

REPRODUCTIVE CYCLE AND ENERGETIC COST OF REPRODUCTION OF THE NEOGASTROPOD *BUCCINUM UNDATUM* IN THE IRISH SEA

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The annual reproductive cycle and cost of reproduction of the common whelk, *Buccinum undatum* L. (Gastropoda: Prosobranchia) were studied off Douglas, south-east of the Isle of Man. Sexual maturity was reached at 60-70 mm shell length. Two years of laboratory observation and field data indicated an autumn to mid-winter breeding season. Egg-laying occurred in the laboratory mainly between December and January, and hatching of juveniles between April and early May, 3-5 months after spawning. The cycles of testis and ovary development were very similar, especially during the breeding period. The annual energy invested in reproduction was estimated to be at least 4.1 kJ m^{-2} . The investment by females ($3.84 \text{ kJ m}^{-2} \text{ y}^{-1}$) was much greater than by males ($0.26 \text{ kJ m}^{-2} \text{ y}^{-1}$).

INTRODUCTION

Several previous studies have examined the reproduction of subtidal Buccinidae (Pearce & Thorson, 1967; West, 1978a,b, 1979; Ito, 1978). However, the only complete observations on seasonal reproductive events for buccinids are those by Takahashi *et al.* (1972) and Fujinaga (1985) for the neptune whelk *Neptunea arthritica* and by Martel *et al.* (1986a,b) for the common whelk *Buccinum undatum*.

Buccinum undatum is one of the commonest species of its family in the North Atlantic. As in most prosobranchs the sexes are separate, the male being distinguished by the large muscular penis which lies folded back within the mantle cavity, posterior to the right side of the head. Dakin (1912), Fretter (1941, 1953) and Johansson (1957) have described the anatomy, histology and function of reproductive organs in this species. The male's gonad resembles the female's in size, shape and appearance and is generally situated dorsal to and in close contact with the digestive gland. Fertilization is internal and the eggs are surrounded by a transparent viscous mass of albumen. They are laid in capsules, large numbers of eggs being deposited, attached to each other. These egg masses are either fixed to floating objects, or to benthic substrata such as mollusc shells, rocks, or crustacean integuments.

In the literature there are variations in the reported breeding season, both between and within localities. In European populations the principal spawning period has been quoted as between October and February (Sykes, 1905, in Europe; Kristensen, 1959, in Holland; Hancock, 1960, east of England; Cunningham, 1899, in Europe), or extending

to April (Moore, 1937, in Europe; Bruce *et al.*, 1963, in the Isle of Man) or even to May (Lebour, 1937, off Plymouth). Fretter & Graham (1984) summarize the records. In the White Sea spawning occurs only between April and August (Kuznetsov, 1963). In the northern Gulf of St Lawrence, Martel *et al.* (1986a,b) reported that the spawning occurred between late May and mid-July. Because information in the earlier literature was so confusing, Thorson (1946) stated that this species spawns all year, though it is clear from more recent studies that *Buccinum undatum*, like most high latitude marine invertebrates, does have a distinct annual breeding cycle. The lack of systematic observation on the timing of reproductive events in the common whelk in northern European waters is surprising, given its wide distribution there and commercial importance.

No previous studies have investigated the energetic costs of reproduction in *Buccinum undatum*. An analysis of this permits evaluation of the relative contributions of different sexes and size groups to the reproductive process.

The present study investigates the annual reproductive pattern and the energetic cost of reproduction for a population in an area of the Irish Sea south-east of Douglas in the Isle of Man.

MATERIAL AND METHODS

Buccinum undatum were collected using whelk pots made from weighted 5-gallon (23-l) plastic drums, following the standard French pattern (Kideys, 1991). Two strings of seven baited pots were set and left for 24 h (unless bad weather delayed recovery). The area sampled was south-east of Douglas, Isle of Man. The samples were taken within a 500-m square centred on 54°8.1'N 4°27.8'W, at a depth of 30 m. Sampling was approximately monthly from February 1989 until June 1990. In February 1990 pot sampling was not possible, but a sample dredged from an adjacent area was used to monitor gonad development.

