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A Comparison of the Reproductive Cycles of *Modiolus modiolus* (L.), *Cerastoderma* (=*Cardium*) *edule* (L.), and *Mytilus edulis* L. in Strangford Lough, Northern Ireland

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Summary. This paper examines the reproductive cycles of three ecologically important marine bivalves – *Modiolus modiolus* (L.), *Cerastoderma edule* (L.), and *Mytilus edulis* L. in Strangford Lough, Northern Ireland over a period of almost five years.

Whilst *Modiolus* does not appear to become sexually mature until it is several years old, *Mytilus* and *Cerastoderma* can reproduce in their first and second years of life respectively. In *Cerastoderma* and *Modiolus* sexual maturity is preceded by a period of rapid somatic growth.

The subtidal *Modiolus* population remained in a more or less fully ripe condition virtually throughout the period of this investigation suggesting that this particular population lacked any marked cyclical reproductive activity. We interpret this as evidence of slow but almost continuous release of gametes throughout much of the year, a suggestion which is supported by recruitment data. A small intertidal population of *Modiolus* in Belfast Lough monitored over a period of two years exhibited a much more seasonal cycle. Here spawning occurred mainly during the autumn and winter. These data suggest that localised environmental factors are exceedingly important in controlling the annual reproductive cycle of this species.

Cerastoderma from the mid-tidal sand flats ripened rapidly during the spring and spawned over a relatively restricted period in the summer. In Strangford Lough *Mytilus* occurs predominantly in the low-shore and while it spawns mainly in the spring and summer the annual cycle is considerably more protracted and variable than in *Cerastoderma*.

Variations in the duration of the spawning periods in these bivalves can perhaps be explained in terms of both environmental stability and the immediate physical conditions experienced by these particular populations. The reproductive strategies exhibited by *Cerastoderma*, *Modiolus*, and *My-*

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tilus in Strangford Lough are considered in relation to population stability and to the different patterns of mortality which characterise these species in their respective local habitats.

Introduction

The three species of bivalved molluscs which form the subject of this paper are widely distributed in their respective habitats around the coasts of Northern Europe. Whereas *Modiolus modiolus* (L.), the horse mussel, is essentially a sublittoral semi-infaunal species occurring at depths of 5–300 fathoms, *Mytilus edulis* L. and *Cerastoderma* (=*Cardium*) *edule* (L.) are principally encountered in rocky and sandy intertidal regions respectively. The high population densities frequently achieved by these bivalves together with their widespread distribution strongly suggests that these species perform exceedingly important roles in the energetics of their respective communities. In addition to their ecological importance *C. edule* (the common codkle) and *M. edulis* (the edible mussel) are also widely exploited by the commercial shellfish industry.

This paper details the reproductive cycles of these bivalves over a period of almost 5 years and represents part of a wider ranging investigation into the ecology of these species in Strangford Lough, Northern Ireland, aspects of which have already been published elsewhere (Seed and Brown, 1975; Brown et al., 1976; O'Connor and Brown, 1977). Data for *Mytilus* are rather less detailed than for the other two bivalves since the reproductive cycle of this species in neighbouring Carlingford and Belfast Loughs is already well documented (Wilson and Seed, 1974).

The literature concerning reproduction in *Cerastoderma* and *Mytilus* in European waters is particular extensive in view of the economic importance of *Cerastoderma* and *Mytilus* (see for details: Boyden, 1971; Seed, 1976). Our knowledge of reproduction in *Modiolus* is, by contrast, lamentably poor; the only detailed published account seems to be that by Wiborg (1946) for mussels from Norwegian waters where *Modiolus* does have a certain limited commercial value. Energy metabolism in relation to the annual reproductive cycle has recently been reviewed by Gabbott (1976) for several marine bivalves though more especially for *Mytilus*.

The Study Area

Strangford Lough in Northern Ireland (Fig. 1) is a Nature Reserve supporting a rich and diverse marine fauna and providing important feeding grounds for numerous overwintering populations of waders. Pollution levels and commercial exploitation within the lough are, as yet, minimal. The lough, which is about 20 miles long and 5 miles across at its widest point, opens into the Irish Sea by a narrow inlet, an area characterised by strong tidal currents. It presents a great variety of habitats from extremely exposed conditions at the mouth of the lough, through the tidal races of the Narrows to the very sheltered sandy and muddy bays towards the north of the lough. Several small rivers enter

