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Seasonal variations in the flesh weights and biochemical content of the scallop *Pecten maximus* L. in the Clyde Sea Area

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Monthly samples of *Pecten maximus* (L.) were obtained from a number of localities in the Clyde Sea Area from May 1966 to March 1968. Statistical analysis of various growth parameters confirm that there are significant differences between populations, and consequently the shell cavity volume has been the parameter used against which other measurements have been compared. The method of volume determination is described.

The wet and dry weights of adductor muscle, gonad, and remaining tissue were estimated each month for a 'standard scallop' of 75 ml, and the weight of carbohydrate and protein (determined from freeze dried sub-samples), calculated for the dried flesh.

The large adductor muscle doubled its weight between March and November, and this was directly related to the increase in the weight of carbohydrate by a factor of 20, and protein by a factor of 1·5. These reserves were depleted during the winter and spring, commensurate with the loss of flesh weights. The digestive gland showed similar weight fluctuations, probably related to the lipid content. Calculation of the calorific value of the reserves indicate that this is only half the equivalent reserve in the large adductor muscle. The gonad showed seasonal variations associated with the sexual cycle, but the biochemical variation was slight. In the main population examined the gonad increased in size during the winter and early spring, whilst other tissue weights and their reserves were falling. Spawning occurred during the early summer, and there was little or no recovery until the following winter.

It is suggested that during the winter the carbohydrate reserves form the basic metabolic substrate for the scallop, whilst the nitrogen reserves in the muscle and digestive gland are utilized to produce the gonad. There is some evidence to suggest that following spawning, gametogenesis and release of gametes may occur continuously, without the development of a large gonad until the winter, when the maturation of the gametes ceases.

Scallops transplanted from a population in a relatively unfavourable environment to an area with no indigenous population showed variations in their growth parameters, and a 50% increase in the weight of flesh compared to the parent population. The range of variation of reserve materials was comparable.

Introduction

Apart from the general biology, the majority of work relating to the scallop has been concerned with its commercial importance. Until recent years the fishery has been restricted to the winter months, at which time the gonad is large, brightly coloured, and therefore most attractive to the consumer. With the increasing use of canning and deep freezing techniques, allowing the fishery to operate throughout the year, more information relating to the weight and biochemical content of the flesh is of increasing commercial importance, as well as biological interest.

The present investigation was made to determine whether there was a seasonal fluctuation in the flesh weight of the scallops in the Clyde. All tissues were included, in order to compare the results with those of other workers dealing with non-commercial bivalves. The biochemical content of selected tissues was also determined.

Material

Scallops were dredged from a number of places in the Clyde Sea Area (Fig. 1). The nature of the substrates varied from a clean coarse sand (Girvan) to a soft muddy sand with clinker and stones (Lion Rock, Cumbrae). Several hundred experimental scallops were transplanted from the Tomont End (Cumbrae) ground to a very soft muddy sand found in a sheltered channel close to Fairlie, here referred to as the Fairlie Ground, and subsequent samples

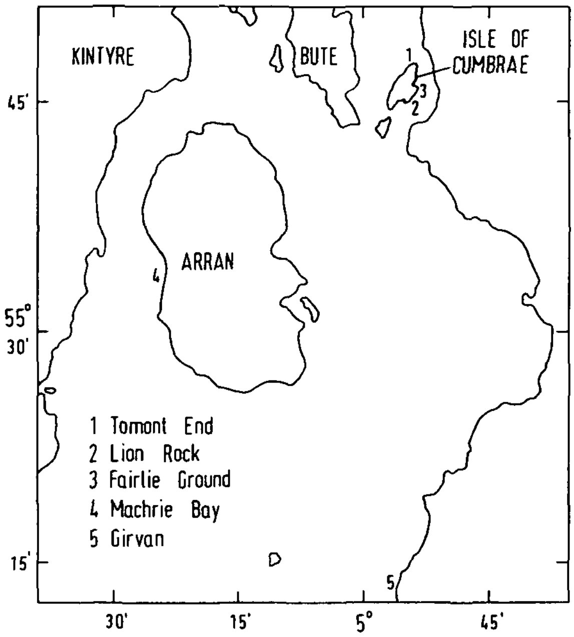

Figure 1. Localities in the Clyde Sea Area from which samples of scallops were obtained.

were recovered by Scuba diving. No indigenous scallops were found there prior to the layings, despite extensive diving in the area.

Regular monthly samples were taken from the Tomont End ground from May 1966 until March 1968, and the other grounds were sampled as occasion allowed.

Methods

Morphology

In species in which the shells are self-sealing, a rapid estimation of volume can be obtained by a simple displacement apparatus (Baird 1958). As *Pecten* is not self-sealing, direct measurement of volume of the entire animal was impracticable because the water in the mantle cavity could not be retained, and a special technique had to be developed.

Volume measurements

These were made with the displacement apparatus (Fig. 2) which consisted of a watertight perspex box with an aperture at the top large enough to take a scallop. A side tube of 3 mm bore was inserted 40 mm below the expected water level and extending vertically to at least 100 mm above the water level. The box was filled with water to a predetermined level, and xylene pipetted into the top of the side arm to give a layer about 5 mm deep on top of the water column. This side tube acted as a measuring column, and the xylene ensured a smooth flow up and down the tube.

A sliding millimetre scale was clipped to the tube so that the scale was visible through the xylene layer, which acted as a lens. The meniscus in the tube could be zeroed by means of the sliding scale, and when an object was immersed in the box the vertical rise of the water level could be read off the scale.

To ensure that the meniscus was always viewed from a constant angle, a 40 mm length of perspex tubing with a 9 mm bore was cut down the mid-line for a distance of 25 mm and one of the lengths of sectioned tube was removed. At right angles to the cut surface a hole was bored in the 15 mm length of intact tubing to clear a 10 mm diameter rod at least 100 mm long which was attached vertically to the perspex box, 30 mm in front, and 10 mm to one side of the measuring column. The tube – the horizontal viewing bar in Figure 2 – could be moved vertically to any desired level. The cut surfaces of the half section of the tubing provided two flat horizontal and parallel surfaces, which when lined up by eye ensured a constant viewing angle. The surfaces were painted red, so that when the viewing angle was properly adjusted, a thin red line was visible: any vertical deviation from the correct angle caused a broadening of the line. The red line was aligned with the meniscus in the measuring tube when readings were made. Easier and quicker readings were made with the cut surfaces directed downwards, and the red line aligned with the top of the meniscus. The apparatus was calibrated by adding known volumes of water to the vessel after it had been set up and zeroed, and the rise in the measuring column read off the scale.

After removal of the meat the paired shells were thoroughly air-dried and fitted together as closely as possible. This necessitated the removal of at least half the ligament. The shell edges were sealed with 2 cm wide strips of a proprietary sealing tape (such as 'Sylglas' or 'Densitape'), particular care being taken to ensure that the very large 'ear' apertures were properly sealed. The sealed shells were placed in luke-warm water for 2–3 min to soak, in order to avoid the formation of adherent surface bubbles when immersed in the apparatus. The soaked shells were roughly dried on a cloth, and immersed in the displacement apparatus. Air trapped in the shells exerted considerable pressure on the sealing tape when the shells were immersed, and speed was essential when taking readings in order to avoid leaks developing, as demonstrated by escaping air bubbles.