Laboratory observations on reproduction

For the two-year period from 1989 to 1991 whelks were maintained in laboratory tanks for observation. Three black plastic tanks, 60x30x30 cm, were kept outdoors provided with an open sea-water circulation at ambient sea temperature, and subject to natural light. The tanks contained over 50 whelks, which were fed at three-day intervals with scallop flesh (*Pecten maximus* or *Chlamys opercularis*). These whelks survived the period of observation.

Quantification of body components

Approximately 20 males and 20 females were dissected each month between April 1989 and March 1990 to quantify specific body components. The complete animal was lightly blotted dry to remove surface fluids, and weighed to the nearest 0.01 g. Shell and aperture length were measured with vernier callipers to the nearest 0.1 mm. The shell was then cracked in a vice and all viscera removed. The soft tissue was allowed to drain onto a paper towel for 2 minutes, and then the whelk was dissected. The ovary, testis,

penis, and the remaining tissues (=somatic weight) were each weighed to the nearest 0.01 g. The length of the penis was recorded. The percentage of gonad weight to somatic weight (plus penis for males) gave the 'gonad index'.

Determination of energy values of gonads

The energy value of the gonads (particularly before and after the spawning periods) was determined seasonally (May, August and November 1989 and January 1990 for females; May, August, September and December 1989 for males). Three mature whelks were used for each determination. The gonad material was dried at 80°C to constant weight, and the dry and wet weights used to calculate a conversion factor. The dried material was then ground to a powder for calorimetric analysis.

The energy content of each sample was determined in triplicate using a Phillipson microbomb calorimeter (Gentry Instruments) and a potentiometer recorder (Tekman TE 200). The instrument was calibrated against benzoic acid, and the general procedure followed that of Phillipson (1964). A Cahn-2 electrobalance was used to determine the weight of samples prior to ignition.

Calculation of energetic cost of reproduction

Crisp (1984) details two methods for measuring reproductive output in annual breeders. The direct method involves collecting and weighing broods from a series of females covering the reproductive size range. It determines only the investment by females, and was in any case not considered feasible in the present study. The indirect method is based on the difference in gonad weight before and after spawning, which is taken as the reproductive output, and this was the method used here. The methods for determining gonad weight, and the calorific value of the gonads, are described above.

RESULTS

Laboratory observations on reproduction

During the two-year period from 1989 to 1991 laboratory-maintained whelks spawned in winter between the last week of December and the end of January. At this time the sea-water temperature was 9-10°C (Figure 1). Each year at least 15 clusters of egg capsules were attached to the walls of the holding tanks, close to the water surface. The majority of egg clusters were produced jointly by several females and then generally hidden by 'nursing' whelks. A sole exception was one female that laid eggs in March.

Juveniles hatched from the egg capsules between April (water temperature approximately 8°C) and early May (9-10°C) in both 1990 and 1991. Embryonic development took between three and five months.

Size at sexual maturity

The relative penis size generally increased rapidly at 60-70 mm shell length (Figure 2), although there were still some individuals exceeding 80 mm with relatively small penes

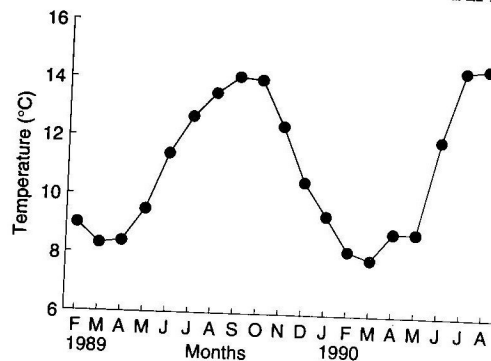


Figure 1. Seasonal variations in monthly mean bottom temperature at 40 m off the south of the Isle of Man (D.J. Slinn, Port Erin Marine Laboratory, unpublished data).

