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REPRODUCTIVE CYCLES OF *CERASTODERMA GLAUCUM* (BRUGUIÈRE) AND *C. EDULE* (L.) WITH SPECIAL REFERENCE TO THE EFFECTS OF THE 1981-82 SEVERE WINTER

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ABSTRACT

Gonadal changes in two species of *Cerastoderma* occurring in discrete populations in South Wales were monitored by stereological analysis during the breeding seasons of 1981 and 1982. Fecundity and spawning efficiencies were determined quantitatively. The relationship between reproductive activity and changes in meat condition are discussed.

Both species are opportunistic breeders. Their normal patterns of reproduction are similar, consisting of minimum activity in winter and peak activity during spring/early summer. The two species were affected differently by the severe winter of 1981-82—*C. glaucum* exhibited a single, 'epidemic' spawning and resumed gametogenesis after a 4-month resting period. *C. edule* adopted a 'polycyclic' pattern without a resting period. Both of these unusual reproductive strategies, augmented by reduced predation resulted in heavy spatfalls.

INTRODUCTION

Sastry (1979) reviewed the reproductive patterns of marine bivalves and demonstrated their great sensitivity to environmental fluctuations. According to Newell *et al.* (1982), the manner in which the exogenous variables and endogenous conditions interact to determine the patterns is only partially understood. There may not be a single reproductive strategy for a species, but rather a variety of different patterns depending on the conditions in a given season. There are, for instance, several records of heavy spatfalls following severe winters (e.g. Thamdrup, 1935; Thorson, 1946; Savage, 1956; Boyden, 1972; Franklin, 1972; Verway, 1981). To the best of my knowledge, explanation of such a phenomenon based on concurrent observations on gonadal activity is lacking.

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As part of an extended study on *Cerastoderma glaucum* and *C. edule* in discrete populations in South Wales, stereological analysis was used to monitor the gonad cycles of the two species. The sampling period was punctuated by the severe winter of 1981-82. This afforded an opportunity to compare the patterns of gonadal activity of the two species of cockle during the breeding seasons prior to and immediately after a severe winter. The results of this comparative analysis are presented here and an attempt is made to explain the observed heavy spatfalls that occurred in 1982.

MATERIALS AND METHODS

Histology

The population of *C. edule* studied was at the Burry Inlet in South Wales (National Grid Reference SS 527962) while the *C. glaucum* population was at the Aberthaw Power Station lagoon (ST 035662), the only known site for the latter species in Wales. Ten to fifteen specimens of each species were examined at approximately monthly intervals from November 1980 to December 1982 for *C. edule*, and from May 1981 to January 1983 for *C. glaucum*. The specimens were fixed for processing within 3 h of collection or else kept in a freezer (−10°C) overnight before fixation after thawing.

Because of the diffuse nature of the gonad the material for processing was obtained by trimming off the gills and the anterior and posterior ends of the viscera and foot, retaining the central piece. Such samples were obtained from animals aged between 1 and 3 years (based on winter rings) and fixed in Bouin's fluid for 24 h. Standard techniques of dehydration and wax embedding were employed before sectioning at 6-8 μm. From each animal 6 'serial' sections were obtained by cutting 2 sections at 3 different depths approximately 1 mm apart. Duplicates of such sections were prepared to ensure against procedural damage. The sections were stained in haematoxylin and counter-stained in eosin.

Stereological analysis of the gonad

The gonadal activity of the two species of *Cerastoderma* was assessed quantitatively by means of stereological analysis of the histologically prepared sections using a Weibel graticule as described for *Mytilus edulis* L. and *C. edule* by Bayne *et al.* (1978), Newell & Bayne (1980), Newell *et al.* (1982). The graticule was superimposed on the gonad area (i.e. the region of the visceral mass adjacent to the foot) and the points coinciding with gonad material were counted and expressed as the 'gamete volume fraction' (GVF). This is the proportion of the gonad area that is composed of follicles containing the cells at various stages of gametogenesis. For each animal 12 separate counts were obtained (i.e. 2 from each of the 6 sections) and the averages computed as GVF%. A standard magnification of ×30 was chosen for convenience.

