgae are the main energy source that are required for scallop growth, including gonad maturation (Farías and Uriarte 2006), and food availability has been suggested as a major driver of reproductive cycles in marine invertebrates. Starr, Himmelman, & Therriault (1990) found that there was a direct coupling of spawning and phytoplankton concentration in green sea urchins and blue mussels. Mussels and urchins spawned progressively earlier with increasing phytoplankton concentrations. The timing of phytoplankton blooms is dependent on a number of different interacting environmental variables beyond simple increases in water temperature. The timing of spawning in *P. maximus* has been linked to blooms of phytoplankton in Galicia, Spain

(Pazos *et al.* 1996). However, energy reserves stored in the adductor muscle and digestive gland can also be used for gonad conditioning in the absence of food (Sastry and Blake 1971; Pazos *et al.* 1997).

Another driver of energy allocation is fishing pressure. It has been shown that scallops exposed to physical disturbance from regular commercial fishing have lower gonad weights in relation to shell size than their counterparts in protected waters (Beukers-Stewart *et al.* 2005; Kaiser *et al.* 2007). Scallops in fished areas may have to allocate energy to repairing tissue and shell damage caused by contact with the towed gear and hence there is less energy for the production of reproductive tissue in closed areas (Beukers-Stewart *et al.* 2005; Kaiser *et al.* 2007).

The present study aimed to i) understand, from fishers' observations, the spatial patterns of spawning around the Isle of Man ii) to test the validity of these observations using independent scientific sampling iii) to explain these observations in terms of key environmental and fishery drivers.

METHODS

For full methods please see Hold 2012 (PhD thesis), but in brief:

- A questionnaire was designed to capture fishers' knowledge of the timing of and patterns in the spawning of *P. maximus*. Questions were administered by face to face interviews. A total of 8 out of 26 (31%) full time Manx scallop fishers completed questionnaires.
- Ten commercial scallop beds in the waters around the Isle of Man were sampled using scallop dredges on the RV Prince Madog across a period of 13 months (Figure 2.1): Bradda Inshore (BRI), Bradda Offshore (BRO), Chickens (CHK), East of Douglas (EDG), Laxey (LAX), Peel (PEL), south of Port St Mary (PSM), Ramsey (RAM), South East Douglas (SED), Targets (TAR). These sites vary in their depths (21m - 69m), oceanographic regime (mixed and stratified water columns) and fishing intensity. Sampling took place in mid October 2009 and 2010 to coincide with the autumn period of gonad maturation and spawning. Sampling was also carried out in June 2009 and 2010 to provide data during a non-spawning period.

- A sample of at least 50 scallops was set aside for gonad maturation analysis from each site. Scallops were dissected on the day of capture and the gonad frozen for wet weight determination back at the laboratory (+/- 0.01g). Shell height (+/- 1mm) was recorded on board the research vessel. The Gonad Observation Index (GOI), as described by Mason (1958), was also recorded. This index categorises a scallop gonad into one of seven stages. Stages one and two relate to virgin scallops, stage three is the first stage of recovery following spawning, stage four and five are filling, stage six is full and stage seven is a spent gonad. We also calculated the Relative Gonad to shell Height (RGH) index which standardises the gonad weight in relation to the size of the scallop.
- The condition and maturity state of the scallops at each site will reflect the circulation history of food availability at that site (Chlorophyll a concentration (Chla)) and exposure to physiological drivers (e.g. water temperature). To understand how spawning may be influenced by these overlying hydrographic conditions, monthly average sea surface temperature (SST) and Chla data was obtained from satellite data (NEODAAS) for the period of November 2008 to October 2010.
- Scallops are benthic species, hence a stratification index (SI) was also calculated (Eq 2). In a mixed water column SST will accurately represent bottom temperatures but in stratified waters the bottom temperature will be lower than SST and the stratification index will help correct for this.
- Water depth was recorded at the time of sampling scallops and was corrected for tidal state using WXTide32 version 4.7 (Hopper 2007) using data for the closest reference location for each site (Douglas, Peel or Ramsey).
- Vessel monitoring system (VMS) data for all vessels fishing in the waters off the Isle of Man was used to create a map of fishing intensity at 1km² resolution for the period of the scallop fishing open season 2008/2009 and 2009/2010. The total fishing intensity for a 2km² area centred over the site reference position was then calculated for each site and fishing season.
- For detailed information on data analysis please see Hold 2012 (PhD thesis).