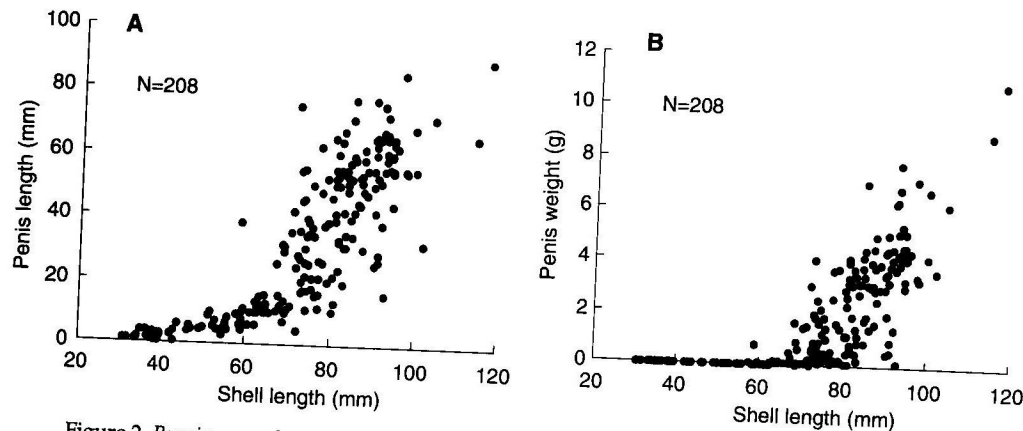


Figure 2. *Buccinum undatum*. (A) Penis length plotted against shell length. (B) Penis wet weight plotted against shell length.

Testis weight showed a similar rapid increase at around the same shell length (Figure 3A). The increase in relative ovary weight showed that females also attained sexual maturity at a size of 60-70 mm shell length (Figure 3B).

Sex ratio

Sex determination was attempted on all pot-caught individuals, most of which were not killed and dissected as they were needed for marking programmes. The presence or absence of a penis was usually easily determined, since the visceral mass came partly out of its shell during inspection. However, a small percentage did not emerge at all, and could not be sexed. Of the 12,498 specimens captured 11,043 were positively sexed, and of these 5,154 were male and 5,889 female. This was significantly different from a 1:1 ratio ($\chi^2=48.92$; $df=1$; $P<0.001$).

The monthly male:female ratios for all size groups and for individuals ≥ 70 mm (mature) showed appreciable variability (Figure 4). For mature specimens there was an increased proportion of females during the autumn and winter, the period of the breeding season.

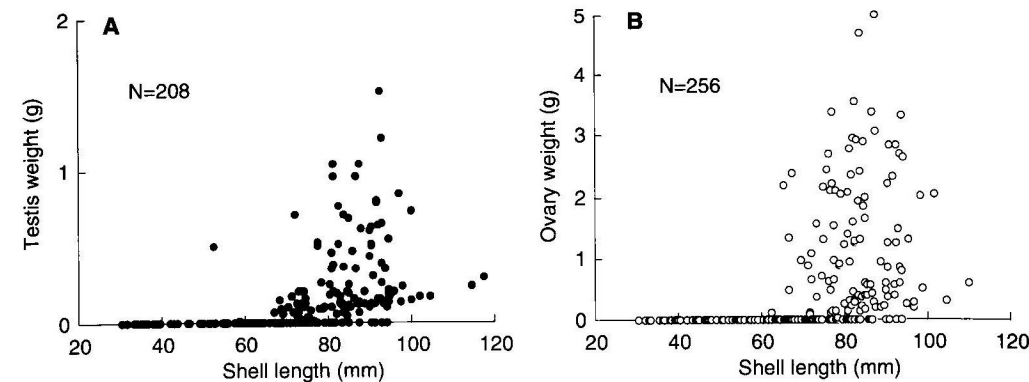


Figure 3. *Buccinum undatum*. (A) Testis wet weight plotted against shell length. (B) Ovary wet weight plotted against shell length.

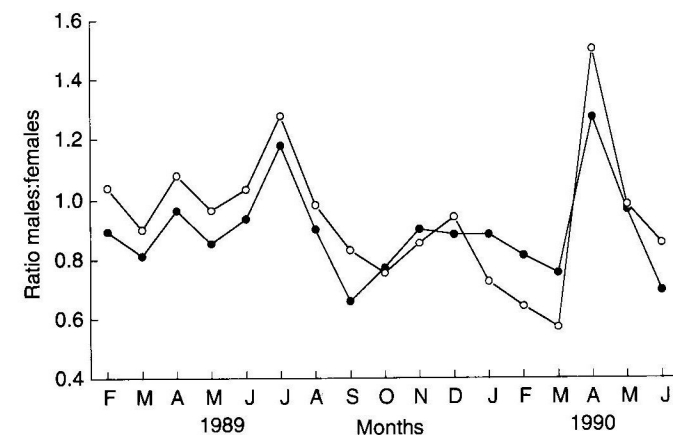


Figure 4. *Buccinum undatum*. Ratio of males to females in each month, for all specimens (●) and for specimens ≥ 70 mm shell length (○).