Estimation of fecundity and spawning efficiency

Various methods have been used to estimate the fecundity of bivalves: (1) gonad weight before and after spawning (e.g. Fox & Coe, 1943); (2) soft tissue weight just prior to and after spawning (e.g. Griffiths, 1977; Bayne & Worrall, 1980; Kautsky, 1982); (3) egg counts in squash preparations (e.g. Oertzen, 1972; Ivell, 1981). The first method is inapplicable to *Cerastoderma* because of lack of discrete gonad. The second is inappropriate because changes in meat condition as a result of spawning may be masked by rapid growth during the same period (see Hancock & Franklin, 1972). The third method precludes the inclusion of males in the estimation. According to Prof. A. Lucas of Laboratoire de Zoologie, Université de Bretagne Occidentale (pers. comm., 1982) the reproductive output of male bivalves is higher than females.

Since the gamete volume fraction (GVF) is a direct measure of the proportion of the gonadal tissue which is actually devoted to gamete production, the difference in the GVF immediately before and after the spawning period was considered as a better estimate of fecundity. The spawning efficiency, i.e. the percentage proportion of the gametes which the animals are able to discharge during the spawning period, was expressed as:

$$\frac{GVF_1 - GVF_2\,(=\text{Fecundity}) \times 100}{GVF_1}$$

where GVF_1 and GVF_2 are the gamete volume fractions before and after spawning respectively. This approach was used to compare the gamete production and spawning efficiencies, where possible, of the two species during the breeding seasons of 1981 and 1982.

Condition index

The condition index (meat condition) of the specimens used for the histological preparations was determined prior to fixation. The displacement method employed by Hancock & Franklin (1972) was used. The samples were pooled to minimise errors involved in the reading of the water levels in the measuring cylinder. The condition index (CI) was calculated as

$$CI = \frac{\text{Meat Volume} \times 100}{\text{Whole volume} - \text{shell volume}}$$

where meat, whole, and shell volumes are the displacements (ml) caused by the meat (wiped dry with blotting paper), the intact animal with the valves closed, and the empty shell valves respectively.

RESULTS

Seasonal changes in the gonad and meat conditions

In both species of *Cerastoderma* the cyclical changes in the gonadal activity during the study period were similar in the two sexes. In order to compare the reproductive cycles of the two species from their typical natural habitats the combined means of all the GVF values of males and females were plotted with 95% confidence limits for each sampling data (Fig. 1). The seasonal changes in condition index (CI) are also illustrated in the same figure to demonstrate the effects of the reproductive activity on the meat condition. Inspection reveals some differences in the reproductive patterns of the two

Table 1. *C. glaucum.* Density variations indicating recruitment (spatfall) patterns in the Aberthaw Power Station lagoon during the breeding seasons of 1981 and 1982. (Notice the heavy spatfall in June 1982 due to epidemic spawning.)

	Density (No. m^{-2})		
		Spatfall	
Date 1981	Total	O-Group	Increase in O-Group
14 May	360	0	0
10 June	451	120	120
15 July	1626	1337	1217
12 August	1931	1621	284
16 Sept.	2022	1776	155
14 Oct.	481	392	0
1982			
12 May	166	0	0
16 June	32,290	32,130	32,130
22 July	28,666	28,500	0

species during the successive breeding seasons which will therefore be described separately.

C. glaucum

The GVF value of 59.2% recorded in May 1981 (Fig. 1a) may be regarded as the maximum pre-spawning gonad condition since specimens collected in April that year did not spawn upon stimulation with temperature shock while some of the specimens collected in May did. Eighty percent of the May sample were at their final stages of maturity while only 20% showed signs of spawning. The progressive decline in GVF from 59.2% in May to 8.0% in August of that year may be attributed to a protracted spawning which was evidenced by continuous recruitment during the same period (Table 1). The post-spawning decline in GVF from August reaching 0.5% in November is probably due to the cytolysis or reabsorption of unspawned gametes. By November there was no sign of revival of gametogenesis.

In 1982 the GVF again peaked in May at 53.8% but decreased rapidly to a minimum of 0.4% in July. This was followed by a 4-month resting period and re-initiation of gonadal activity in November. The GVF then increased from 8.1% in November 1982 to only 11.1% in January 1983 indicating a rather slow gametogenic activity over the winter months.