The volume of tape used to seal the shells was

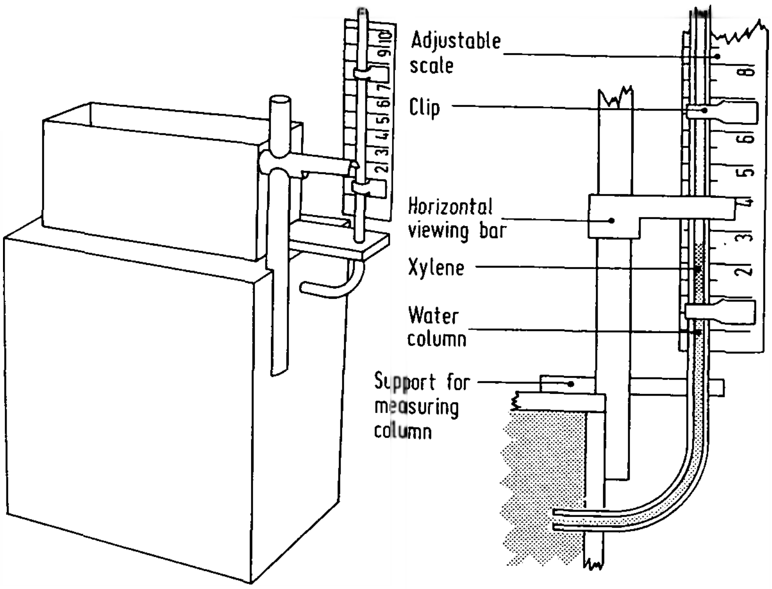

Figure 2. Apparatus to determine the shell cavity volume of individual scallops.

determined, and subtracted from the total volume.

The volume of the shells was determined by suspending them in the vessel on a corlene loop, care being taken to ensure that no air was trapped in the concave proportion of the shell.

Linear measurements

Mason (1957) has given an account of the relationship between length (anterior – posterior axis), breadth (dorso – ventral axis), thickness or width (lateral axis), and age of the scallop in Manx waters. The same method of measurement has been adopted for this investigation. Total length or breadth relates to the values obtained for the curved right valve, whilst values derived from measurements of the growth rings relate to the flat valve.

The degree of curvature of the valves was measured by placing each one, inner surface downwards, on a level surface and measuring the height from the surface to the highest point of the shell by means of an engineers set square. A 'population regression', based on the length and volume measurements of 50–100 shells, was calculated for each collecting ground and was used to estimate the volume of all subsequent scallops obtained from that ground.

Flesh Weights

Each month approximately fifty scallops were collected from Tomont End and used to determine the flesh weights, biochemical content and various growth parameters. Scallops from other grounds were similarly treated, but the numbers varied according to availability. Each individual was divided into three main fractions; (1) large and small adductor, (2) gonad (including the entire testis which was excised close to the digestive gland, and consequently included the foot which represented approximately 4·2% of the dry weight of the spent gonad), and (3) the rest of the body which included the gut, gill and mantle. During the last nine months of sampling the small and large adductor muscles were weighed separately, and in a few of the later samples the digestive gland was also weighed separately. For each fraction the fresh wet weight and the weight after drying to constant weight at 85–90°C were determined. The dry weights have been used as the main basis of all comparisons throughout this paper.

All weights were plotted against the shell cavity volume and a line fitted by eye (Fig. 3). From this line the weight of a 'standard animal' of 75 ml shell cavity volume was estimated and used to compare the various monthly samples obtained from the same or from different populations (Barnes, Barnes and Finlayson, 1963; Ansell and Lander, 1967; Ansell and Trevallion, 1967).

Gonad Condition

Determination of gonad condition as defined by Mason (1958) proved difficult as there was no correlation between a 'full' gonad and a gonad in spawn-

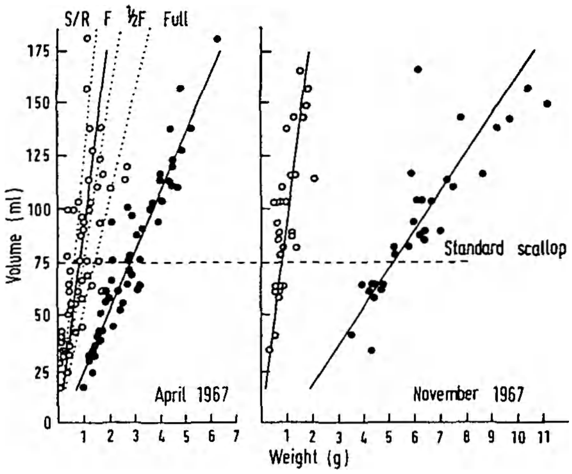

Figure 3. Plots of the dry weights (g) of the gonad (open circles) and combined large and small adductor muscle (solid circles) against the shell cavity volume (ml) of samples of scallops collected in April and November 1967. Trend lines fitted by eye. Classification of gonads: SR, spent-recovering; F, filling; ½F, half-full; and Full.

ing condition. Thus it was possible to have a population with mainly large distended gonads which were obviously 'full' but not in spawning condition, concomitant with a population with thin, meagre gonads which were ready to spawn, but which by comparison with the condition of the first population were barely 'half full'. To standardise the assessment of condition as much as possible, the dry weight of the gonad was used as the basis of classification (Fig. 3). The lower limit was set using weights obtained from obviously 'spent' scallops, and the upper limit from weights obtained from readily recognisable 'full' animals. 'Filling' and 'half-full' values were arbitrary points between the two set values. Thus for the 'standard' scallop, gonads with a dry weight of 0–0·6 g were 'spent recovering', 0·6–0·95 g were 'filling'; 0·95–1·5 g were 'half-full'; and over 1·5 g were 'full'. It is possible that in populations with consistently large gonads the amount of non-germinal material may be greater than in populations with small gonads, but it was assumed that the difference was not of such magnitude as to require a correction factor for each population examined.

Biochemical Analysis

At least 5 scallops were selected from the Tomont End monthly sample as being of approximately the same size, age and condition. A representative sample of large adductor, small adductor, testis, ovary and digestive gland was taken from each individual, the respective tissues amalgamated, homogenised in a Buhler homogeniser, freeze dried and stored in a desiccator. The dry weight of the individuals from which the samples were taken was corrected by calculation. In a number of cases the tissues from individual animals were analysed separately in order to estimate the variation to be expected between animals and groups of animals of the same length or age in a population (Table 1). Where few scallops were obtained, as, for example, from the Fairlie Ground and the populations from the southern Clyde, the analysis was carried out on each individual.