Sexual dimorphism of the shell

It has been suggested that it is possible to sex the common whelk by the ratio of aperture size to shell length (Hallers-Tjabbes, 1979). To test this, aperture length was plotted against shell length for each sex (Figure 5). The slope of the regression was significantly steeper for males (ANCOVA: $t=5.66$; $df=426$; $P<0.001$).

Gonad indices

Gonad indices were calculated only for mature individuals ≥ 60 mm shell length (Figure 6). The mean testicular index varied from 0.2 to 1.7, compared to 0.6 to 4.3 for the ovary. There was much less inter-individual variation for the testis than for the ovary (compare standard deviation bars, Figure 6).

The testis index showed a well-defined annual cycle (Figure 6A), increasing gradually from April to October when the highest value of 1.7 was observed. The index decreased substantially between October and November, and then more gradually to reach its

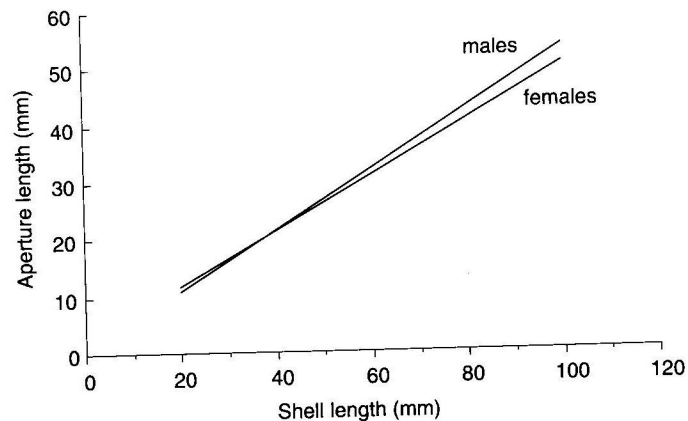


Figure 5. *Buccinum undatum*. Regressions of aperture length plotted against shell length. Males: $y=0.087+0.534x$; $r^2=0.956$. Females: $y=1.814+0.487x$; $r^2=0.957$.

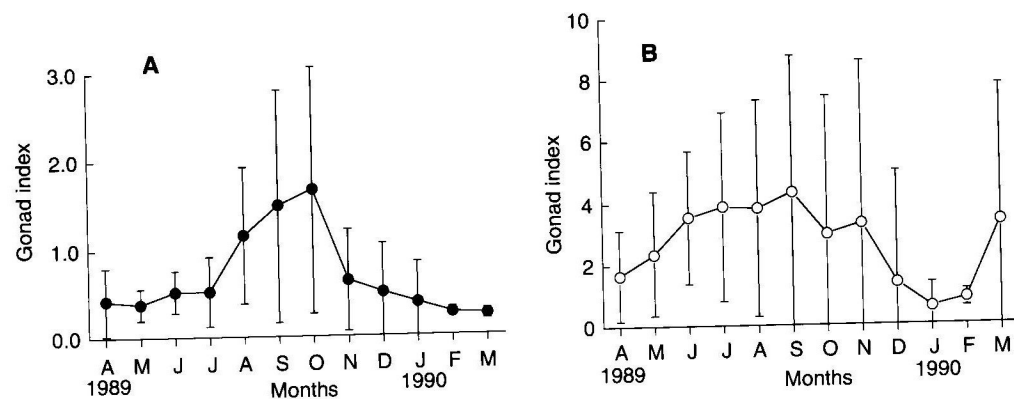


Figure 6. *Buccinum undatum*. Gonad index plotted monthly for specimens ≥ 60 mm shell length. (A) Testis, (B) ovary. Vertical bars show ± 1 standard deviation. For N, see Table 2.

lowest value of 0.2 in March. There was also a distinct ovarian cycle (Figure 6B). The ovary index gradually increased from April to September, reaching 4.3. It then decreased from September to a minimum of 0.6 in January.