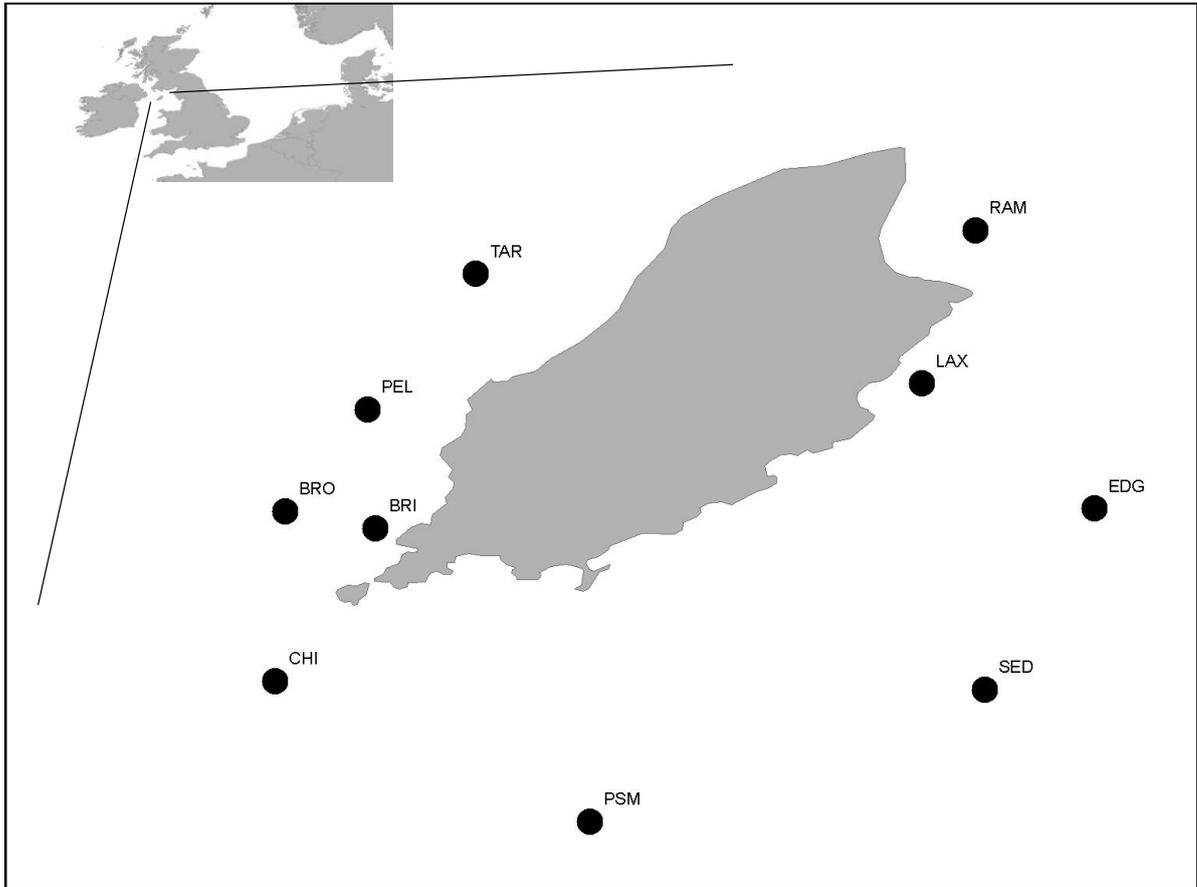


Figure 2.1. Survey sites around the Isle of Man in the Irish Sea. Site Codes: Bradda Inshore (BRI), Bradda Offshore (BRO), Chickens (CHK), East of Douglas (EDG), Laxey (LAX), Peel (PEL), South of Port St Mary (PSM), Ramsey (RAM), South East Douglas (SED), Targets (TAR)

RESULTS

FISHERS QUESTIONNAIRE

The main hypotheses identified from the fishers' questionnaire were:

- The autumn spawning event has been occurring later recent years, as fishers used to see good quality roe by the time fishing commenced on November 1ST whereas recently the gonads have been empty and poor quality indicating recent spawning.
- Spawning of scallops occurs at different times at different fishing areas around the Island.
- There is temporal variation in the timing of spawning on an inter-annual basis, with the spring spawning occurring primarily in April and May and the autumn spawning occurring in September and October.
- Scallop spawning within a single site is synchronised with the majority of scallops spawning within a day or two of each other.

- Spawning events occurred after a large spring tide.
- Deeper sites spawn later than shallower ones.

Analysis of scallop survey data

The analysis of differences in gonad maturation indices between sites and years indicated that, although there are differences among sites, these are not consistent between years. There was no grouping of gonad maturation by geographical or oceanographical pattern (for example; inshore v offshore, east v west) (Figure 2.5). The proportion of scallops with gonads that fell within each class of the Gonad Observation Index (GOI) is shown in Figure 2.6 showing a similar pattern to the gonad maturation index. In 2009 the majority of scallops were classed as stage five (filling) whereas the majority were classified as stage three (first stage of recovery after spawning) in 2010.