Carbohydrate

Determination of carbohydrates was carried out photometrically using the method of Trevelyan and Harrison (1952). The sample of tissue was suspended in 1 ml of distilled water and 5 ml of 0·2% anthrone in 6 parts H_2SO_4 and 2 parts H_2O added, mixed rapidly and placed in a boiling water bath. The tissue was not deproteinised, any colour interference being corrected using blanks without anthrone. In practice only the digestive gland and to a lesser extent the ovary and testis gave significant interference colours. Trevelyan and Harrison (1952) specify 5 H_2SO_4: 2 H_2O but at this concentration some precipitation of the anthrone occured on cooling, and the ratio was increased to 6:2 to overcome this problem. The solutions were read at 620 nm, and the results plotted against standard glucose solutions of 25, 50 and 100 µg/ml.

Nitrogen

Determination of nitrogen was carried out using the normal Kjeldahl technique. The NH_3 released during the steam distillation was passed into 2% boric acid with bromol-cresol green and methyl red as indicator. The solution was titrated with standardised HCl calibrated against ammonium sulphate. It was assumed that all the nitrogen was in the form of protein and the figure obtained by the above method was multiplied by the factor 6·25 to give the estimated amount of protein present.

Ash

Samples were oven-dried at 85–90°C, weighed after cooling in a desiccator, placed in a muffle furnace at 500°C for at least 3 h, cooled in a desiccator and weighed. The difference in weight between the material before and after oven-drying was on average 2·7%, and the biochemical results have been corrected to allow for this residual water. All values

Table 1. Results of the analysis of the large adductor muscle from individual scallops from Tomont End and Fairlie Ground

July 1967	Tomont End											
	Group 1					Mean	Group 2				Mean	Grand mean
Breadth (mm)	76	78	80	81	82	79	106	106	106	109	107	92
Age (yr)	4+	4+	6+	5+	4+	5+	6+	8+	8+	9+	8+	6+
% Protein ...	77·02	72·23	76·01	70·47	81·13	75·38	76·58	75·09	73·50	71·24	74·10	74·61
% Carb......	11·47	15·58	12·55	14·37	8·13	12·42	9·58	13·95	15·81	12·81	13·04	12·69

July 1967	Fairlie Ground								Tomont End November 1967					
								Mean	Group 1					Mean
Breadth (mm)	101	107	107	109	110	113	114	109	88	89	89	90	90	89
Age (yr)	6+	5+	9+	9+	7+	6+	8+	7+	4+	4+	4+	4+	4+	4+
% Protein ...	70·54	67·68	67·40	59·64	63·63	67·80	60·54	65·32	70·37	65·98	74·05	64·59	66·79	68·36
% Carb......	20·54	30·30	30·48	30·08	32·39	28·43	35·14	29·62	21·66	24·47	18·88	26·57	24·27	23·17

November 1967	Tomont End												
	Group 2					Mean	Group 3					Mean	Grand mean
Breadth (mm)	103	103	103	103	105	104	113	114	114	116	117	115	103
Age (yr.).....	5+	6+	6+	7+	9+	7+	7+	7+	8+	9+	9+	8+	7+
% Protein ...	60·36	56·09	65·44	68·38	58·85	61·82	67·98	67·65	65·98	62·64	68·37	66·52	65·67
% Carb......	25·39	26·63	18·89	21·10	22·98	23·00	24·88	22·98	23·68	21·50	21·19	22·85	23·01

therefore relate to oven-dry weights. Results are expressed throughout either as percentages of dry weight of tissue (Tables 1 and 7) or as the estimated total weight of dried material calculated from the dry weight of tissue present in a scallop with a shell cavity volume of 75 ml – generally referred to as a 'standard scallop' (Tables 6 and 9).

Results

Morphology

Regressions of various parameters are given in Tables 2 and 3, and a covariance analysis based on Fisher's test has been used to compare regressions from different populations or different months (Table 4).

The figures indicate that there is a high degree of correlation between the majority of parameters used, including volume. The low correlation between the curvature of the flat shell and the breadth is possibly related to the change in shape, from concave to convex, during the first three growth periods. The variations between Fairlie Ground and Tomont End scallops, from which the former were taken, are probably related to transplantion, the new growth pattern not having stabilised during the period of collection.

Covariance analyses on population regressions show significant variations at the 5% level for at least one parameter between most of the populations. The noticeable exception is the Machrie Bay and Lion Rock populations which showed no significant differences at all (Table 4).

There was no significant difference between the slopes of the regression lines for curvature of the curved shell between Tomont End and Lion Rock populations, but there was a significant difference between the intercepts at the 1% level. There was a significant difference in slope between the flat shell regressions of curvature at the 5% level.

Seasonal fluctuations in weight have been recorded for *Tellina tenuis* da Costa (Ansell and Trevallion, 1967) and *Mytilus edulis* L. (Boje, 1965), but measurements on Tomont End and Lion Rock scallops indicate no significant monthly changes. The February 1967 figures for Tomont scallops are significantly different from the months in 1966, but on the present evidence this must be treated as an anomaly.

Seasonal variations in flesh weight and biochemical content

Using the percentage composition of the various tissues examined, the actual weight of each consti-

Table 2. Regression constants and correlation coefficients (log-log plots) of shell weight (W) on breadth of flat shell (B_f) for Tomont End and Lion Rock scallops

	Tomont End			Lion Rock		
	b	*a*	*r*	*b*	*a*	*r*
1966						
Aug	2·803	−3·744	0·981	–	–	–
Oct	2·735	−3·607	0·973	–	–	–
Nov	2·812	−3·762	0·964	–	–	–
1967						
Feb	2·569	−3·261	0·971	–	–	–
Apr	2·890	−3·910	0·969	–	–	–
May	–	–	–	2·414	−2·903	0·918
Jun	2·581	−3·294	0·956	3·039	−4·185	0·919
Jul	–	–	–	2·721	−3·550	0·974
Aug	2·475	−3·070	0·963	2·548	−3·202	0·969
Sep	–	–	–	2·122	−2·333	0·924
Means	2·727	−3·587	0·968	2·650	−3·399	0·950

tuent was calculated for a scallop with a shell cavity volume of 75 ml. Where the weight of the large adductor muscle was not known by direct weighing, it was estimated by subtracting the average percentage weight of the small adductor muscle calculated from the record of known weights. Thus the average dry weight of the small adductor muscle was 8·5, 7·2 and 8·2% of the combined large and small adductor muscle of Tomont End, Fairlie Ground and Machrie Bay populations respectively (Table 6). The ovary and testis have been amalgamated as gonad, calculations being based on the assumption that each tissue accounted for half of the entire organ. Total flesh weights are also given (Table 5; Fig. 4).

Muscle

Analyses of individual scallops (Table 1) show a reasonable degree of uniformity between size groups, although individual variations can be considerable. The fluctuations in the body weight of the Tomont End scallops were followed for the entire 27 months of the investigation, except for a break in March 1966 (Figs 4, 5, 6).