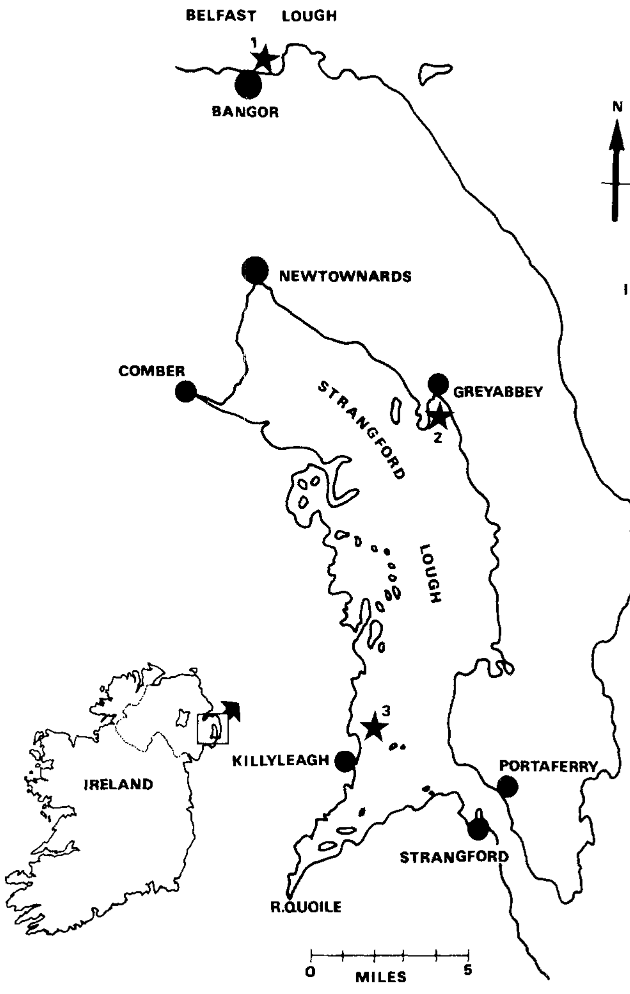

Fig. 1. Map of the study area. Sampling sites are shown by numbered asterisks

the lough but tidal mixing is such that salinities show relatively little seasonal variation.

Although *Cerastoderma* is locally abundant in the mid-shore regions of many of the numerous bays, the population selected for detailed investigation was at Greyabbey about 7 miles south of Newtownards. This area is fairly typical of the sandy beaches in which *Cerastoderma* is a dominant macrofaunal species. Rocks and stony reefs in the low-shore at Greyabbey also support a patchy population of *Mytilus*. The full extent of the *Modiolus* beds in Strangford L. is not yet fully established, but these are known to be extensive. The bed situated amongst the numerous small islands off Killyleagh at depths of 6 to 9 fathoms which were sampled regularly during this investigation, appears to be well over one square mile in extent. *Modiolus* is principally a subtidal species though intertidal populations are occasionally encountered. Such a population was discovered at Bangor in the spring of 1975 on the southern shore of Belfast Lough (Fig. 1) where scattered individuals inhabitating shallow pools and damp cervices occur in the lower reaches of the intertidal region.

Materials and Methods

The course of the annual reproductive cycle in marine bivalves can be assessed in a number of direct or indirect ways each having its own specific advantages and limitations (Seed, 1975). In this investigation, information was obtained from what was considered by us to be the most reliable (and most laborious) method – microscopic examination of the gonad. Here the actual cytological changes during the entire reproductive cycle can be monitored in some detail.

The three Strangford populations were sampled at approximately monthly intervals between January 1972 and August 1976. Smaller samples of the intertidal *Modiolus* population were collected during 1975 and 1976 for comparison with the more extensive subtidal population. Reproductive tissues were removed immediately after collection. In *Cerastoderma* this entailed the removal of much of the descending portion of the muscular foot which, in addition to housing the reproductive tissues, also contains part of the alimentary canal. In *Modiolus* the bulk of the reproductive tissue is contained in a prominent fleshy mesosomal lobe posterior to the foot while in *Mytilus* it extensively pervades the mantle lobes. Tissues were fixed overnight in Bouin's fluid and stored in 70% alcohol. They were later embedded in paraffin wax (as many as 5 to 10 individuals could be accomodated in each block) sectioned at 10 to 15 μm and stained in haematoxylin. From such sections gonads could be arbitrarily classified according to their degree of development and density of gametes. Details of this classification are presented in Table 1 while photomicrographs of various stages in the cycle are illustrated in Figure 2. The relatively rapid rate with which the cycle proceeded in *Cerastoderma* meant that fewer stages could be reliably identified in this species compared with either of the mussel species (see later). The general reproductive condition of each sample was assessed by calculating a mean gonad index. This was obtained by multiplying the number of individuals in each stage by the numerical ranking of that stage and dividing the resulting value by the number of individuals in the sample. Thus a value of 0 is obtained if all the population is completely

Table 1. Arbitrary scheme of classification of gonad condition

	Brief description of gonad	Stages in *Mytilus* and *Modiolus*	*Cerastoderma*
i)	*Resting or spent gonad:*		
	Undifferentiated; no gametes present	0	0
ii)	*Developing stages:*		
	Developing gametes appear; no ripe gametes detectable	1	1
	Ripe gametes appear but majority still developing	2 }	
	Gonad half full of ripe gametes	3 }	2
	Majority of gametes ripe; a few developing gametes still present	4 }	
iii)	*Ripe gonad:*		
	Gonad full of ripe gametes	5	3
iv)	*Spawning stages:*		
	General reduction in density of gametes occurs	4 }	2
	Gonad half empty; unlike developing gonad very few early gametes are present	3 }	
	Gonad approx. three quarters spawned	2 }	1
	Only residual gametes present; cytolysis may be in progress	1 }	

spent whereas a value of 5 (or 3 in the case of *Cerastoderma*) indicates that the entire population is fully ripe. Reproductive development leads to an increase in the index while a falling index suggests that spawning is in progress.

Results

Reproductive tissues of *Cerastoderma* and *Modiolus* of different sizes were examined in order to determine the size at which these species first attain sexual maturity. *Mytilus* is known to mature at a very early age, the precise size at which this occurs depending on local growth rates (Seed, 1969). Figure 3 shows that all individuals of *Modiolus* were mature by the time they measured 40–50 mm in shell length (estimated to be between 4 and 6 years of age). However, a few, possibly slower growing individuals, did show some evidence of gamete development when measuring only 10 to 20 mm. *Cerastoderma*, by contrast, first matures and spawns during its second summer, the first year having been devoted entirely to somatic growth. These cockles, which are then approximately 18 months old, generally measure between 15 and 20 mm in shell height.