Calorific values

The calorific values of ovary and testis tissue were determined on four occasions (Table 1) to enable the calculation of gonadal energy before and after spawning. Testis contained significantly less energy per unit mass than ovary (ANOVA, $F=27.69$, $df=23$, $P<0.001$), with mean values of 19.6 and 23.4 kJ g^{-1} respectively. The testicular energy level was lowest in May, was higher in August, and changed little thereafter. Calorific values of the ovary for May and August were higher than those for November and January. However, seasonal variation in energy value was not significant either for testis or ovary (ANOVA: ovary, $F=2.38$, $df=11$, $P>0.05$; testis, $F=2.28$, $df=11$, $P>0.05$), so the mean annual values have been used in calculations.

Table 1. *Buccinum undatum*. Calorific content of gonads per unit dry weight determined at different seasons. Mean values \pm standard error.

	Gonadal energy (kJ g^{-1})	
	Ovary	Testis
May	23.6 ± 0.66	18.0 ± 1.02
August	25.2 ± 0.18	20.2 ± 0.50
September	-	20.4 ± 0.72
November	22.9 ± 1.02	-
December	-	19.9 ± 0.72
January	21.9 ± 1.50	-

Table 2. *Buccinum undatum*. Monthly mean and maximum gonad weights for different shell length classes.

Shell length (mm)	60-69				70-79				80-89				≥ 90			
Month	Mean	SD	Max	N	Mean	SD	Max	N	Mean	SD	Max	N	Mean	SD	Max	N
Males																
Apr 1989	0	-	0	1	0.05	0.03	0.08	5	0.23	0.22	0.61	5	0.15	0.06	0.24	5
May	0.08	0.01	0.09	2	0.08	0.05	0.12	4	0.14	0.07	0.21	5	0.16	0.02	0.18	5
June	0.02	0.04	0.06	3	0.16	0.06	0.21	6	0.11	0.08	0.19	4	0.21	0.05	0.26	4
July	0.08	0.11	0.15	2	0.12	0.11	0.26	4	0.17	0.13	0.35	5	0.2	0.22	0.43	5
Aug	0	-	0	6	0.22	0.25	0.5	3	0.33	0.3	0.76	5	0.67	0.14	0.78	3
Sep	0	-	0	3	0	-	0	2	0.75	0.5	1.03	4	0.73	0.62	0.16	4
Oct	0	-	0	2	0.25	0.34	0.71	5	0.57	0.36	0.95	5	1.21	-	1.21	1
Nov	0	-	0	2	0.04	0.04	0.07	4	0.1	0.11	0.25	5	0.62	0.14	0.84	5
Dec	0	-	0	2	0.03	0.05	0.12	5	0.19	0.14	0.38	5	0.3	0.29	0.64	6
Jan 1990	0	-	0	2	0.02	0.03	0.09	6	0.27	0.18	0.47	4	0.14	-	0.14	1
Feb	-	-	-	-	-	-	-	-	-	-	-	-	0.18	0.07	0.29	6
Mar	0	-	0	1	-	-	-	-	0.1	0.03	0.13	4	0.17	-	0.17	1
Females																
Apr 1989	0.19	0.24	0.47	3	0.42	0.4	0.88	5	0.6	0.63	1.86	6	0.56	0.22	0.84	4
May	0.33	0.56	0.98	3	0.56	0.52	1.23	5	0.98	0.78	1.93	5	0.54	0.49	1.24	5
June	0	-	0	1	0.77	0.49	1.3	5	1.27	0.79	2.37	5	1.12	0.81	2.22	5
July	0	-	0	3	0.84	1.03	2.22	6	1.43	0.97	2.08	4	1.95	1.16	2.84	5
Aug	0.33	0.66	1.33	4	0.45	0.67	1.52	6	1.68	1.5	3.06	4	2.15	0.6	2.63	3
Sep	0	-	0	4	0.8	1.25	2.69	6	2.23	2.02	4.69	5	2.1	1.62	3.33	3
Oct	0.48	1.06	2.38	5	1.22	1.16	2.44	5	0.48	1.08	2.42	5	0.01	0.01	0.01	2
Nov	1.1	1.54	2.18	2	1.11	1.58	3.38	5	0.75	1.24	2.95	5	0.28	0.12	0.36	2
Dec	0	-	0	4	0.09	0.16	0.36	5	1.06	2.2	4.99	5	0	-	0	1
Jan 1990	0	-	0	7	<0.01	<0.01	0.01	5	0.32	0.35	0.93	6	0.53	0.04	0.56	2
Feb	-	-	-	-	0.14	-	0.14	1	-	-	-	-	0.6	-	0.6	1
Mar	<0.01	<0.01	0.01	2	0.09	0.14	0.25	3	1.55	1.38	3.55	6	0.61	-	0.61	1

SD, Standard deviation; Max, Maximum value; N, number of observations; -, no calculation possible.