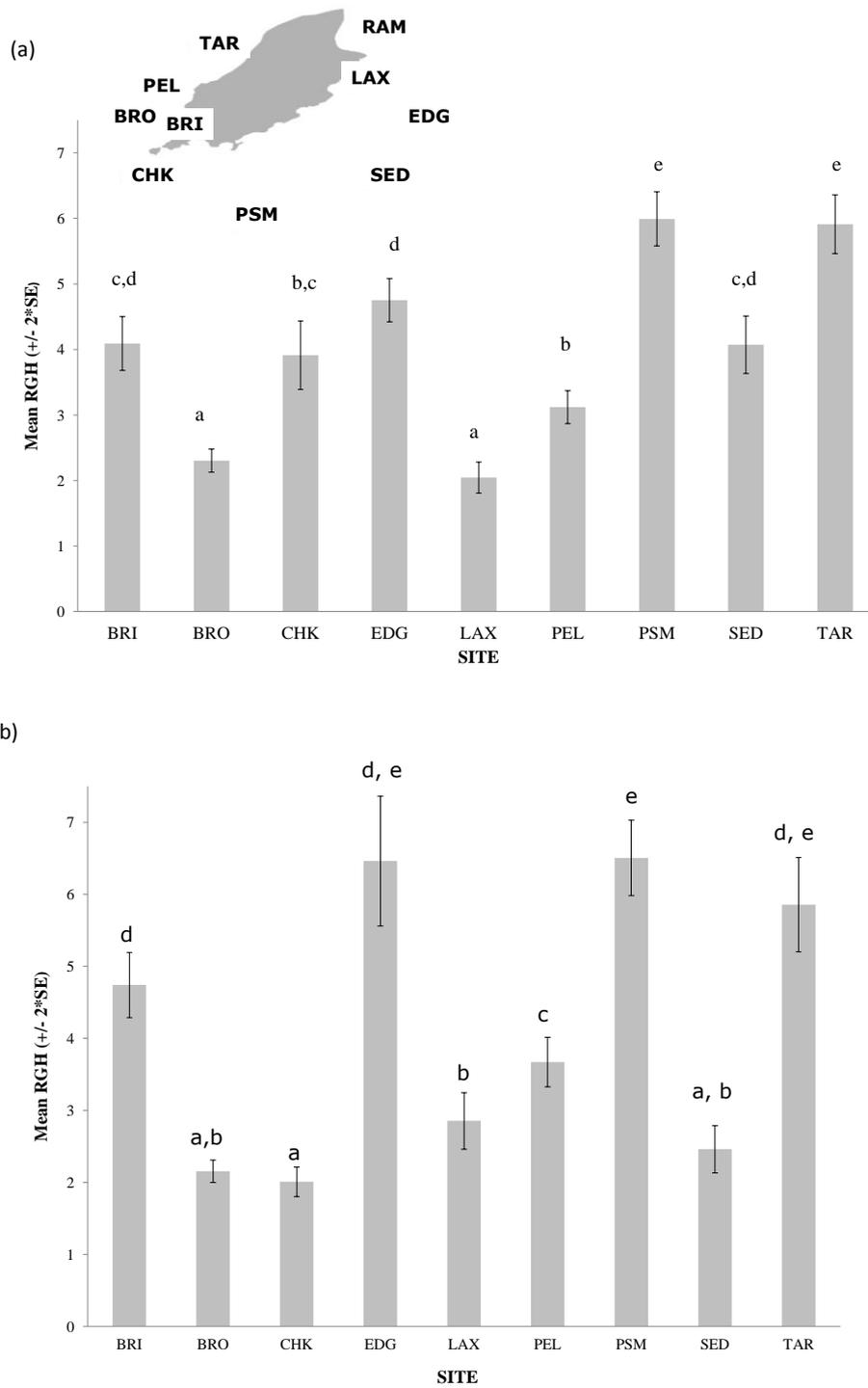


Figure 2.5. Mean relative gonad weight to height index (RGH) for scallops sampled from different beds around the Isle of Man in (a) October 2009 and (b) October 2010. Letters above chart indicate significance results of Tukey's HSD pairwise comparisons. Insert shows map of sampling sites around the Isle of Man