The seasonal trend in the combined adductor muscle weight shows a fall throughout the late autumn and winter, and a rise throughout the late spring to early autumn, the lowest values being recorded in March or April and the highest from

Table 3. Regression constants and correlation coefficients of various morphological parameters for 4 scallop populations in the Clyde Sea Area, and for Tomont End scallops transplanted to the Fairlie Ground. Symbols are as follows:

L – length of curved shell
T – thickness or width of shell
W – weight of shell
V – volume of shell cavity
B_c – breadth of curved shell
B_f – breadth of flat shell
C_c – curvature of curved shell
C_f – curvature of flat shell

		L on B_c	L on B_f	T on B_c	V on B_f (log-log)	W on B_f (log-log)	C_f on B_f	C_c on B_f
Tomont End	*b*	1·253	1·583	0·295	3·209	2·727	0·110	0·226
	a	1·289	−0·409	−1·550	−4·494	−3·587	−1·773	0·678
	r	0·990	0·986	0·910	0·961	0·968	0·755	0·926
Fairlie Ground	*b*	–	1·187	–	2·395	2·132	–	–
	a	–	−2·172	–	−3·575	−2·332	–	–
	r	–	0·932	–	0·820	0·810	–	–
Lion Rock	*b*	1·160	1·164	0·287	3·086	2·650	0·077	0·239
	a	−2·375	−0·642	0·119	−4·185	−3·399	2·527	0·168
	r	0·973	0·967	0·822	0·951	0·950	0·540	0·817
Machrie Rock	*b*	1·166	1·197	0·313	2·998	2·451	–	–
	a	−3·327	−4·473	−2·423	−4·005	−3·000	–	–
	r	0·976	0·977	0·916	0·977	0·961	–	–
Girvan	*b*	1·136	1·163	0·310	3·531	2·473	–	–
	a	−0·871	−2·349	−0·831	−5·100	−3·011	–	–
	r	0·961	0·963	0·841	0·941	0·951	–	–

Table 4. Analysis of covariance (Fisher's test) on the regression constants given in Tables 2 and 3; a* and b* indicates level of significant difference for intercept and slope term respectively at 5% (*) and 1% (**) levels. ns = not significant; 0 = test not carried out. Intercept terms are only comparable if there is no significant difference in slope. Degrees of freedom are given in parentheses

Monthly W on B_f (log-log)

Tomont End	Aug	Oct	Nov	Feb	Apr	Jun	Lion Rock	May	Jun	Jul	Aug
Oct	ns (1,92)						Jun	(1,62)			
Nov	ns (1,92)	ns (1,97)					Jul	ns (1,53)	ns (1,54)		
Feb	a* (1,92)	a* (1,97)	a* (1,97)				Aug	ns (1,43)	ns (1,44)	ns (1,35)	
Apr	ns (1,94)	ns (1,99)	ns (1,99)	b* (1,98)			Sep	a* (1,49)	b* (1,50)	b* (1,41)	ns (1,31)
Jun	ns (1,92)	ns (1,97)	ns (1,97)	ns (1,97)	ns (1,99)						
Aug	b* (1,84)	a* (1,90)	b* (1,89)	ns (1,90)	b* (1,91)	ns (1,90)					

Population Regressions

V on B_f (log-log) (above diagonal); L on B_f (below diagonal)

	Tom	F G	L R	Gir	Mac
Tom		a** (1,179)	a** (1,245)	a** (1,183)	a** (1,176)
F G	a* (1,111)		b* (1,136)	*b (1,74)	b* (1,67)
L R	ns (1,157)	ns (1,157)		b* (1,40)	ns (1,134)
Gir	ns (1,106)	a** (1,106)	a** (1,152)		b* (1,71)
Mac	ns (1,112)	a* (1,112)	ns (1,158)	a* (1,107)	

T on B_c (above diagonal); W on B_f (log-log) (below diagonal)

	Tom	F G	L R	Gir	Mac
Tom		0	a* (1,157)	a** (1,106)	a** (1,112)
F G	b* (1,393)		0	0	0
L R	a** (1,460)	b* (1,176)		a** (1,152)	ns (1,158)
Gir	b* (1,388)	a* (1,106)	a** (1,172)		a** (1,107)
Mac	b* (1,420)	a** (1,138)	ns (1,204)	a** (1,133)	

September to November. Year to year variations were marked; thus in November 1967 the muscle was over 20% heavier than in October 1966, whilst in March 1968 it was over 30% heavier than a year earlier.

At Lion Rock the scallops, although geographically close to those at Tomont End, showed different variations but a similar trend (Fig. 5). Thus the seasonal maximum occurred a month earlier.

In scallops from Machrie Bay the muscle weight was noticeably greater than in the Tomont End or Lion Rock populations, and was greater still in scallops from Fairlie Ground.

Calculation shows that for a standard 75 ml scallop the percentage weight changes in the small adductor are comparable to those in the large adductor (Table 6).

Carbohydrate. The percentage of carbohydrate in the large adductor increased steadily throughout the year to a peak of 23·76% in November for Tomont End

Table 5. The total dry weight of flesh estimated for scallops of standard volume from three populations in the Clyde. The ages are based on a growth curve derived from the number of rings and the breadth of the flat shell

	Volume (ml.)	Length of curved shell (mm)	Breadth of flat shell (mm)	No. of rings	Dry weight of total flesh (g) May 1967	Sep 1967
Tomont End	50	98	85	4+	5·0	6·6
	75	111	96	5+	6·5	8·6
	100	122	106	7+	8·1	10·5
	130	132	115	10+	10·1	13·9
Lion Rock	50	93	81	3+	3·9	5·4
	75	106	92	4+	6·3	8·2
	100	117	101	5+	7·8	10·9
	130	127	110	6+	10·2	14·3
Machrie Bay	50	91	80	3+	6·6	7·8
	75	105	92	4+	8·6	10·7
	100	116	101	5+	10·7	13·6
	130	127	110	6+	13·1	17·1

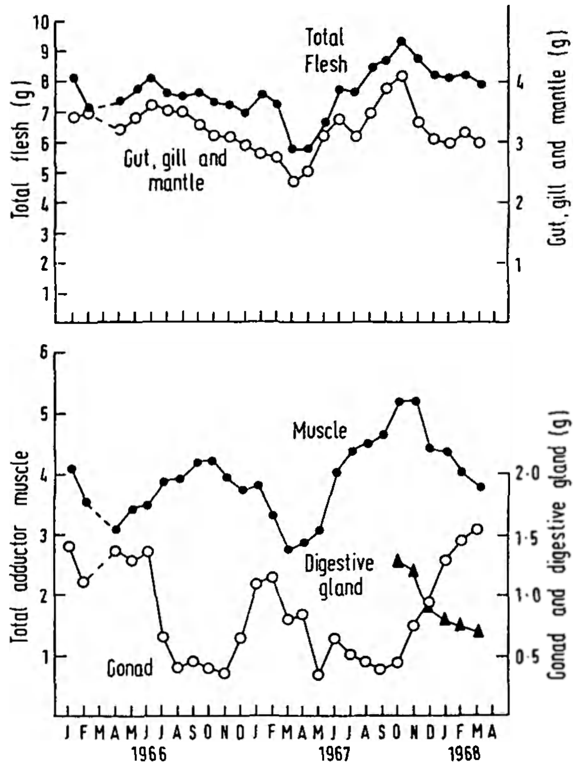

Figure 4. Monthly dry weights (g) of adductor muscles, digestive gland, gut, gill and mantle, and the total flesh, of a "standard scallop" from Tomont End, January 1966 to March 1968.

scallops. The increase in the small adductor was comparatively small, the maximum of 6·31 % being recorded in October, and the decrease a month before that of the large adductor (Table 7).