The pattern of changes in the meat condition (CI) followed that of the gonad condition in a similar manner. In both years the CI peaked in May and attained minimum values during the post-spawning resting period. The lower values

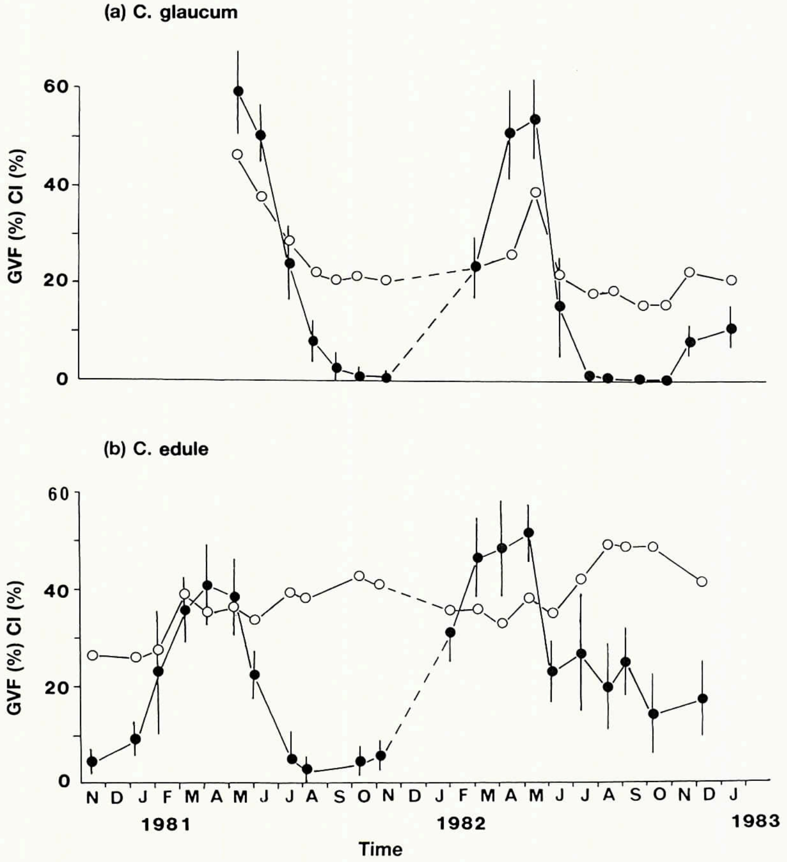

Fig. 1. Seasonal changes in gonad condition (GVF%) and condition (meat) index (CI%). 95% confidence limits for combined male and female GVF are indicated by vertical bars. Closed circles, GVF (%); open circles, CI (%). (a) *C. glaucum* from the Aberthaw Power Station lagoon; (b) *C. edule* from the Burry Inlet.

of the peak CI and GVF in 1982 compared with 1981 may reflect poorer feeding conditions in this lagoon following the severe winter (1981-82). This is strengthened by the lower growth rates (to be reported elsewhere) recorded during 1982 compared with 1981.

C. edule

During the 1980-81 winter there was a slow increase in the mean GVF from 4.6% in November to 8.8% in January (Fig. 1b). The GVF attained a peak value (41%) in April 1981 after which it declined progressively to 4.9% in July due to spawning. The July and August samples showed evidence of gametic reabsorption and by October, re-development had begun. The GVF attained a value of 30.8% in early February 1982 compared with 23% at the same time in 1981. The GVF then peaked at a higher value (51.1%) in May. Following an initial spawning between May and June, subsequent gonadal activity, indicated by the histology of the gonad, was marked by repeated development and spawning through the rest of the summer and autumn. During this period individuals with GVF's ranging from 2.4-61.5% were recorded. These included cockles at stages 1-4 of Kingston's (1974) classification. The gonads of 20% of the July sample contained 'mixed' follicles some of which were at the initial stages of development while the others were partially empty. No spent individuals of *C. edule* were encountered throughout 1982.

The condition index values of *C. edule* were generally higher, and unlike *C. glaucum* the pattern of changes in CI did not follow that of the GVF. In both years there was a slight drop in CI at the period of maximum gonadal activity followed by a rise after the major spawning period. The values of CI during the summer of 1982 were higher than those of the same period in 1981. This suggests better feeding conditions in the environment during the summer of 1982 which in turn supported the repetitive reproductive activity described above.

Another useful comparison of the reproductive biology of the two species would be the degree of synchronisation of gametogenic activity among individuals within the population. In Fig. 2 the variance in GVF estimated for the various samples (10-15 per sample) is illustrated together with the mean GVF for the two species. It is seen that during the spawning period of 1981 the GVF variance of *C. glaucum* declined relatively slowly compared with the rather sharp decline recorded for *C. edule*. This indicates a more protracted spawning in the *C. glaucum* population than *C. edule* in that year. In 1982 the pattern was reversed, with *C. glaucum* exhibiting better synchronisation and completing spawning by the end of June, while spawning in *C. edule* extended into Autumn.