Reproductive cycle and energy cost of reproduction

Whelks ≥ 60 mm shell length were divided into 10-mm size groups and the mean and maximum gonad wet weights for each size group calculated monthly (Table 2). Standard deviation of mean gonad weight was very high for both sexes, particularly during September to January when gonad weight was decreasing. These high deviations were partially caused by very low gonad weights (<0.01 g) in spent individuals.

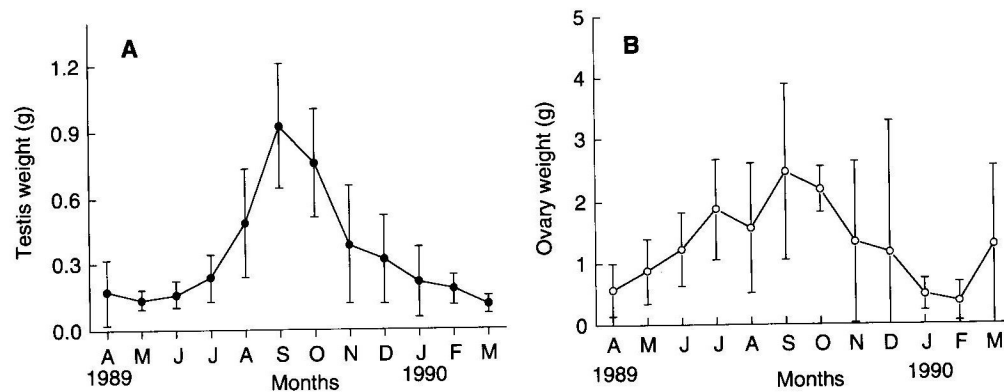


Figure 7. *Buccinum undatum*. Monthly values for mean gonad wet weight (excluding spent animals) for specimens ≥ 60 mm shell length. (A) Testis, (B) ovary. Vertical bars indicate ± 1 standard deviation.

After excluding spent animals, the mean gonad wet weights (for all size groups of 60 mm and over combined) were recalculated (Figure 7). The mean annual weight of the ovary (1.28 g) was much higher than for the testis (0.34 g). There was a gradual increase in the mean testis weight from April to September, when the highest mean (0.93 g wet wt) was obtained. Thereafter, testis size decreased until March when the lowest value (0.04 g wet wt) was observed. The same seasonal trend was observed for ovaries. Mean weight increased from 0.57 g in April to 2.47 g in September and thereafter decreased gradually until February when the lowest value of 0.37 g was obtained. Weights of both ovary and testis decreased through autumn to mid-winter. This long period of gamete release probably contributed to the high standard deviations in gonad weight (Table 2). In view of this the maximum gonad weights observed during the year for each mature size group (Table 2) will form a better basis for determining the loss during reproduction.

To present this loss by reproduction in terms of energy, maximum gonad wet weights were converted to dry weights using the following regressions.

Table 3. *Buccinum undatum*. Annual energetic cost of reproduction.

Size class (mm)	¹ Wet wt (g)	Gonad ² Dry wt (g)	Σ Energy (J)	³ Density (no. m ⁻²)	Energy cost (J m ⁻² y ⁻¹)
Males					
60-69	0.15	0.043	843.5	0.0215	18.14
70-79	0.71	0.157	3075.9	0.0352	108.27
80-89	1.03	0.222	4351.6	0.0221	96.17
≥ 90	1.21	0.258	5069.2	0.0055	27.88
Total					250.46
Females					
60-69	2.38	1.234	28833.3	0.0229	659.30
70-79	3.38	1.798	42008.9	0.0374	1570.67
80-89	4.99	2.706	63221.6	0.0235	1484.7
≥ 90	3.33	1.770	41350.1	0.0059	242.77
Total					3957.44
Grand total					4.21 kJ m ⁻² y ⁻¹

¹from Table 2; ²regressions in text; ³from Kideys (1991).