Data for the years 1972–1976 are summarised in Tables 2–5 and in Figure 4. The bivalves in Strangford L. exhibit marked differences in their breeding cycles. Subtidal *Modiolus* appears to lack any obvious cycle of development and spawning (except possibly for 1976). The gonad index in this species was consistently high (usually >4.50) with over 80% of the individuals in any one sample in the ripe condition. This apparent absence of any marked annual cycle could perhaps be interpreted as evidence of a slow but more or less constant release of gametes throughout the year, a suggestion which is supported by the continual presence of small mussels (<10 mm) within the population throughout the year. These, however, rarely account for more than 10 to 20% of the total popultion (Seed and Brown, unpub. data).

The reproductive cycle in *Cerastoderma* by contrast shows marked seasonal trends. Most cockles overwinter in the spent condition but once sexual development starts in the spring months it progresses rapidly such that by midsummer the major part of the population is fully ripe. Spawning occurs rapidly over the summer and by August or September most cockles are once again in the spent condition. The brevity of the spawning period is again clearly demonstrated by the relative numbers of new recruits present in the population during the year. The percentage of small cockles (<5 mm) is at its lowest in the summer months but once spatfall has commenced (August–September in most years) numbers rise dramatically such that by the early winter these small individuals frequently account for well over 50% of the total population (Seed and Brown, unpub. data). Winter storms can, however, drastically reduce the numbers of small cockles in the Greyabbey population.

Situated in the lower reaches of the shore at Greyabbey *Mytilus* has to survive the rigors of an intertidal existence for only a relatively short period each day. Compared with the subtidal *Modiolus* population, *Mytilus* has a relatively marked annual cycle though development and spawning is considerably

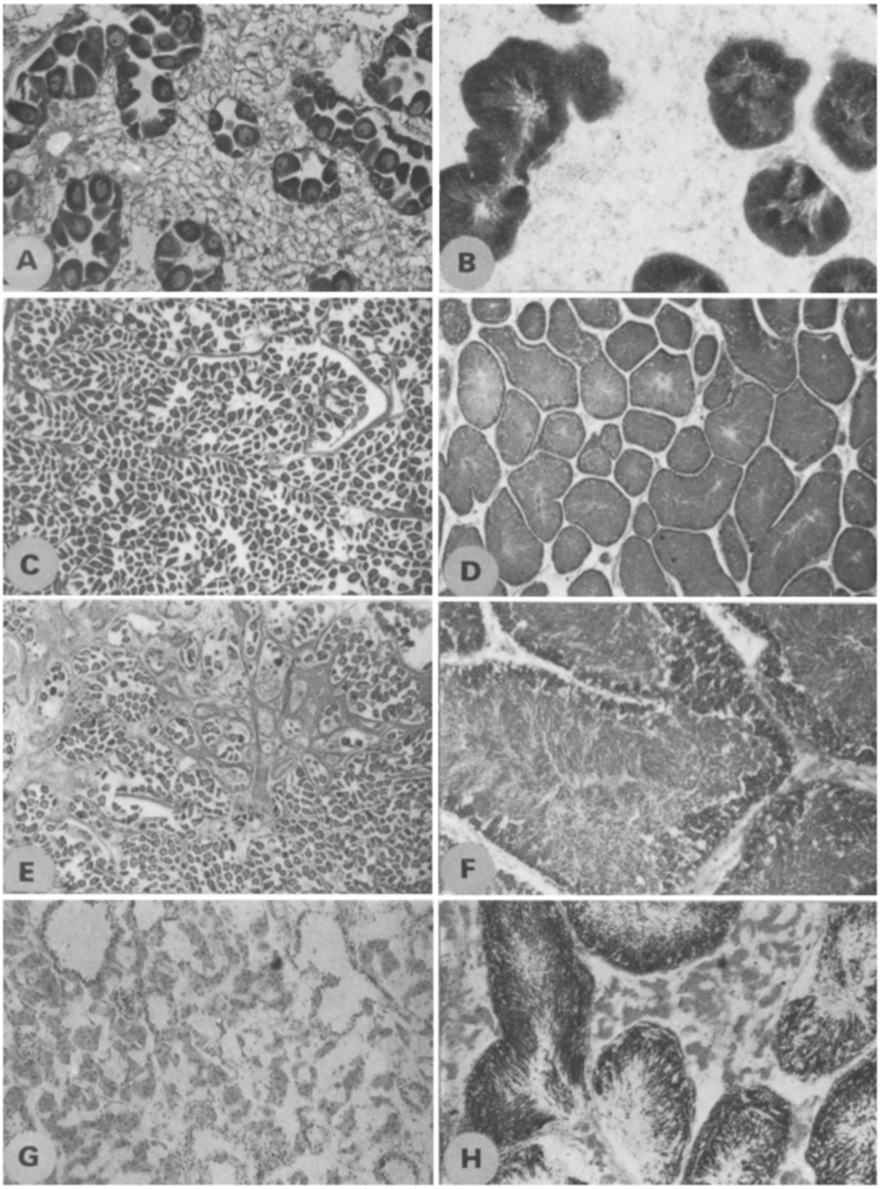

Fig. 2a. Photomicrographs of various stages in the reproductive cycles of *Mytilus* and *Modiolus*. *A* Developing female *Mytilus* (stage 3). *B* Developing male *Mytilus* (stage 3). *C* Ripe female *Modiolus* (stage 5). *D* Ripe male *Modiolus* (stage 5). *E* Spawning female *Modiolus* (stage 3). *F* Ripe male *Modiolus* (stage 5). Note dark peripheral band of early stages of gametogenesis. *G Mytilus*, spent (stage 0). *H* Spawning male *Modiolus* (stage 3). Note general reduction in sperm density