The weight of carbohydrate in the large adductor (Fig. 6) showed a steep increase from May until November 1967. The fall in
indeed between November ai
tinued more gradually after a slight increase in December to January. The overall trend was very similar to that for the dry weight fluctuations. The weight fluctuations were similar, but much less, in the small adductor (Table 6).

In Machrie Bay scallops the small adductor had a very low content in April 1967, equivalent to that found for Tomont End, but the increase was slightly greater. Fairlie Ground scallops retained a comparatively high content throughout the year but nevertheless showed a marked increase during the summer months. The loss of carbohydrate occurred a month prior to that in the large adductor, as noted for Tomont End scallops. The carbohydrate content of the large adductor in both the Machrie Bay and

Table 6. The dry weight of the small and large adductor muscle calculated for a 'standard scallop' of 75 ml from Tomont End, and the weight of protein and carbohydrate present in the small adductor

Month 1967/68	Dry weights (g) Large	Dry weights (g) Small	Small add./total add. %	Weight (g) in small adductor Protein	Weight (g) in small adductor Carbohydrate
Jul	4·05	0·35	7·88	0·28	0·011
Aug ...	4·13	0·37	8·23	0·31	0·016
Sep....	4·28	0·37	8·02	–	–
Oct....	4·80	0·40	7·78	0·31	0·025
Nov ...	4·85	0·43	8·28	0·35	0·024
Dec....	4·08	0·37	8·32	0·26	0·009
Jan	4·01	0·39	8·80	0·31	0·009
Feb....	3·69	0·36	8·95	0·26	0·004
Mar ...	3·48	0·32	8·48	0·25	0·004

Fairlie Ground scallops was considerable, but the latter were characterised by retaining a large proportion of the reserve, unlike the other populations observed, which utilised the majority of the reserve throughout the winter and early spring.

Protein. With such a marked increase in the percentage of carbohydrate present it follows that a commensurate fall in the percentage protein content should be observed. The weight of protein, however, increased markedly from April until July 1967, after which there was virtually no increase until October when a peak of 6·8 g was recorded. A rapid loss of weight occurred during the following two months, a slow decrease in weight until January and then a rapid fall till March 1968. The noteable appearance of the graph is the 'plateau' period from July to January when the amount of protein remained relatively constant except for the October peak.

but the fluctuations were slight throughout the year. The weight of ash rose very slightly throughout the year with a sharp drop in the December/January period and a slow rise thereafter.

Water. The percentage of water present in both the large and small adductor varied slightly throughout the year. In the large adductor of Tomont End scallops there was an increase of approximately 4 % from the time of peak condition (November) until the seasonal low in the succeeding March. During the corresponding period the water content of the small adductor muscle increased by approximately 2 %. The same trend could be seen in the results obtained from the other populations examined. The

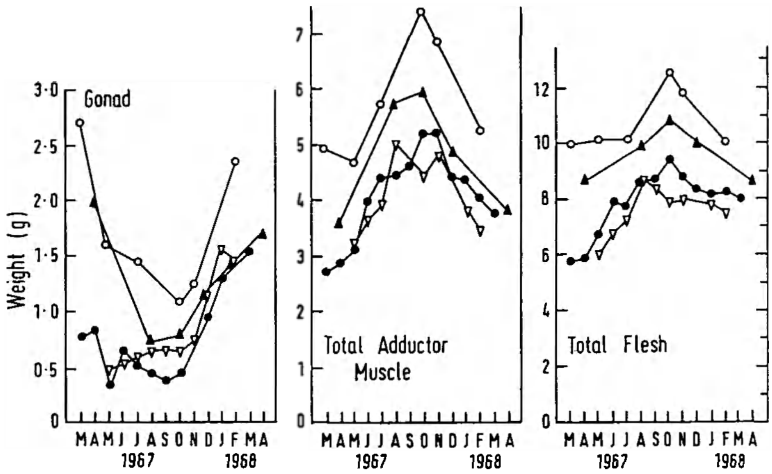

Figure 5. Monthly dry weights (g) of adductor muscles, gonad, and total flesh of "standard scallops" from various localities from March 1967 to April 1968. Tomont End, solid circles; Lion Rock, open triangle; Machrie Bay, solid triangle; Fairlie Ground, open circle.

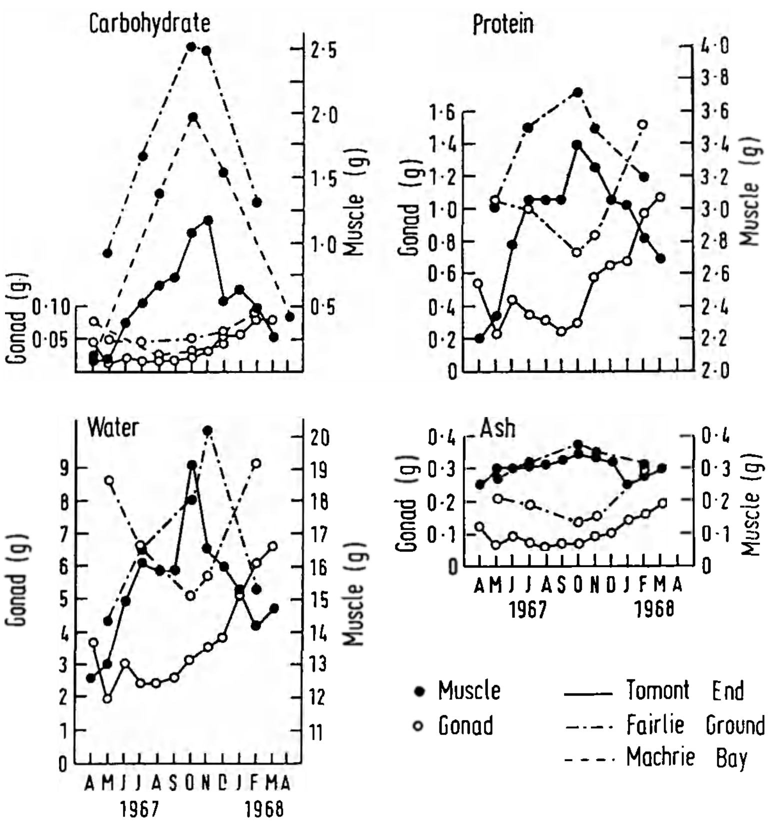

Figure 6. Monthly weight (g) of carbohydrate, protein, water, and ash in the large adductor muscle and gonad of a "standard scallop" at different localities.