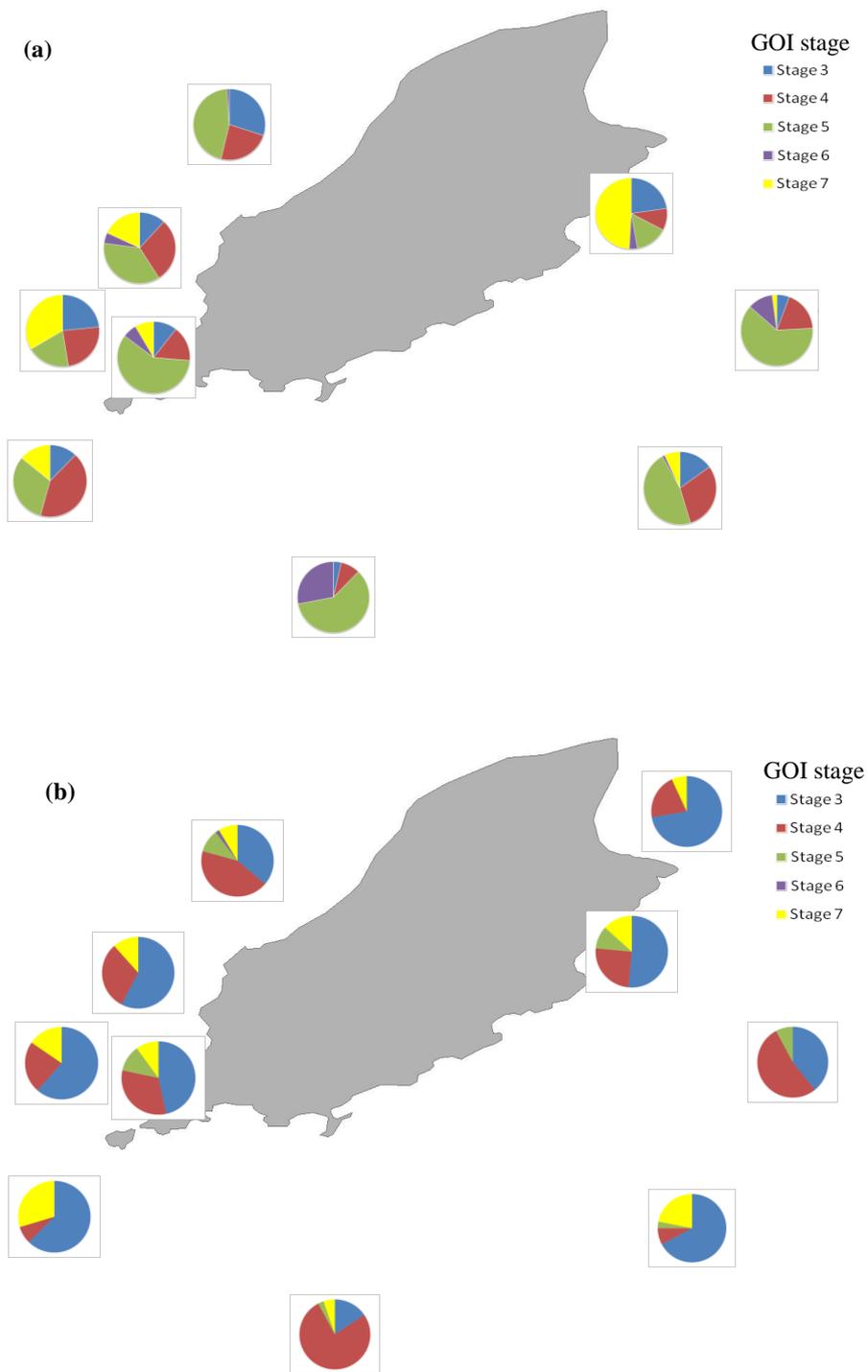


Figure 2.6. Pie charts representing the proportion of scallops from each site with gonads at each stage of the gonad observation index (GOI) (Mason 1958). (a) October 2009 (b) October 2010

The coefficient of variation (CV) of the gonad index varied from 0.19 to 0.78 across different sites in June and October 2009/2010 (Table 2.1). This suggests a large variation in the synchronicity of gonad maturation state between sites and dates, but generally the synchronicity was poor (mean CV = 0.46) compared to the synchronised spawning in Bay St Brieuc (CV < 0.1 all year) (Mackie and Ansell 1993).

Table 2.1. Coefficient of variation (CV) of the relative gonad weight to shell height (RGH) index of scallops caught off the Isle of Man in June and October 2009 and 2010. (For site codes see Figure 1)

Site	CV			
	June 2009	June 2010	October 2009	October 2010
BRI	0.41	0.41	0.55	0.53
BRO	0.49	0.32	0.43	0.42
CHK	0.47	0.38	0.54	0.77
EDG	0.54	0.26	0.41	0.62
LAX	0.40	0.35	0.67	0.78
PEL	0.43	0.39	0.48	0.55
PSM	0.40	0.22	0.37	0.45
SED	0.50	0.27	0.50	0.67
TAR	0.34	0.19	0.50	0.54

Modelling Environmental Drivers of Gonad Maturation State

The generalised additive model to assess the effect of different environmental drivers on gonad weight was created with a total sample size of 1546. However, most of these samples were within sites and the interactions between variables could not be included due to lack of replicates in the covariate axis.

The starting model included temperature change over the month prior to sampling, annual average chlorophyll a, scallop density, shell height, water stratification, sampling period/year, depth and fishing pressure. Sampling period, fishing pressure and depth were not significant and were dropped from the optimum model. This resulted in a final model that related gonad weight to temperature change over the

month prior to sampling, annual average chlorophyll a, scallop density, shell height and water stratification.

The model explained 42.8% of the deviance or variation in the gonad weight data. Figure 2.7 shows the effects of each parameter on gonad weight. Greater rates of change of temperature over the month prior to sampling initially had a larger positive effect on gonad weight up to a rate of 0.8°C decrease per month, beyond which the effect of > 0.8°C change in temperature per month had a reduced effect on gonad weight. Increasing shell height had a positive effect on gonad weight as would be expected. Increasing scallop densities initially had a small negative effect on gonad weight but changed to a rapid increase in gonad weight at densities greater than 8 per 100m². Initially increasing average annual chla had a positive effect on gonad weight however this levelled out and decreases slightly at chla levels greater than 3.5 mg m⁻³. However, it should be noted that this part of the graph has only a single data point driving the relationship. There was a negative linear relationship of gonad weight with increasing intensity of stratification (Table 2.2).