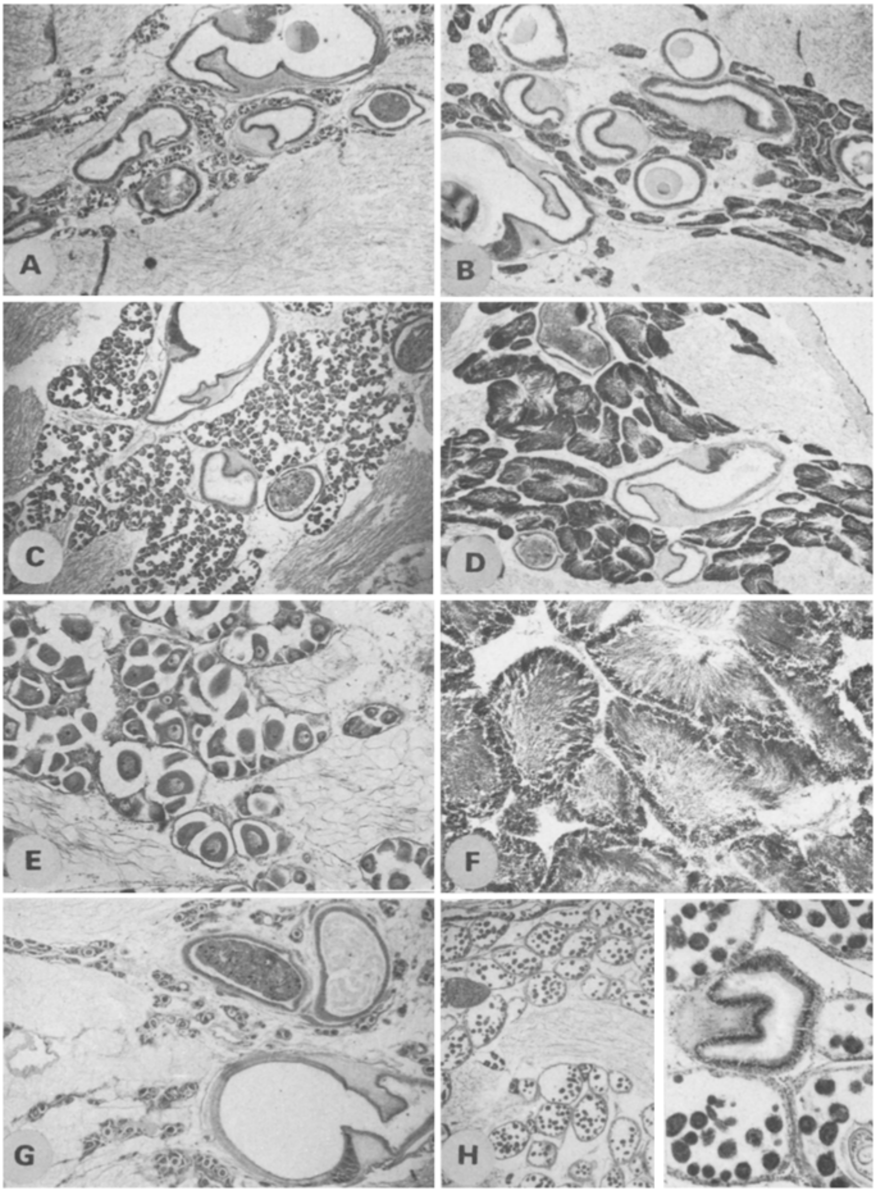

Fig. 2b. Photomicrographs of various stages in the reproductive cycle of *Cerastoderma*. *A* Developing female (stage 1). Note sections through alimentary canal. *B* Developing male (stage 2). *C* Ripe female (stage 3). *D* Ripe male (stage 3). *E* Developing female (stage 2). *F* Ripe male (stage 3). Note dark peripheral band of early stages of gametogenesis. *G* Spawning female (stage 1). *H* Gonad completely castrated by trematode sporocyst

Table 2. Distribution of gonad stages in samples of *Modiolus* from Strangford Lough

Date	Male									Spent	Female									No.	Index
	Developing					Spawning					Developing					Spawning					
	1	2	3	4	5	4	3	2	1	0	1	2	3	4	5	4	3	2	1		
1/12/71				3	12	4					1	1	2	3	13	2				41	4.43
13/1/72			2	1	18		1			1			1	3	17	4				48	4.56
18/2/72				1	11	1									12					25	4.92
23/3/72				6	21	1		1							11	6	3	1		50	4.50
20/4/72				5	13	4				1					25	6				54	4.63
16/5/72				16	12	8						1			16	6	1			60	4.41
13/6/72				15	16	1									28					60	4.73
4/7/72				1	12	1	2								13	2	1			32	4.69
4/8/72					23	2									31	2				58	4.93
5/9/72					24	2									23	1				50	4.94
4/10/72					46	1									25					72	4.98
7/11/72					38								1	1	34					74	4.96
18/12/72					32										24	1				57	4.98
29/1/73					22	2		1		1					24	3	2		1	56	4.63
1/3/73					37		1								19	1				58	4.95
10/4/73				2	24			2						1	34	4		1		68	4.76
14/5/73				7	8										14	5				34	4.65
21/6/73				3	9										29					41	4.92
26/7/73					20										23	1	1			45	4.93
23/8/73				1	25										15					41	4.98
11/9/73					21	1								4	23	1				50	4.88
9/10/73					22									2	25		1			50	4.92
19/11/73					20										17					37	5.00
19/12/73					4										14					18	5.00
8/2/74					25										14					39	5.00
13/3/74					18		1							4	7	1				31	4.77
10/4/74					23	3									12	3	2			43	4.77
3/6/74				4	15										18	2				39	4.85
2/7/74					17	1									14	1				33	4.94
31/7/74					12	2									13		1			28	4.90
30/8/74					7	1									7	1				16	4.90
14/10/74					12										16	1				29	4.97
11/11/74					19	1									13					33	4.97
12/12/74					18										9					27	5.00
10/1/75					10	2									7					19	4.89
11/2/75					11	1		1							6	2			1	22	4.59
13/3/75					5	1									8			1		15	4.73
10/4/75					6	3									9	1	1			20	4.70
9/5/75					8										6	1	1			16	4.81
10/7/75					9	1								1	8					19	4.89
14/8/75					10										6					16	5.00
17/11/75					7	4									6		1			18	4.67
15/12/75					5										10					15	5.00
6/2/76					4										8		1			13	4.85
12/3/76					13		1								5	1				20	4.85
28/4/76					2	1	5	1									2	1		12	3.25
24/6/76					1	6	2								9	1				19	4.42
3/8/76					3	3									3	3	2			14	4.28
25/8/76						2	3									4	1			10	3.60