Table 7. The percentage of carbohydrate (C), protein (P), ash (A) and water in five of the tissues of the scallop *Pecten maximus* from the Clyde. Water is based on the original wet weights, and the other components on the oven dried weights of the tissues

	Large adductor				Small adductor				Testis			Ovary			☿	Digestive gland				Total flesh
	C	P	A	H_2O	C	P	A	H_2O	C	P	A	C	P	A	H_2O	C	P	A	H_2O	H_2O
Tomont End																				
1967 Apr ...	1·99[1]	83·40[1]	8·65[1]	81·22[1]	–	–	–	–	5·40	64·46	13·67	5·40	64·46	13·67	80·97	–	–	–	–	85·87
May...	2·50	82·40	9·78	80·74[1]	2·20	–	10·22	–	2·88	69·53	15·14	2·39	64·45	24·20	84·24	–	–	–	–	84·88
Jun....	10·39	75·00	7·30	78·63[1]	4·20	–	–	–	2·03	73·05	11·57	4·70	54·03	15·66	81·94	–	–	–	–	82·21
Jul....	12·88	75·32	7·09	78·55	3·09	79·54	7·59	79·82	2·34	69·55	12·36	3·36	–	14·02	81·43	–	–	–	–	83·06
Aug...	16·0	73·80	7·08	77·86	4·19	83·41	7·82	79·24	2·82	75·13	14·02	3·55	60·94	14·23	84·02	–	–	–	–	81·96
Sep ...	17·00	71·60	7·02	77·25	–	–	–	79·37	3·88	67·11	14·27	3·29	58·01	22·44	86·57	–	–	–	–	82·92
Oct ...	22·52	70·60	6·52	78·62	6·31	77·20	6·50	79·12	3·06	72·63	11·08	5·04	58·10	18·38	87·25	7·28	35·78	5·54	72·61	83·18
Nov...	23·76	67·04	6·33	75·86	5·68	80·64	6·76	78·78	3·50	79·63	9·82	4·44	58·79	12·88	82·35	6·95	31·05	7·64	71·20	82·70
Dec ...	13·36	74·68	7·23	77·05	2·52	70·94	7·26	79·12	4·70	81·15	9·67	5·58	55·80	11·89	79·86	9·23	35·71	7·46	72·36	81·21
1968 Jan....	15·76	75·25	5·62	77·64	2·31	79·95	7·23	79·60	3·28	78·27	10·04	4·95	56·79	10·88	78·20	6·62	39·27	9·18	73·78	82·52
Feb ...	13·14	76·09	6·83	77·83	2·97	72·91	7·39	79·07	4·21	79·28	11·13	6·68	54·84	10·60	80·80	4·37	40·97	10·26	74·95	83·16
Mar...	7·44	77·61	7·84	79·45	1·30	77·51	8·75	80·86	3·67	79·92	10·52	6·50	55·97	14·10	81·08	9·59	44·96	10·58	77·10	83·60
Fairlie Ground																				
1967 May...	21·00	68·96	6·09	76·74[1]	5·86	81·28	7·80	–	1·84	76·87	11·06	4·46	55·22	17·21	84·32	–	–	–	–	81·73
July...	31·00	65·60	5·85	76·12[1]	–	–	–	–	1·72	80·55	10·49	4·36	56·86	15·51	81·87	3·16	–	–	–	80·48
Oct ...	36·40	53·99	5·29	72·49	11·50	75·64	5·25	77·71	3·42	77·53	10·42	5·67	55·23	14·47	82·21	4·03	22·11	3·30	60·44	79·98
Nov...	38·64	54·51	5·46	73·17	10·51	70·57	8·08	80·70	3·75	77·45	10·19	5·56	55·31	14·76	81·99	2·88	20·83	5·82	62·54	80·00
1968 Feb ...	27·09	66·16	6·39	76·23	6·34	78·14	8·55	78·96	2·31	78·98	10·89	5·59	50·75	14·02	79·54	2·65	–	5·41	67·04	80·79
Machrie Bay																				
1967 Apr ...	3·27	89·84	8·12	80·08[1]	2·15	–	–	–	2·72	87·15	10·61	4·91	56·82	12·22	79·15	–	–	–	–	83·03
Aug...	26·00	71·21	6·08	74·68	–	–	–	78·71	2·78	67·27	13·12	4·24	51·99	13·64	79·99	3·64	30·58	9·47	–	78·36
Oct ...	35·55	59·94	5·41	74·01	8·84	78·96	7·40	75·52	2·90	84·92	10·70	5·07	59·76	12·45	80·15	8·49	30·65	6·05	67·72	80·01
Dec ...	33·81	50·02	5·96	74·94	6·87	73·67	7·91	78·59	1·81	76·37	18·60	5·09	63·56	11·23	78·58	5·28	24·84	7·01	68·36	80·03
1968 Apr ...	12·22	79·14	7·70	78·22	4·37	86·52	8·10	79·60	–	77·92	13·53	–	53·69	12·30	79·34	–	33·20	16·18	75·28	82·60
Lion Rock																				
1967 May...	5·50	–	–	80·20[1]	–	–	–	–	–	–	–	–	–	–	84·92	–	–	–	–	84·31
Jun....	11·00	–	–	78·95[1]	–	–	–	–	2·49	–	–	3·52	–	–	85·88	–	–	–	–	83·93
Jul....	8·00	–	–	78·92[1]	–	–	–	–	2·65	–	–	3·70	–	–	85·71	–	–	–	–	83·56
Sep ...	21·87	–	–	77·29[1]	–	–	–	–	2·34	–	–	–	–	–	85·02	–	–	–	–	82·16
Nov...	38·64	–	–	76·98[1]	–	–	–	–	2·87	–	–	5·67	–	–	82·95	–	–	–	–	82·87

[1] Combined large and small adductor muscle.

weight of water present followed the general pattern shown by the protein weights.

Gonad

The weight of the gonad varies considerably in relation to the spawning cycle. Wet weight is a particularly inaccurate method of assessment owing to the large amounts of water retained in the lumen of spent and also filling and half full gonads (Mason, 1958) and the variable amount lost when the organ is excised. In the present investigation the dry weight of the gonad has been used as a measure of the amount of flesh, and hence as a measure of condition (Fig. 3).

The gonad of Tomont End scallops showed little change in weight from January until June 1966 (Fig. 4). Spawning occurred in June to July, with a corresponding fall in the dry weight to a very low level. Recovery did not commence until December and continued until February 1967, when the highest value of the year (1·15 g) was recorded. Spawning

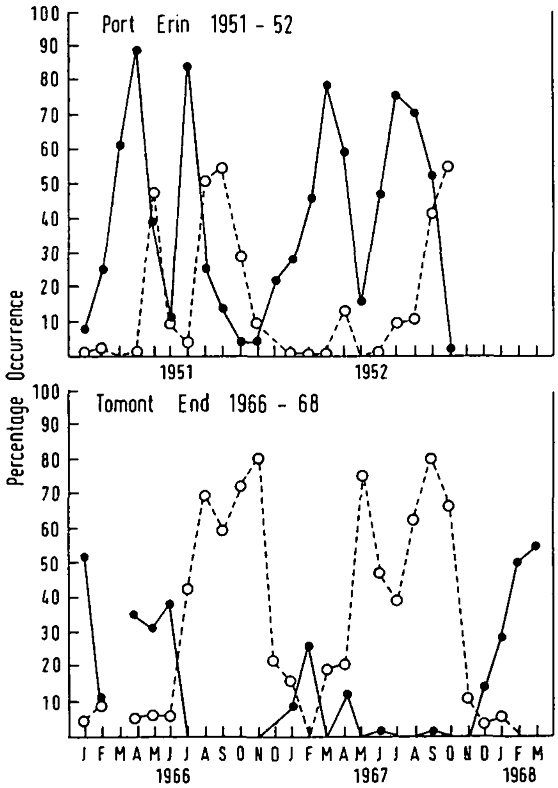

Figure 7. Monthly percentage of spent-recovering (open circles) and full (solid circles) gonads in scallops from Port Erin, Isle of Man (data from Mason, 1958), and Tomont End.