Table 2.2. Results of preferred GAM model

<u>Parametric coefficients</u>				
Parameter	Estimate (SE)	SE	t value	p value
intercept	2.03 (0.13)	0.13	15.63	<0.0001
Stratification	-0.25 (0.04)	0.04	-5.55	<0.0001
<u>Smoothed terms</u>				
Parameter	edf	F	p value	
Temperature decrease	6.3	34.41	<0.0001	
Density	2.49	33.06	<0.0001	
Average chlorophyll	2.96	11.51	<0.0001	
Shell height	2.64	68.21	<0.0001	

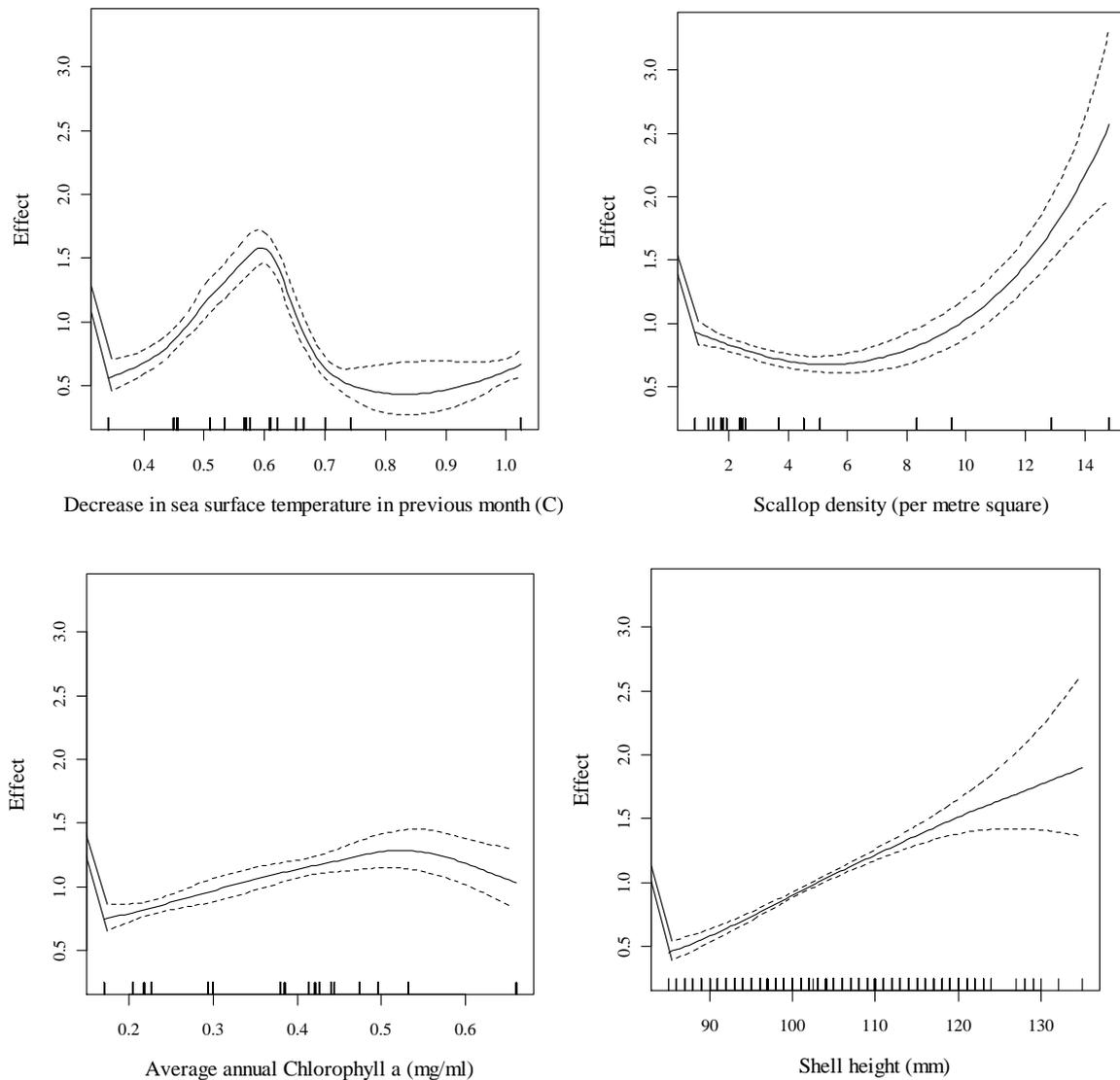


Figure 2.7. Smoothers of the effect of the 4 non-parametric terms on gonad weight (g) in the preferred GAM model. Dashed lines indicate 2 standard errors.

Predicting the gonad weight based on different shell sizes showed that the greatest gain in gonad weight was found between a shell length of 85 and 90 mm (Figure 2.8). However it can be seen that gains in gonad weight with shell size appear to be indeterminate for the sample range used.