It is also evident from Fig. 2 that the GVF variance of both species increased during the maturation periods and dropped briefly just before the initiation of spawning. The beginning of spawning was marked by a sharp increase in variance followed by a decline towards the resting period. It may be inferred that gonad maturation and initiation of spawning in both species do not take place uniformly throughout the population. The temporary drop in GVF variance prior to the initiation of spawning coincides with the time when the gonads of most specimens are full and probably undergoing physiological ripening.

Fecundity and spawning efficiency

From Table 2 it is seen that the fecundity of 1-3 year old *C. glaucum* was higher than that of *C. edule* of similar age (51.2 and 36.1 respectively) during the 1981 breeding season. The spawning efficiencies, however, were almost the same, that of *C. glaucum* (86.5%) being slightly lower than *C. edule* (88.0%). This means that individuals of *C. glaucum* which had recently completed spawning contained more unspawned gametes than *C. edule*. In other words the spawning of *C. glaucum* in 1981 was partial while that of *C. edule* was relatively complete. This agrees with the findings of Kingston (1974) who studied allopatric populations of the two species on the south-eastern coast of England. In 1982 however, the method could not be successfully applied to *C. edule* because of the overlapping spawnings and re-development which took place from spring through autumn.

It is also evident from Table 2 that both the fecundity and spawning efficiency values of *C. glaucum* were higher in 1982 than in 1981. The massive shedding of gametes which took place over a relatively shorter period (i.e. 'epidemic' spawning) resulted in the heavy spatfall recorded during that year (see Table 1). With regard to *C. edule*, although the fecundity and spawning efficiency could not be determined in 1982, non-quantitative observations on recruitment, supported by verbal communication with the Fisheries Officer in charge of the Burry Inlet cockle fishery, suggest that recruitment in 1982 was higher than in 1981. Both species therefore