21*

occurred throughout March and April 1967, with the lowest recorded weight (0·35 g) in May. A slight increase in weight in June was followed by a gradual decrease until November, when a sharp increase was recorded, continuing until March 1968, to give the highest value of the investigation (1·55 g).

Lion Rock scallops showed a slow increase in weight from May to November (0·5–0·75 g) and a more rapid increase until January 1968. This was followed by a slight fall in weight in February, possibly due to a small number of individuals spawning (Fig. 5).

Machrie Bay scallops had a very high value when sampling was started in April 1967, (2·0 g), but this had fallen to a very low level (0·75 g) by August. Recovery was apparently very slow, although owing to the wide intervals between the samples it is possible that a recovery and subsequent spawning may have taken place between December 1967 and April 1968. The transplanted scallops from Fairlie Ground retained a very large gonad at all times. The weight decrease from March until October 1967 (2·7–1·1 g) and the subsequent recovery in November 1967 and February 1968 (2·35 g) indicate, however, that spawning occurred at least once during the period from April to October.

Carbohydrate. The carbohydrate content in both the ovary and testis remained at a low level throughout the sexual cycle (Fig. 6). The highest recorded value for the testis was 4·7% and for the ovary 6·7% in the Tomont End population, and these figures corresponded with samples obtained from half full or full animals. For spent scallops the figures were 2·88–3·88% and 2·39–3·29% for testis and ovary respectively, but the lowest percentage recorded for the testis (2·03%) did not correspond with the samples of scallops known to be spent. In the other populations the fluctuation was less marked, but the values obtained were comparable with the Tomont End population. The weight of carbohydrate present was very small and was directly related to the weight of the organ.

Protein. In the testis the percentage protein increased conconmittant with size for the period October to March in Tomont End population, ranging from 67·11% (September 'spent' sample) to 81·15% (December sample). Although the gonad size continued to increase throughout the period from December to March, the percentage of protein remained virtually constant, and compared closely with the one value recorded from the Fairlie Ground scallops, which retained a large testis throughout the year.

The ovary showed a decrease in the percentage of protein with increase in size but this could well be due to the percentage increase of other constituents, – in particular lipid which was not measured. The very low percentage of protein found (54·03–64·45 %), associated with the large discrepancy in the total of the three constituents measured, indicates that another important constituent is present.

The other populations examined had values comparable to those from Tomont End.

As with carbohydrate, the protein weight was directly associated with the amount of reproductive tissue present, with a low value throughout the summer corresponding to the small gonad which was present during this period.

Ash. Both the testis and ovary showed a higher percentage of ash when spent than when the gonad was in better condition. The testis showed a curious phenomenon when ashed. The residue in the majority of cases consisted of a black, vitreous mass which proved resistant to the common inorganic and organic solvents, and to heating to red heat in a bunsen flame. The ash obtained from other tissues was a soft, grey or white powder.

The weight of ash appeared to be directly related to the size of the gonad. Throughout the summer and early autumn only a small weight was recorded, increasing as the gonad size increased throughout the winter.

Water. Water content is only known for the combined ovary and testis. In general the percentage content was higher in the spent gonad than in the filling or full organ, whilst the weight was least in the spent or filling gonad, and greatest in the full gonad, but there was an increasing weight of water present throughout the summer whilst the actual weight of the gonad, reflected in the weight of protein, was falling.

Gut, gill and mantle (Fig. 4)

In general these tissues show the same trend as the muscle. For Tomont scallops there was a slight increase in weight until June 1966, followed by a steady decrease until May 1967, and then a recovery until October when a peak weight of 4·1 g was recorded. The following decrease was initially very sharp, but levelled off in January 1968 at 3·0 g.

Digestive gland (Fig. 4)

The weight of the digestive gland alone was estimated for only a small number of selected animals from each sample beginning in October 1967. This is sufficient to show that the weight changes of the amalgamated tissues referred to above are not due to marked weight changes in the digestive gland as first anticipated. The fall in weight of the digestive gland was an estimated 0·6 g, compared to a fall of 1·1 g in the amalgamated tissue, and whilst most of the weight loss of the latter occurred between October and November, i.e. within the first month, the weight loss in the digestive gland was very small during this period, and occurred more or less evenly throughout the five months during which records were kept.

Carbohydrate. The carbohydrate present in the Tomont End scallops varied throughout the six months of the investigation from 4·37 to 9·59 % with no apparent relation to any of the other fluctuations noted. The figures obtained for the Fairlie Ground scallops were approximately half those obtained from Tomont End and there was little evidence of any marked fluctuation throughout the year. Machrie Bay scallops showed intermediate values, with indications that there were possibly noteable fluctuations as found in the Tomont End population.

Protein. The amount of protein found in the Tomont End scallops was relatively high compared to the values obtained for the other grounds, particularly Fairlie Ground, and the trend was for the percentage to increase with the advent of spring. Thus a steady increase was found from November 1967 (31·05 %) to March 1968 (44·96 %). The discrepancy between the total percentages of the known constituents and the total weight indicates that there is an important constituent not accounted for, most probably lipid, and the possible variations in the amount of this material cause fluctuations in the percentage content of the other constituents, as suspected in the ovary.

Ash. For Tomont End scallops an increase in the percentage of ash occurs throughout the winter and spring. A similar trend is detectable in the figures for Machrie Bay, although the April 1968 figure of 16·18 % is suspect, being so much larger than results obtained from other populations. Fairlie Ground scallops are again characterised by their apparent uniformity throughout the year.

Water. All three populations show a rise in the percentage water content throughout the winter and spring, with Tomont End showing the largest percentages, and Fairlie Ground the least.

Total flesh (Figs 4 and 5)

Water. The indications are that associated with loss of weight in the muscle throughout the winter and

Table 8. The percentage dry weights of glycogen, protein, lipid, ash and the percentage of water calculated from the results of Mason (1959) on the biochemical content of Bay Fine (Isle of Man) scallops in 1952

Percentage analysis											
Muscle (Large and small adductor)						Gonad					
	Jan	Feb	Apr	Jun	Sep		Jan	Feb	Apr	Jun	Sep
Glycogen	14·50	18·98	13·66	17·29	17·36	Glycogen	0·83	1·96	1·16	1·55	0·72
Protein	70·93	74·54	82·93	78·50	66·04	Protein	71·49	72·54	72·83	76·16	70·29
Lipid	2·20	2·31	2·44	1·87	1·51	Lipid	10·33	12·25	4·05	10·88	5·07
Ash	6·17	6·94	6·83	6·54	5·28	Ash	9·09	9·31	12·72	9·33	14·49
Water	77·30	78·40	79·50	78·60	75·50	Water	75·80	79·60	82·70	80·70	86·20

spring there is a commensurate increase in the water content. In the Tomont End population, the lowest recorded percentage (81·21 %) occurred in December, and the highest in the preceeding April. In the other two populations recorded, the trends were similar but the percentage figures slightly lower.