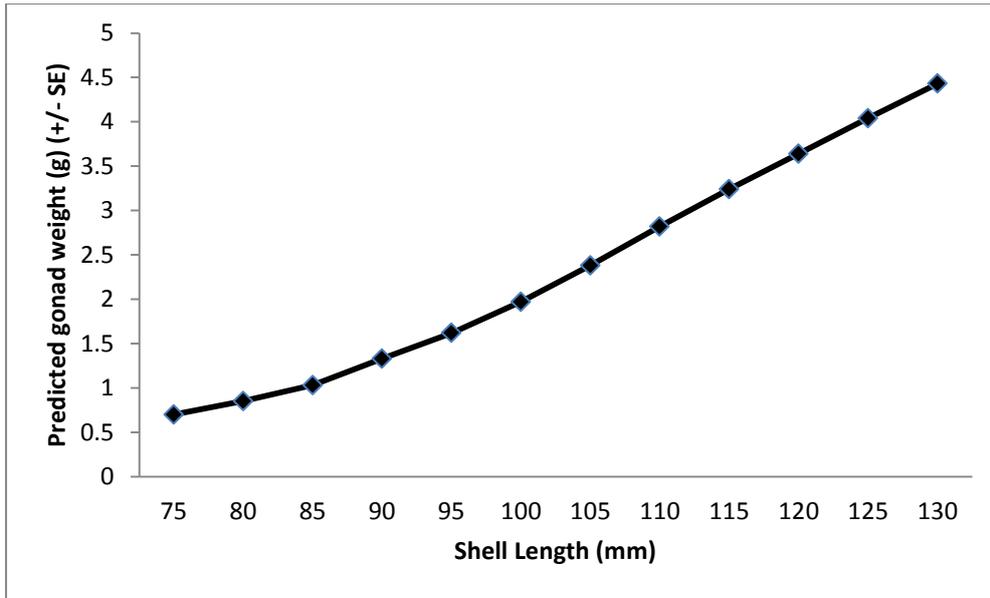


Figure 2.8. Predicted gonad weight (g) at varying shell lengths (mm) based on the preferred GAM model with all other parameters held constant at average values. Maximum measured scallop was 131mm in shell length

DISCUSSION

Timing of scallop spawning.

Mason's (1958) observations of scallops at a single site off the south west coast of the Isle of Man and these of the present study agree with the fishers' observation that there are two main spawning events per year for *P. maximus* in the waters surrounding the Isle of Man. The months in which these two spawning events take place were considered by the majority of fishers to be April/May and September/October. The timing of the spring spawning observed by the fishers matched well with Mason (1958) who found the majority of the spawning occurred in April (1952) or May (1951). However Mason reported that the autumn spawning occurred in August or September, a month earlier than that observed by the fishers in the present study. Interestingly the fishers also noted that they felt there was a trend towards later spawning, particularly in the autumn. The results of the gonad maturation survey in the second week in October 2010 suggested that spawning recently had taken place with the majority of scallop samples at all sites observed in stage three or four on the gonad observation index. This agrees with Mason's (1958) observations of gonad state in October 1952 which had a spawning event in the middle of September. Mason (1958) recorded that spawning occurred in August in 1951 and by October the majority of scallops had recovered to stage four of the GOI with few stage three gonads

observed. The condition of the gonads in October 2010 therefore suggest a September spawning event rather than an earlier August event. In 2009 our survey showed a different picture, with the GOI stage with the greatest representation across all sites being stage five. However, Laxey and Bradda Offshore both had mostly spent gonads at stage seven which suggested a very recent spawning event. It was also noted that in 2009 there were significant numbers of scallops at four out of the five GOI stages at most sites. Masons' (1958) work observed that stage five did not predominate until December following a full spawning in August or September but did occur following a small, partial summer spawning event. Therefore, this suggests a partial spawning event at some sites where the scallops have recovered quickly to stage five and a full spawning at others which are seen as spent. Presence of stage seven gonads suggests that the full spawning event in 2009 occurred in October, later than the August/September found in the 1950s, supporting the observation from some fishers that recent spawning is later than in historic years.

Implications of changes in the timing of spawning

Residual flow in the Irish Sea is generally slow (0.01 ms^{-1}) and northward towards the North Channel (Bowden 1955). The mean residual flow out of the North Channel towards the Malin shelf is estimated to be $0.02 - 0.03 \text{ ms}^{-1}$ (Knight and Howarth 1999). This residual flow is primarily wind-driven hence storms and storm surges are particularly important. A large 48 hour winter storm in February 1994 displaced a volume of water equivalent to 34% of the Irish Sea through the North Channel (Knight and Howarth 1999). During low wind events some density driven currents can become important due to the temperature and salinity differences between the Irish Sea and the Malin Shelf water (Knight and Howarth 1999), but during the summer months it would be expected that residual flow is minimal due to decreased wind forcing. This low residual flow may enhance the retention of larvae within the Irish Sea. The consequence of later spawning is that scallop larvae are present in the plankton for the onset of the increased autumn wind forcing and hence increased residual flow through the northern channel. Thus a biannual spawning strategy is important for connectivity beyond the Irish Sea to the west coast of Scotland, especially if it occurs in autumn rather than late summer.

The inter-annual variation in the timing of spawning shown by our survey and others (Mason 1958) was also observed by the fishers who stated that the annual spawning events

can vary by three to four weeks. This variability in the timing of spawning can mean that the scallop larvae experience different oceanographic conditions from one year to the next which may help explain the temporal variability in recruitment of *P. maximus*.