$$\text{Testes: dry wt (g)} = 0.012 + 0.203 \text{ wet wt (g); } r^2 = 0.87, N = 12 \quad (1)$$

$$\text{Ovaries: dry wt (g)} = -0.108 + 0.564 \text{ wet wt (g); } r^2 = 0.94, N = 12 \quad (2)$$

The dry weights were then converted to energy values using the mean energy values given above (19.64 kJ g⁻¹ dry wt for testes and 23.36 kJ g⁻¹ dry wt for ovaries). The results of these calculations are given in Table 3. The mean density in the study area of each size group exceeding 59 mm shell length is also given (from Kideys, 1991). This enabled the minimum energy cost of reproduction by each sex to be calculated per unit area, 0.25 kJ m⁻² y⁻¹ for males and 3.96 kJ m⁻² y⁻¹ for females. Of the size classes, the highest contribution to annual reproductive production (P_r) was by the 70-79 mm class, 0.11 and 1.57 kJ m⁻² y⁻¹ for males and females respectively. Total reproductive output (P_r) was estimated as 4.21 kJ m⁻² y⁻¹.

DISCUSSION

The onset of sexual maturity in *Buccinum undatum* is indicated in both sexes by a sharp increase in relative gonad weight at a shell length of 60-70 mm. In males there is also an increase in relative penis size at the same length. This size at maturity is lower than the 70-80 mm found in the northern Gulf of St Lawrence (Martel *et al.*, 1986a). However, Martel (unpublished data, cited in Martel *et al.*, 1986a) reported a population on the Gaspé coast of Quebec which reached sexual maturity at approximately the same size (60-65 mm) as in the present study.

All samples taken together indicated a small but significant surplus of females, with a male:female ratio of 1:1.14. Ratios close to unity have generally been found in other gastropods. Thus *Nucella lapillus* (L.) had a ratio of 56:44 (male:female) which was not significantly different from 1:1 (Feare, 1969). Hughes (1971) detected a 1:1 sex ratio in *Nerita tessellata* Gmelin. Pearce & Thorson (1967) reported a 47:53 (male:female) ratio for another prosobranch, *Neptunea antiqua*, which again was not significantly different from a 1:1 ratio. Possibly the variations in sex ratio during the year in the present study resulted from reproductive behaviour. Fretter & Graham (1962) and Martel *et al.* (1986a,b) both reported that during egg laying, females move towards shallower water. In the laboratory spawning occurred primarily between December and January. Since the sampling area was only a few hundred metres from the shore, the proportional increase of mature females during winter could result from such an inshore movement.

According to Martel *et al.* (1986b) egg laying takes place between three weeks and two months after copulation. So October should mark the start of copulation for the population off Douglas, as the marked decrease in testis weight at this time indicates. The fall in the proportion of mature females from October to December may be due to an influx of mature males during this period. Attraction of males to females during the copulation period has been observed for *B. undatum* (Martel *et al.*, 1986b) and for other neogastropods (Magalhaes, 1948; Pearce & Thorson, 1967; Edwards, 1968; D'Asaro, 1970). The decrease in the proportion of males following the copulation period is therefore to be expected.

Sexual differences in shell morphology have been described in several prosobranch

gastropods (Kitching *et al.*, 1966; Bernard, 1968; Webber, 1977; Anderson *et al.*, 1989), including *B. undatum* (Hallers-Tjabbes, 1979). She regarded the aperture as the most labile feature of the whelk shell, being the area where differences might relate to sexual function. She used a three-dimensional system to analyse aperture form. However, the simpler aperture-length to shell-length relationship examined in the present study was adequate to show that adult males have a longer aperture than females in relation to shell length, supporting Hallers-Tjabbes (1979) conclusion. This was not true for smaller individuals though. Thus a female of 20 mm length had an aperture length of 11.9 mm, a similar sized male one of 10.6 mm, and the relatively longer aperture in males became apparent only above about 55 mm shell length. Smaller whelks were not investigated by Hallers-Tjabbes (1979), so she made no comment on the sexual dimorphism of juveniles.