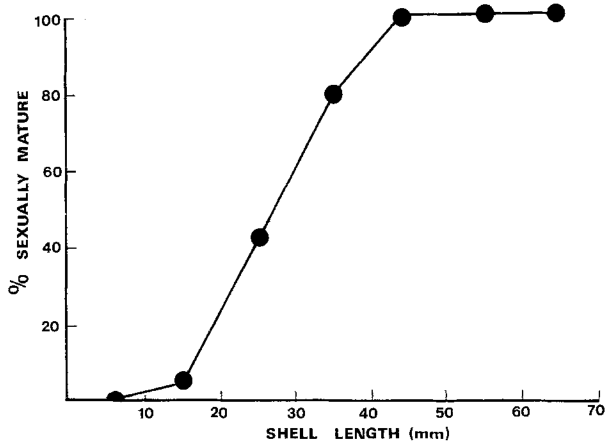

Fig. 3. The relationship between the onset of sexual maturity and size in *Modiolus*

Table 3. Distribution of gonad stages in samples of *Modiolus* from Bangor

Date	Male									Spent	Female									No.	Index
	Developing					Spawning					Developing					Spawning					
	1	2	3	4	5	4	3	2	1	0	1	2	3	4	5	4	3	2	1		
2/5/75			3	2										4	1					10	3.80
29/5/75			1	4	2										3					10	4.40
8/7/75					3										2					5	5.00
12/9/75					2		3									1	2	1		9	3.44
13/10/75		2	1			2	2	1							1			2		11	2.45
11/11/75						1		1	1			1	4	1			1			10	2.80
11/12/75				1		3	3								3					10	4.00
8/1/76					1	1	1	1							2		1	2	1	10	3.20
4/3/76			3				2						1		3		1			10	3.60
22/4/76			5										1	3	2					11	3.63
5/6/76				2	1										7					10	4.80
18/7/76					2	2									5					9	4.78
29/8/76		1											3	1		4	2			11	1.55

more protracted than in the mid-tidal cockle population. Individual mussels could be found in the spawning condition more or less throughout the year while the actual duration of the main spawning period (spring and summer) varied somewhat from one year to another. During the spawning period there was some evidence that gamete release was periodically punctuated by phases of redevelopment. Extended and repeated spawning in *Mytilus* has elsewhere been shown to result in exceedingly large numbers of small mussels persisting in the population throughout the year (Seed, 1969). However, the correlation between spawning periods and the numbers of young mussels entering the population at any particular time is complicated by the process of primary and secondary settlement previously described in this species by Bayne (1964).

Table 4. Distribution of gonad stages in samples of *Cerastoderma* from Strangford Lough

Date	Male					Spent	Female					No.	Index
	Developing			Spawning			Developing			Spawning			
	1	2	3	2	1	0	1	2	3	2	1		
7/1/72		2				20	2	1				25	0.32
16/2/72	2	1				40	6					49	0.20
22/3/72	4	1				10	10					25	0.64
25/4/72	7	13	1			2	21	13				57	1.46
28/5/72		7	9			1	1	3	8			29	2.48
15/6/72		10	15	13				4	15	3		50	2.60
4/7/72		2		13	3	1				6	10	35	1.57
7/8/72	3	23	1	1	2	15	8	4			9	66	1.23
19/9/72					12	27					7	46	0.41
19/10/72					2	56					1	59	0.05
16/11/72	3					44	2					49	0.10
13/12/72	7					34	8					49	0.31
11/1/73	2					44	8					54	0.19
9/2/73	9					30	14					53	0.43
13/3/73	11					17	17					45	0.62
4/5/73	6	6				3	14	6				35	1.26
20/6/73	1	9	4				1	12	3			30	2.17
28/7/73			5	4	1	1			6	1	1	19	2.37
24/8/73					2	9						11	0.18
2/10/73	1					16	1					18	0.10
30/10/73						31						31	0.00
3/12/73						20	1					21	0.05
14/1/74	2					22	11					35	0.37
18/2/74	2					6	4					12	0.50
25/3/74	4					11	1					16	0.31
25/4/74		11	2				1	19	5			38	2.16
30/5/74		1	24	1				5	10	1	1	43	2.77
26/6/74		1	1	6	2				5	2	5	22	1.95
9/8/74				2	14	6					3	25	0.84
30/8/74	1	1			3	17					6	28	0.43
14/10/74					2	10						12	0.16
19/11/74						26	1					27	0.03
19/12/74						20						20	0.00
7/2/75						15	2				2	19	0.21
6/3/75	5					12	9					26	0.53
6/5/75	1	7	5	1			3	7	2			26	2.11
6/6/75			10	2	1			2	10	1		26	2.73
25/7/75			7	5		3		3	3	1	2	24	2.08
30/9/75						11						11	0.00
10/11/75						14						14	0.00
11/12/75						19						19	0.00
8/1/76						10						10	0.00
4/3/76	2					19	4					25	0.24
22/4/76	3					7	5					15	0.53
5/6/76		2	6	3	1			2	6			20	2.55
3/8/76			2	4		3	1		3	2	1	16	1.81
29/8/76			1	1	1	4				3	1	11	1.18