Synchronicity of spawning

Fishers' observations that most scallops spawn within a day or two of each other suggests a highly synchronised spawning event. However, this is not seen in our results with the coefficient of variation (CV) being, on average, high in both June and October (Table 2.2). Previous work has compared the CV of the highly synchronised population in the Bay St Brieuc, France with less synchronised populations of Scotland and Bay of Brest, France (Mackie and Ansell 1993). Bay St Brieuc showed low CV (<0.1) all year apart from during the spawning event where it rose to just greater than 0.5. Scottish scallops that generally showed a bimodal spawning pattern showed a brief period of synchronisation with low CV (<0.1) immediately following spawning in the spring and autumn (Mackie and Ansell 1993). At other times the CV rose and remained between 0.1 and 0.4. Bay of Brest scallops which show year round "trickle" spawning, never showed a period of synchronisation with CV alternating between approximately 0.1 and 0.35 (Mackie and Ansell 1993). Our scallops showed CV values of up to 0.78 following spawning in October. Even in June, outside of the spawning period, the majority of sites showed values over 0.3. This suggests that scallops around the Isle of Man are not synchronised in their gonad maturation state and spawning. The discrepancy between the fishers' observations and the survey results is possibly due to the interpretation of the question and a matter of perspective. Fishers will seek the site with the best quality gonads in a high proportion of their catch. So if, for example, a third of the catch has spent gonads they likely will seek alternative sites, with the perception that spawning has taken place. However for a scientist a third of the population spawning whilst two thirds have not does not constitute a synchronised event. The result of this perception of synchronisation is that when the fishers move on to new sites, there will be a large proportion of scallops remaining that have ripe gonads and will be able to spawn. Therefore the fishing strategy of targeting scallops with ripe gonads will have less of an impact in the "bet hedging" reproductive strategy than on a tightly synchronised spawning strategy. The lack of synchronisation can mean that reproductive failure due to a single environmental event is less likely than in populations with a single synchronised event (Paulet *et al* 1988).

However, “bet hedging” as a reproductive strategy, by having multiple spawning events, can cause difficulty in fertilisation due to Allee effects; a decreased probability of two gametes meeting compared to a large peak in spawning (Sastry 1979). This can also be compounded if sedentary species, such as *P. maximus*, occur in low densities as on commercially fished grounds. Work on sea urchins found that fertilisation success dropped significantly when the distance to the nearest neighbour increased above just a few metres (Levitan 1991; Levitan *et al.* 1992). The densities of scallops found on the commercial beds in the Isle of Man were extremely low at a maximum of 14 individuals per 100m² (Brand and Prudden 1997). However this is an average over the length of the tow and the variance between tows suggests it is likely that the distribution is patchy with aggregations at higher densities between areas of low or no scallops.

Spatial variation in gonad maturation state

The fishers reported that scallops found at different sites around the Isle of Man spawn at different times. Our survey showed that there was a significant difference between the RGH at different sites which supported this observation. The information regarding the order in which sites spawn is more difficult to interpret. There was no consensus among fishers regarding which sites spawned first and this was mirrored in our results, such that most sites had at least some scallops at the same GOI stage (Table 2.1). However, five out of eight fishers reported that scallops at the deeper Chickens site spawned last. This was the case in our survey in 2010 when chickens had the highest percentage of recently spent, stage seven gonads while other sites were showing signs of recovery from spawning (Table 2.1). The 2009 results were confused by the presence of the partial spawning, making it very difficult to work out which sites had spawned first or last.

The observation of the fishers that scallops at deeper sites spawn later in the year than shallower ones could not be validated by our data.

Modelling drivers of gonad maturation state

The generalised additive model found that shell height, rate of decrease in temperature over the previous month, the degree of thermal stratification, scallop density and average annual chlorophyll a concentration all had a significant effect on the gonad weight. The effect of shell height is not surprising as larger the scallops would be expected to have larger

gonads. Using the model to predict gonad weight at different shell sizes shows that the greatest gain in gonad weight for an increase in shell length of 5mm is found between 85mm and 90mm. Small gains are then made up to a shell size of 100mm where-after the relationship is approximately linear with around 0.4g gonad weight added per 5mm of shell. With the mean gonad weight equalling 3.99g this equates to around 20% gain in gonad size between the lower United Kingdom (UK) MLS of 100mm and the higher MLS implemented in the Isle of Man of 110mm and other parts of the UK. The relationship between large parental size and larger eggs which, in turn, increases offspring fitness is well documented in fishes (for example: Eium and Flemming 2000, Vallim and Nissling 2000, Chambers and Leggett 1996, Parker and Begon 1986). However, in marine invertebrates there appears to have been less focus on this issue in the literature. A study by Valentinsson (2002) found that the maternal size in whelks led to a greater number of eggs and hatchlings but not larger offspring. To our knowledge there have been no similar studies in Pectinids, however given larger gonads one would expect the production of greater numbers of egg and sperm. Therefore, the difference between the lower landing size limit of 100mm found in some parts of the UK and 110mm in other areas and the Isle of Man could equate to considerable increase in reproductive output. However, growth rates vary considerably around the UK and in some areas scallops rarely reach 110mm due to food limitation (David Palmer, CEFAS, Pers. COMM.) and therefore in those areas a MLS of 110mm would be inappropriate. It is also important to note that Mason (1958) found that scallops only spawn once a year in their first two breeding seasons (age two and three). Unpublished survey data from Isle of Man shows that the average shell length at age 3 ranges from 92mm at BRO to 107mm at RAM with a mean size across all sites of 102.2mm. At age four this increases to 105mm at LAX to 121mm at RAM with a mean of 110.9mm across all sites. All sites except LAX have an average size over 110mm by age five. Scallops from the majority of sites in waters off the IOM, by virtue of the 110mm MLS, are protected until they reach an age at which they will spawn twice in a single year. Therefore a larger scallop protected from fishing mortality to 110mm is likely to produce this 20% increase in the amount amount of eggs and sperms twice in a year. So scallops protected from fishing mortality until 110mm (age 4) will produce 3.4x the amount of eggs and sperm in their lifetime compared to a scallop that suffers fishing mortality at 100mm (age 3) (Table 2.3).