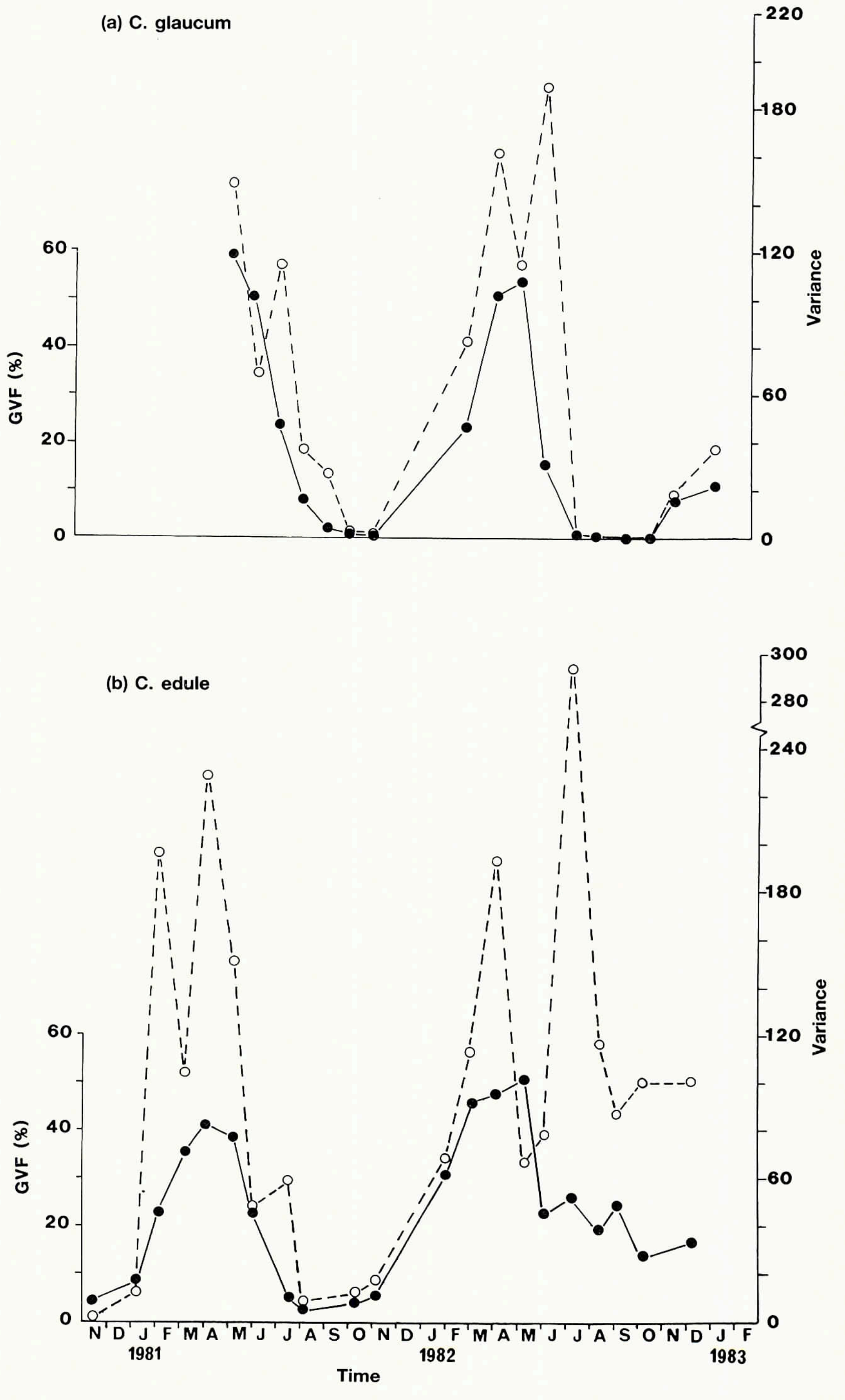

Fig. 2. Seasonal changes in mean GVF and GVF variance. Closed circles, GVF (%); open circles, GVF variance.

Table 2. Fecundity, spawning efficiency and changes in condition index in *C. glaucum* and *C. edule* (Values extracted from Fig. 1). In 1982 similar calculations for *C. edule* were not possible due to the overlapping spawnings and re-development.

Year	Species	GVF_1 (%)	GVF_2 (%)	Fecundity $(GVF_1 - GVF_2)$	Spawning Efficiency $\left(\frac{GVF_1 - GVF_2}{GVF_1} \times 100\right)$	% Change in CI	Spawning Period
1981	*C. glaucum*	59.2	8.0	51.2	86.5	(−)51.9	May-Aug./Sept.
	C. edule	41.0	4.9	36.1	88.0	(+)8.9	April-July
1982	*C. glaucum*	53.8	0.4	53.4	99.3	(−)54.2	May-June
	C. edule	51.1	—	—	—	—	May-

exhibited improved reproductive effort in 1982 following the preceeding severe winter.

Table 2 also shows that although both species shed similar proportions of gametes during the 1981 spawning period, *C. glaucum* lost 51.9% in meat condition during that period while *C. edule* gained 8.9%.

DISCUSSION

The overall annual patterns of gonadal activity recorded here for the two species of *Cerastoderma* follow the general boreal temperate pattern of maximum activity during the warm spring/early summer months. However, two of the main features of the present results are outstanding and therefore of particular importance—(1) the differences in the relationship of the spawning activity to the meat condition; (2) the impact of a severe winter on the reproductive patterns of the two species.

C. glaucum from an Italian lagoon population is reported to undergo a depletion of glycogen reserves and a decrease in dry weight during and after spawning, and a build-up in these parameters during gametogenesis (Ivell, 1979a). This is paralleled by the present results which show concurrent decreases followed by increases in gamete volume fraction and condition index during spawning and gametogenesis respectively. *C. edule* on the other hand, is reported as being able to grow and accumulate carbohydrates during the spawning period (Hancock & Franklin, 1972; Newell & Bayne, 1980). This also agrees with the present observation of increase in condition index at the time when gamete volume fraction values were falling as a result of spawning. It may however, be argued that this difference between the two species may be environmentally imposed rather than genetic. For example, Boyden (1971), studying a mixed population of *C. glaucum* and *C. edule* in the Crouch estuary (Essex) concluded that both species undergo fattening after spawning. Secondly, Jones (1979) reported a gradual decrease in dry weight due to loss of reproductive products and regression on gonads in *C. edule* on a high level sand flat population. In the lagoon studied by Ivell (1979a) as well as the Aberthaw Power Station lagoon (in this study), food becomes a limiting factor during the late summer post-spawning period resulting in a decrease in productivity. It is also not difficult to envisage less productivity on the high level sand flat studied by Jones (1979) where food may be more limiting than in the more productive estuarine habitats studied by Boyden (1971), Hancock & Franklin (1972), and Newell & Bayne (1980).