Table 5. Distribution of gonad stages in samples of *Mytilus* from Strangford Lough

Date	Male									Spent	Female									No.	Index
	Developing					Spawning					Developing					Spawning					
	1	2	3	4	5	4	3	2	1	0	1	2	3	4	5	4	3	2	1		
7/1/72	2	3	1	2			2			4	12	2								28	1.46
16/2/72		5	5	3				4		1	7	7	1							33	2.09
22/3/72		1	4	14			1	1		1		2	1	1	9	3	4	1		43	3.65
25/4/72				4	3	6								4	12	4	2	1		36	4.31
28/5/72		6	19	1			2	1		2		2	2				2	5	5	47	2.38
15/6/72				17		5	1	4					1		10	7	6	5	1	57	3.67
4/7/72		1			15	2	2	1							4	3	4	1	1	34	4.12
15/8/72		1	4		3	2	2	2		9			2		6	1	1		5	38	2.50
19/9/72					1		3	8	4	18							4	4	8	50	1.24
19/10/72	6	3							1	29	8									47	0.45
16/11/72	9	7	1					1	2	8	22									50	1.04
13/12/72	3	11	9	3						1	18	2						1		48	1.83
11/1/73	1	7	8	3				2		2	12	7								42	1.93
9/2/73		15	4	4	2			1	1	1	6	10	7							51	2.31
13/3/73		2	6	8	3	5	1	1			3	6	14	7	4			1		61	3.30
10/4/73		3	3	15	8		1				1	6	8	7	5					57	3.54
20/6/73			3		13	3	4	2	1		2	3	6	1	16	4	2	1	4	65	3.71
28/7/73					13	2	3	2		1					9	4	8	6		48	3.81
24/8/73					14	2	3	1	2	1					8	5	3	4	2	45	3.78
2/10/73					3		2	1	8	24							4	2	2	46	1.07
30/10/73					4	1	7	2	4	8	6	1			1	1	3		2	40	2.02
3/12/73					2	2	4	3	3	3	7	1					5	1	3	34	2.00
14/1/74		5	1	1	2	2	3	2	3	1	12	13	1						1	47	1.98
18/2/74		2	6	2		2	1		1		6	2	4							26	2.46
25/3/74			8	6	3	1	2				1	4		2	3	3	4			37	3.49
25/4/74				9	14		1							4	21	1				50	4.68
30/5/74			6	5	2	5	1	1		2		2	2	2	1	3	10	2	2	46	3.13
26/6/74								2	3	8									9	22	0.73
9/8/74		2	2		1					5								2	7	19	1.37
30/8/74		6					1	7		1		2						1	3	21	1.81
14/10/74		1			1		1	2	1	5								1		12	1.41
19/11/74		1				1	5	6	2	7	5									27	1.48
19/12/74	1	2	3	2							7	4								19	1.95
7/2/75		2	2					1		1	5	8	2	1						22	1.95
6/3/75		1	3	7						1		3	2							17	3.00
6/5/75					7	1				1				1	7	2		1		20	1.40
5/6/75					13										10	1				24	4.96
25/7/75					5										7	4	3			19	4.47
13/8/75			1			1	2	1	2	4							1	2	2	16	1.63
30/9/75					1	2		2	2	5									2	14	1.50
10/11/75		2						1	1	14	1									19	0.42
11/12/75		1					3	2	1	6	8									21	1.14
8/1/76		1					1	2	3	2	1							1		11	1.36
4/3/76		1	5	3	1	2	3					5	1		1		1	1	1	25	3.00
22/4/76				3	3						2				1	3	5	1		18	3.50
5/6/76			2	2				1			1	2	2	1	2	1	2	1	2	19	2.89
3/8/76					4	1				1				1	7	1			1	16	4.25
29/8/76					3		1		1	3					5		1	1	1	16	3.12