Table 2.3. Calculation of increase in reproductive output of a scallop experiencing fishing mortality at 110mm (4 years) scallop compared to a scallop experiencing fishing mortality at 100mm (3 years), including a 20% increase in gonad weight between 100m and 110mm

Fishing mortality	Yr 1	Yr2	Yr 3	Yr 4(spring)	Yr 4(autumn)	Total
100mm (age 3)	Virgin	Virgin	1x	dead	dead	1x
110mm (age 4)	Virgin	Virgin	1x	1.2x	1.2x	3.4x

Rate of change of temperature

The decrease in temperature over the month prior to sampling suggests that the rate of change in temperature is a trigger for the onset of gonad maturation and spawning in the autumn. The sites with the smallest change in temperature had low gonad weight and a GOI suggestive of recent spawning and early stages of recovery (stages three and seven). The scallops sampled from the sites associated with the largest changes in temperature exhibited a larger effect on gonad weight and had GOIs suggestive of less recent spawning with greater evidence of recovery (stage four). The drop in effect with a higher rate of temperature change seemed to be driven primarily by LAX in 2009 which had a large proportion of spent, low weight gonads (stage 7) but also had recovered gonads suggesting a partial spawning earlier followed by the more recent spawning event.

Long term drivers of gonad weight

The effect of the rate of change of temperature on weight represents a short-term response associated with a biannual spawning event. The remaining parameters in the model were needed to explain the portion of the spatial variation in gonad weight that caused long-term responses to spatial heterogeneity in the environmental drivers.

The effect of scallop density on gonad weight suggested that greater densities of scallops lead to higher gonad weights. This perhaps sounds counter-intuitive considering the potential effects of increased competition but may be due to the fact that the sites with higher scallop densities may be associated with favourable conditions for scallop growth, greater investment in gonad production and higher survival. In general, higher average annual chlorophyll concentration had a positive effect on gonad weight. A single scallop sampling site had high chla with a lower effect on gonad weight (RAM). This site is unusual in the fact that it is very shallow and is exposed to inputs from a sewerage outflow and

hence high inputs of particulate organic matter (POM) that stimulate primary production. However the potential positive effect of gonad growth associated with these high food levels is perhaps counteracted by the negative effect that high levels of turbidity have on growth. High turbidity decreases growth rates as it is energetically expensive to expel silt (Morel and Bossy 2001) and large aggregations of POM can clog the gills (Chauvaud and Paulet 1998). The only parametric term in the model was the stratification index. Increased stratification was associated with lower gonad weights in scallops compared to scallops from sites experiencing a mixed water column. This is to be expected; with such sites experiencing bottom temperatures around two degrees cooler than mixed waters (Shammon 2007) which would lower metabolism and decrease growth rates (Chauvaud and Paulet 1998). In addition sites with stratified waters will not experience the same rate of bottom temperature decrease in the autumn as those sites with a mixed water column. This could lead to later onset of gonad maturation due to lack of this environmental stimulus.

Conclusions

In general fishers' observations on the spatial and temporal variability in scallop gonad status and spawning events in the Isle of Man were accurate and validated by this study. When fishers' observation deviated from empirical data it might be explained by the differences in perspectives of fishers compared to scientists. This highlights that questions should be explicit and avoid language that can take on different quantitative meanings depending on an individuals' priorities. However, when appropriate questions are asked the knowledge of the fishers can provide useful insights into the ecology and biology and focus research towards specific hypotheses.

This study shows that the reproductive status of king scallops in Isle of Man's waters is spatially variable over just a few kms and that rate of change in temperature acts as an environmental stimulus for the autumn spawning event. However, the within site variation is also very high, so these scallops are adopting a strategy which spreads the risk associated with environmental unpredictability by having an extended spawning season, thereby avoiding complete reproductive failure due to unfavourable conditions, which is more likely in a single synchronised event. Some years show higher within site variation in gonad maturation status than others, this poor synchronicity could cause decreased fertilisation

success, especially in low density locations. Therefore areas closed to fishing which allow accumulation of high densities of adult scallops can ameliorate this risk.

The fishers perceive that scallops at a single site spawn within a day or two at which time they will then fish at alternative sites. The current study suggest that the spawning event within a site is much less synchronised than the fishers perceive and as a result, when the fishers move on to new sites, there will be a large proportion of scallops remaining that have ripe gonads and will be able to spawn. Therefore the fishing strategy of targeting scallops with ripe gonads will have less of an impact in the “bet hedging” reproductive strategy than on a tightly synchronised spawning strategy.

Gonad weight increases significantly with shell size and the 110mm landing size in the Isle of Man may increase reproductive output by up to 3.4 times over a 100mm landing size.