It is not easy to ascribe a particular spawning pattern (complete or partial) to either of the two species. The reproductive patterns exhibited by both species in 1981 are different from those in 1982. The 1981 patterns agree generally with those described by most previous workers (e.g. Rygg, 1970; Hancock & Franklin, 1972; Kingston, 1974; Ivell, 1979b; 1981; Lucain & Martin, 1974; Newell & Bayne, 1980). The 1982 patterns, on the other hand, have not been encountered in the literature as far as northern populations of *Cerastoderma* are concerned. Since the 1981-82 winter was rather unusual (severe), the 1981 reproductive patterns which fit those described by other workers may be regarded as 'normal' and the unusual 1982 patterns as 'abnormal'. The abnormal reproductive cycle of *C. glaucum* in 1982 was characterised by an epidemic, non-partial spawning followed by re-initiation of gametogenesis in autumn as against the protracted, partial spawning followed by redevelopment in winter or early spring of the normal pattern. In *C. edule* the abnormal pattern consisted of an incomplete (partial) initial spawning followed by repeated redevelopment and spawning without a resting stage in contrast to the normal pattern in which spawning is complete and non-repetitive followed by a short resting period prior to redevelopment which trails into the next year.

It is of interest to note that the abnormal reproductive strategies of both species after the severe winter resulted in heavy spatfalls in agreement with previous observations cited earlier. Savage (1956) surmised that a severe winter seems to synchronise spawning during the following spring. This explanation seems to apply to *C. glaucum* which exhibited epidemic spawning, but not to *C. edule* which responded to the severe winter by adopting a polycyclic reproductive pattern typical of populations of southern latitudes. It is also possible that the severe winter caused a reduction in the numbers of predators. The mortalities in marine life resulting from the severe winter of 1962-63 in Britain for example, are well documented (see Crisp, 1964). The adult cockles themselves are major predators on their own larvae (Kristensen, 1957; Kingston, 1972; Brock, 1980) and eggs (present observations). Table 1 shows that the density of adult cockles prior to the spawning period of 1982 was less than half that of 1981. This agrees with the suggestion by Smidt (1944, cf. Boyden, 1972) that there was an inverse relationship between the established cockles and numbers of settling individuals.

The heavy spatfalls of 1982 may therefore be explained for the two species as follows:

C. glaucum: There was an improvement in spawning efficiency which was also highly synchronised. Predation was probably minimal and hence more larvae survived through to settlement.

C. edule: Circumstantial evidence based on condition index determinations indicated an improved feeding condition in the estuary after the severe winter. This resulted in improved fecundity and protracted breeding. Predation was probably minimal and hence there was high larval and juvenile survival rates.

It should however, be recognised that the differences in the reproductive strategies adopted by the two species after the severe winter could also be environmentally related. Nevertheless, one possible generalization for both species is that the heavy spatfall resulted from an improved reproductive effort enhanced by reduced predation. The 'abnormal' reproductive patterns exhibited by the two species may thus be regarded as adaptations for re-establishing their populations after suffering high mortalities during the preceeding severe winter.

SUMMARY

The meat condition of *C. glaucum* deteriorated during and after the spawning period, and improved during gametogenesis. That of *C. edule* improved during and immediately after spawning and dropped during the initiation of gametogenesis. This difference in the relationship of reproductive activity and meat condition may be induced by the environment.

Both species of *Cerastoderma* have more than one reproductive strategy. In 1981 the spawning of *C. glaucum*, indicated by changes in the histology of the gonad was 'partial' and protracted (May-August/September). This resulted in an extended period of spatfall from June to September. The spawning of *C. edule* in the same year was relatively 'complete' and less protracted (April-July). In 1982, following the severe winter of 1981-82, *C. glaucum* exhibited 'complete' and epidemic spawning (May-June), while *C. edule* adopted a 'partial' and repetitive spawning throughout the summer and autumn. Fecundity and spawning efficiency estimates indicated that there was improved reproductive effort in both species after the severe winter.

This, probably aided by reduced predation, resulted in the heavy spatfalls of 1982.

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