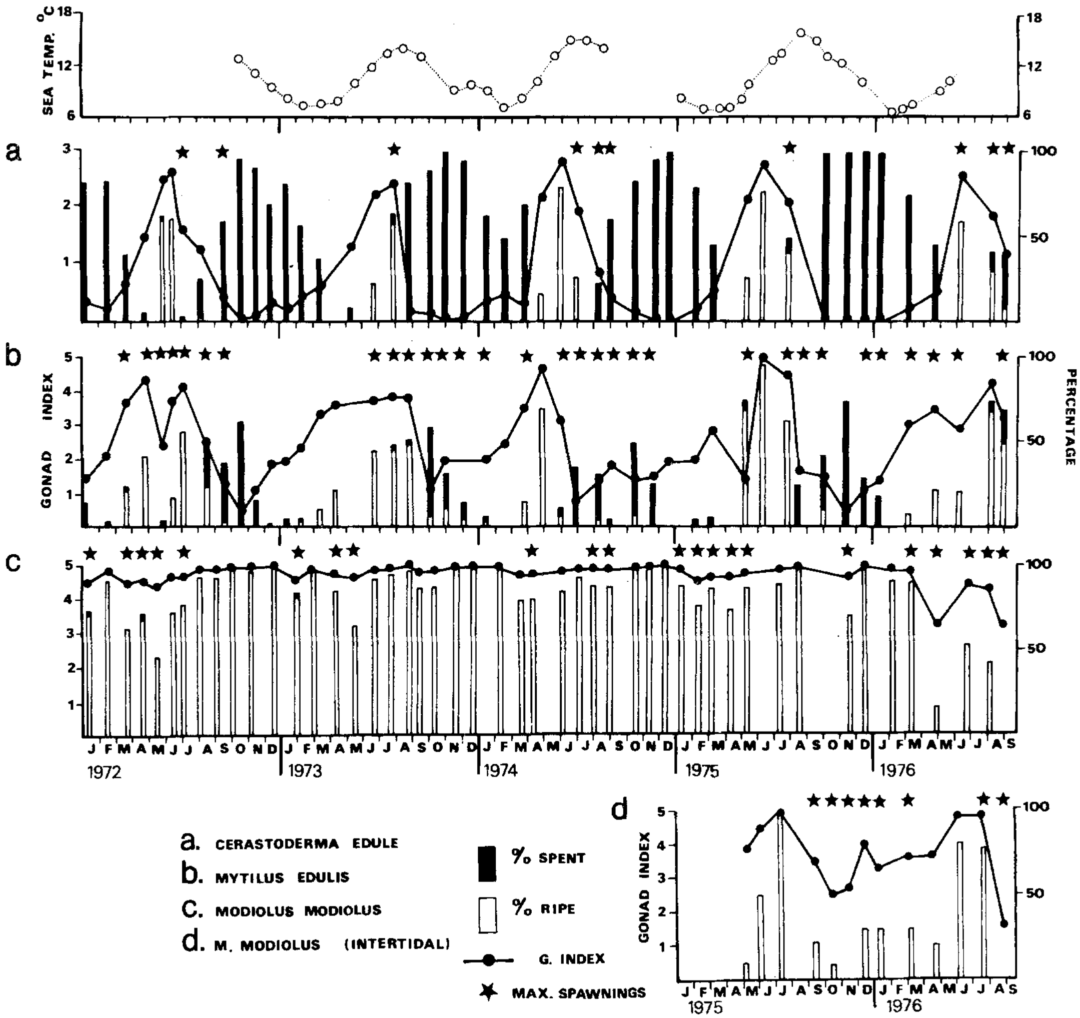

Fig. 4a–d. Reproductive cycles of **a** *Cerastoderma*, **b** *Mytilus*, **c** subtidal *Modiolus*, and **d** intertidal *Modiolus* showing the percentage of ripe (*open columns*) and spent individuals (*dark columns*) together with the gonad index (●). Periods when over 20% of the *Cerastoderma* and *Mytilus* populations were spawning (over 10% in the case of *Modiolus*) are marked by asterisks

The intertidal *Modiolus* population at Bangor was monitored in order to determine whether the more rigorous intertidal conditions had any significant influence on reproduction in this predominantly subtidal species. Despite the rather small sample sizes (dictated by availability) this population did exhibit a much more marked seasonal reproductive cycle. During 1975 gamete development occurred during spring and early summer while spawning commenced about August or September and continued until March. A similar pattern occurred for 1976 though the onset of spawning appeared to be somewhat earlier. During the spawning period 60 to 80% of this population could be found in the spawning condition, a marked contrast to the subtidal population where, apart from 1976, it was rare to find more than 20% of the population spawning at any one time. However, intertidal and subtidal populations were similar in that spent individuals were rarely, if ever, encountered. Instead, partially spawned animals started their redevelopment during the winter when individuals with both residual and developing gametes could be found. The duration of spawning and the process of redevelopment of partially spawned animals in the intertidal *Modiolus* population thus more closely parallels the situation in *Mytilus* (which is also found along with *Modiolus* at Bangor) though the actual periods of spawning do differ quite markedly. Whether it is permissible to regard these mussels as truly intertidal is perhaps questionable since they occur in shallow pools and crevices and are therefore relatively better protected from the full rigors of a truly intertidal existence. In spite of this the marked seasonal reproductive cycle of these animals compared with their subtidal conspecifics strongly suggests that local environmental variability plays a major part in influencing the nature of the annual reproductive cycle in this particular species.

Discussion

Of the numerous environmental variables which potentially influence reproduction in marine invertebrates the relationship between geographical distribution and breeding seems to be controlled principally by sea temperature, although for intertidal species air temperature may be equally as important. Although reproduction in *Mytilus* has been particularly well documented (reviewed by Seed, 1975, 1976) the literature for *Cerastoderma* (Table 6) and even more especially for *Modiolus* (Wiborg, 1946; Schweinitz and Lutz, 1976) is unfortunately much less extensive and at present it is impossible to assess the precise relationship between temperature, reproduction and distribution for these two bivalves in Northern Europe.