Spawning cycle

In scallops from around Cumbrae, the pattern indicated that the majority spawned in the late spring or early summer. In the period from January to April 1966, however, it appeared that partial spawning of the population occurred, followed by the main spawning in June and July. In 1967 the spring spawning extended from February to May despite the very poor condition of the gonad, whilst in 1968 there was no indication of spawning occurring up to the cessation of sampling in March.

There was little evidence of recovery during the summer and autumn of 1966, but the reduction in the numbers of 'spent/recovering' animals in June, July and August of 1967 indicates that a general partial recovery must have occurred, with subsequent spawning in August and September. In both years the highest percentages of 'spent/recovering' individuals were recorded in September and November.

Discussion

In the past the majority of measurements made on the scallop have been related to length of shell or to age – assessed from the number of growth rings. The comparative biology of scallops from different populations requires a parameter of size to which other measurements may be related, although the fishery would be more concerned with the flesh content at a given age which gives a real estimate of productivity relative to time. As the shell form of lamellibranchs varies between populations owing to crowding, nature of substrate and other environmental factors, (Fox and Coe, 1943; Swan, 1952; Lent, 1967; Seed, 1968) either the shell cavity volume or total weight has been used in oysters and mussels (Havinga, 1928; Baird, 1958). These are difficult to assess in the scallop, but the present results confirm that linear measurements are unsatisfactory for comparing populations.

The weight and appearance of the large adductor muscle was found to vary seasonally, from year to year, and area to area. The appearance of the dried muscle varied from off-white in winter to dark mahogany brown in autumn and this could be related to the amount of carbohydrate which had been stored. This accords with the statement by Tang (1941) that Manx scallops lost condition during spawning, although Mason (1959) found no evidence to substantiate this observation (Table 8). In Tomont scallops partial or complete resorption of the crystalline style occurred when the lowest weights of flesh were recorded, signifying unfavourable conditions (Yonge, 1925).

In the gonad the main variations were associated with spawning, but there was an inverse relationship with the muscle weight during the winter and spring. This suggests that the material for gametogenesis was not derived from the environment, but from a food reserve in the scallop, possibly the muscle.

Fluctuations in the weight of tissues other than the muscle and gonad were only partly accounted for by the digestive gland, but any storage which occurs in the gill or mantle is probably transitory. Thus Lopez-Benito (1956) concluded that there was no storage in these tissues in *Pecten jacobeus*, although his results for the other tissues were comparable to those given here for *P. maximus*.

The calorific values calculated from the carbohydrate and protein measured, and the lipid estimated as the unaccounted fractions showed that the large adductor muscle possessed approximately twice the calorific reserve of the digestive gland. The figures assume that all the nitrogen was present as protein, but in *Tellina tenuis* da Costa (Ansell and Trevallion, 1967) only 75–80 % was represented by protein, the remaining fraction being unaccounted for.

The evidence suggests, therefore, that there is con-

Table 9. The changes in relative and actual weights of the large adductor muscle and gonad, and the monthly incremental weights (in g) of protein and carbohydrate calculated from the dry weights for a 'standard scallop' from Tomont End

Month	Gonad weight	% Variation muscle wt.	Carbohydrate	Protein
Apr–May	–	+ 7·2	+0·02	+0·13
Jun	+	+30·6	+0·30	+0·44
Jul	–	+ 9·2	+0·14	+0·27
Aug	–	+ 2·0	+0·14	+0·00
Sep	–	+ 3·6	+0·07	+0·01
Oct	+	+12·2	+0·35	+0·33
Nov	+	+ 1·0	+0·07	−0·14
Dec	+	−15·9	−0·61	−0·20
Jan	+	− 1·7	+0·09	−0·03
Feb	+	− 8·0	−0·15	−0·21
Mar	+	− 5·7	−0·23	−0·11

siderable accumulation of carbohydrate and protein in the large adductor muscle, and a substantial amount of lipid in the digestive gland during the summer and autumn. This reserve is utilised during periods of environmental food shortage, the carbohydrate supplying the main metabolic substrate, and the nitrogenous reserves the material for gametogenesis. The lack of synchronisation between the gonad and muscle weight relationship in 1966, where the muscle weight fell prior to an increase in the weight of gonad, and in 1967 when both organs were increasing at the same time, supports the view that, as in *Mercenaria mercenaria* (Ansell and Lander, 1967), storage and utilisation can occur independently of gametogenesis and spawning.

The maximum and minimum weights achieved by various tissues differed from year to year, and as has been suggested for other bivalves (Ansell and Lander, 1967; Ansell and Trevallion, 1967), and supported by the present results, this variation in the amount of reserves available must influence the size of the gonad developed in the following spring, and hence the fecundity of the animal. Thus the low reserves in 1966 were followed by a small gonad, whilst the higher reserves in 1967 were followed by a considerably larger gonad.

Mason (1957) found that Manx scallops had an incomplete spawning in the spring, followed by a complete spawning in the late summer, with full recovery during the intervening months. In Tomont scallops the spring spawning proved to be the most important with only partial or no recovery during summer and autumn. During this period both carbohydrate and protein reserves were accumulating, although not necessarily at a comparable rate (Table 9). Laboratory observations showed that viable eggs could be obtained from 'filling' ovaries during the summer months, and also that partial spawning occurred amongst a small percentage of individuals, as reported by Mason (1957). It would appear possible, therefore, that in Tomont scallops gametogenesis and release of gametes took place constantly throughout the summer and autumn, without the intervention of a storage period in the gonad. This would account for the differential storage rates of carbohydrate and protein. It is also possible that gonadial development only occurs if the environmental food sources exceeds a minimum amount, as suggested by the June and October figures (Table 9). Thus in a relatively unfavourable environment, as at Tomont End, the environmental food supply was sufficient to supply the nitrogen for the constant drain of gamete production and release, and some degree of reserve storage, but only occasionally to allow a build up of gonad. In more favoured areas enough food was available to allow greater storage, and also increase in gonad size. The data relating to the animals transplanted to Fairlie Ground illustrate the potential which animals from a mediocre ground can achieve.

It is evident that the relationships between food supply, the accumulation and mobilisation of reserves, and the cycle of gonad maturation and spawning are complex. The present study has suggested some of these relationships, and indicates the need for further research. As the main storage and sexual organs are easily separated, the scallop is a useful animal, but it is difficult to maintain in the laboratory for experimental studies. It is suggested that the other Pectinidae, notably *Chlamys opercularis* (L.) (the 'Queen') or *C. varia* (L.), probably have the same basic physiology, and may prove to be more amenable to laboratory experimentation and control.

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