In each sex a sharp decrease of the gonad index between September and February indicated that gamete release occurred during that period. The mean gonad weights of mature animals showed the same pattern, indicating that the breeding period off Douglas is from autumn to mid-winter. This was supported by laboratory observations, where egg laying occurred between December and January over two consecutive years. This agrees with most other studies in Europe (Table 4), but contrasts with that in the northern Gulf of St Lawrence (Martel *et al.*, 1986a,b), where spawning occurred between late May and July, some seven months later. A similar phenomenon has been observed for *Neptunea*. Thus Martel *et al.* (1986b) noted that *Neptunea despecta* lays during late spring and early summer in the Archipel de Mingan, contrasting with the winter reproduction of *Neptunea antiqua* in Europe (Pearce & Thorson, 1967). These differences probably relate to sea-water temperature, since winter temperature in Europe is higher than the average summer temperature in the Archipel de Mingan. So reproduction in the northern Gulf of St Lawrence is delayed until summer to permit more rapid development of the embryos in the capsules (Martel *et al.*, 1986b).

Table 4. Literature on breeding period of *Buccinum undatum*.

Mating	Egg laying	Hatching	Locality	Reference
Mid May-June	late May-mid July (occasionally until Aug)	late autumn to winter	Northern Gulf of St Lawrence	Martel <i>et al.</i> (1986a,b)
-	Nov-Feb	-	Europe	Cunningham (1899)
-	Nov-Apr	-	Europe	Sykes (1905)
-	Apr-Aug	-	White Sea	Moore (1937)
Nov	Dec-Jan	-	Holland	Kuznetsov (1963)
-	Winter	-	Europe	Kristensen (1959)
-	Oct-May	-	Plymouth	Fretter & Graham (1962)
-	Feb-Sep	-	Kristineberg	Lebour (1937)
-	Winter	-	Holland	Auruvillius (1898)
Oct-Nov	Nov	-	East of England	Havinga (1922)
-	Nov	late Jan-Mar	East of England	Hancock (1967)
-	Jan-Apr*	-	Isle of Man	Hancock (1960)
-	late Dec-Jan (rarely until Mar)	Apr-early May	Isle of Man	Bruce <i>et al.</i> (1963)
				This study

* egg masses collected from field; -, not reported.

The only previous observation on the hatching period of *B. undatum* in Europe gives it as August (Sykes, 1905). However, our two years of laboratory observations indicated that it always occurred between April and early May, approximately 3-5 months after spawning. This contrasts with an autumn to winter hatching (5-8 months after spawning) in the northern Gulf of St Lawrence. A further difference is seen in gonad development. Martel *et al.* (1986a,b) reported a lack of synchrony in the development of the testis and ovary in the northern Gulf of St Lawrence, which contrasts with our observations of closely synchronized gonad development between the two sexes. Martel *et al.* (1986a) attributed the differences in the timing of testis and ovary development to long-term storage of sperm in the seminal vesicle of the male prior to copulation. No attempt was made to quantify the sperm held in the seminal vesicles in our study. It is of interest that while there were these major differences in the periods of egg laying and hatching between Europe and the northern Gulf of St Lawrence, seasonal changes in testis size showed a very similar pattern. In both areas testis size suddenly decreased in September. The relationship of testis development cycles to the timing of copulation and laying requires further study.

It is clear that *B. undatum*, like most high latitude marine invertebrates, has a seasonal breeding cycle. Therefore the difference in gonad weight before and after spawning can be regarded as indicative of reproductive effort in the construction of energy budgets, such as those done for several other gastropods (Paine, 1971; Davis & Wilson, 1985; Horn, 1986). This method will, however, tend to provide conservative values. Over the prolonged breeding period there may be an element of recovery during mid-season: this is particularly likely in males, and in *Buccinum* little is known of the frequency and periodicity of copulation by individual males. In females energy is used for secretion of the capsule by the pallial oviduct, as well as by the ovary for egg production. An additional source of error will arise if some females of reproductive size fail to breed in a given season, as is the case in the Gulf of St Lawrence (Martel *et al.*, 1986b). The calculated yearly reproductive cost to males (0.26 kJ m^{-2}) was much lower than for that to females (3.84 kJ m^{-2}). However, for the reasons discussed above, the actual cost may be greater for each sex. In both sexes the 70-79 mm size group provided the highest contribution to the yearly reproductive production, but this was only because of their abundance compared to other size groups. Reproductive investment per male continued to increase to the largest size class, whilst in females it appeared to peak at 80-89 mm, though the limited number of individuals studied makes these conclusions tentative.

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