In Strangford Lough *Cerastoderma* spawns during the summer when sea temperatures are reaching their maximum values. After spawning most cockles

Table 6. Spawning and settlement periods of *Cerastoderma*

Area	Authority	Spawning period	Spatfall	Method of assessment
Millport (Scotland)	Stephen (1931)	–	End of July	Sieving
Plymouth (England)	Lebour (1938)	May–August	–	Appearance of gonad
Waddensea (Holland)	Baggerman (1953)	–	May–August	Sieving
Cardigan Bay (Wales)	Creek (1960)	End of May–June		Sections of gonad
Vigo (Spain)	Figueras (1967)	–	April–May and August–September	Population size frequency distributions
Kent (England)	Kingston (citedin Boyden, 1971)	End of May–End of June	–	–
Trondheim (Norway)	Rygg (1970)	Early July	–	Sections of gonad
Essex (England)	Boyden (1971)	Mid May	–	Smears of gonad
South Wales	Hancock and Franklin (1972)	June	–	Smears of gonad

overwinter in the spent condition and only when temperatures rise again the following spring does any appreciable redevelopment occur. *Mytilus* has a more variable and extended cycle than *Cerastoderma*. Here spawning generally commences with rising temperatures in the spring, continues throughout the summer and sometimes extends into late autumn when temperatures are approaching their lowest values; redevelopment during late winter and early spring occurs more slowly than in the cockle. While *Mytilus* and *Cerastoderma* in this locality thus appear to spawn predominantly during the warmer months, intertidal *Modiolus* spawns principally thoughout late autumn and winter. Spawning in the subtidal population, on the other hand, seems to be more extended though there was a *slight* tendency for the number of spawning individuals to increase during the early months of the year when temperatures were at their lowest. In Norway *Modiolus* spawns in March and April with possibly two or more years elapsing between successive spawning periods (Wiborg, 1946). Spatfalls were small when compared with *Mytilus* a feature which we too have noted in our Strangford populations. We interpret our data for the subtidal population as evidence of a slow but more or less continual release of gametes thoughout the year. This is supported by recruitment data and contrast sharply with the more seasonal nature of the annual cycle in the intertidal mussel populations and in *Cerastoderma*. The marked differences between intertidal and subtidal *Modiolus* reported here are apparently paralleled in *Hiatella arctica* (Hunter, 1949).

Results for both our *Modiolus* populations during 1976 are puzzling; spawning in subtidal animals was not only unusually intense but occurred during the warmer months. Intertidal animals also spawned earlier than in the previous year. No explanation for these differences can be given, but if the exceptionally warm summer was in any way contributory then the results are rather surprising for a species which is predominantly northerly in its distribution.

Species which spawn more or less continuously (particularly those with a protracted pelagic phase) might be expected to have more stable adult populations than seasonally breeding species since damage caused by unsuccessful recruitments is likely to be reduced. This appears to be true of the Strangford *Cerastoderma* and *Modiolus* populations, the latter showing little change in population structure over a period of five years. *Cerastoderma,* on the other hand, exhibits quite marked seasonal fluctuations in abundance. Most benthic invertebrates, however, reproduce seasonally and frequently exhibit varying degrees of population instability. Mileikowsky (1971) considers the two major disadvantages accruing from such a reproductive strategy; considerably overcrowding during periods of heavy settlement and reduced ability to cope with the higher levels of competition during periods of poor recruitment. Nevertheless, unpredictable and often exceedingly heavy spatfalls frequently enable *Mytilus* to become the competitively dominant organism on many exposed and semi-exposed rocky shores (Seed, 1976).

Growth of *Mytilus* in Strangford Lough has not been documented, but in *Cerastoderma* and *Modiolus* maximum growth occurs *prior* to sexual maturity. *Cerastoderma* grows most rapidly in its first year and only in its second summer, when approx imately 18 months old, do the majority of cockles first mature. The size at which this occurs depends on the precise time of spatfall relative to the seasonal growth pattern though most cockles by this time measure about 15 to 20 mm. This was also noted by Hancock and Franklin (1972) who further remark that large cockles (> 15 mm) may mature in their first year, a fact which suggests a link between size and sexual maturity. The relative uniformity in size achieved by Strangford cockles after their first year's growth, regardless of any earlier size differences which may have been apparent, supports this suggestion especially if one accepts that some mechanism of compensatory growth may exist, enabling cockles to grow beyond a certain minimum size before they first mature (see also Kristensen, 1957; Hancock, 1965).

The majority of Strangford *Modiolus* do not mature until they are 40 to 50 mm in shell length, a finding which appears to be broadly in keeping with previous reports (Wiborg, 1946; Mikulich and Rodin, 1963).

The different emphasis placed on somatic growth relative to the reproductive cycle may reflect different strategies each operating through a need to reproduce as efficiently as possible within a framework of heavy mortality. Mortality in *Modiolus* especially from crabs and starfish tends to be most acute amongst smaller mussels (< 50 mm). Once *Modiolus* has 'escaped' prediation through rapid growth during this critical period, longevity is greatly enhanced and the emphasis then changes from somatic growth to reproductive development. *Cerastoderma*, on the other hand, experiences heavy mortality in all size classes and, being intertidal, from a double set of predators. Flatfish and to a lesser extent crabs, take large numbers of small cockles while larger cockles are particularly attractive to waders such as oystercatchers. These take the various size groups more or less in proportion to their availability (Brown and O'Connor, 1974). Since fecundity is proportional to body size in most marine bivalves, gamete production in any one year which reduces the capacity for growth must be weighed against increase in size and thus the expectation of higher fecundity the following year. The onset of sexual maturity in cockles during their second year following a year of rapid growth may therefore provide a compromised strategy for maximising production before excessive predation severely limits the numbers within any particular age group. *Mytilus*, however, is known to mature during its first year, often at a very small size (Seed, 1969). This highly gregarious species, which occurs in dense patches in the rocky intertidal, frequently settles erratically in exceedingly large numbers; small mussels can, therefore, obtain substantial protection amongst the weft of byssus threads provided by the established population. Nevertheless, intense predation in many localities, including Strangford L. can virtually exclude this species from the sublittoral while even within the intertidal, *Mytilus* may sometimes only escape predation by virtue of the spatial refuge provided by the high shore from which its major predators are largely excluded (Seed, 1969, 1976).

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