Physiological energetics of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man (the Irish Sea)

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Abstract: Physiological energetics of the common whelk (*Buccinum undatum*) were studied in a population off Douglas, Isle of Man and an energy budget was constructed for the period February 1989 to January 1990. The components of the energy budget (in kJ m^{-2} year^{-1}) for the population can be summarized thus: consumption (C)=753; growth production (P$_g$)=34; reproductive production (P$_r$)=4; mucus production=218; respiration (R)=96; ammonia excretion (U)=8; and faecal production (F)=393. Assimilation efficiency was 47.7%. P/B (annual production/biomass) was calculated as 1.40 representing an intermediate life span for this species.

Key Words: *Buccinum,* Ecology, Energetics, Energy budget, production.

Man Adasının Douglas kenti açıklarında (İrlanda Denizi) gastropod *Buccinum undatum*'un fizyolojik enerjetiği

Özet: Man adasının Douglas kenti açıklarındaki bir adi salyangoz (*Buccinum undatum*) populasyonunun fizyololojik enerjetikleri çalışıldı ve Şubat 1989 ile Ocak 1990 arasındaki süre için bir enerji bütçesi hesaplandı. Populasyonunun enerji bütçesinin unsurları (kJ m^{-2} yıl^{-1} olarak) şöyle özetlenebilir: tüketim (C)=753; büyüme için biriktirilen üretim (P$_g$)=34; üreme için biriktirilen üretimi (P$_r$)=4; mukus üretimi=218; solunum (R)=96; amonyak salgılanması (U)=8; and dışkı üretimi (F)=393. Asimilasyon elverişliliği 47.7% idi. P/B (yıllık üretim/biyokitle) 1.40 olarak hesaplandı ki bu değer söz konusu türün orta uzunlukta bir yaşam süresinin olduğunu gösterir.

Anahtar Sözcükler: *Buccinum,* Ekoloji, Enerjetik, Enerji bütçesi, üretim.

Introduction

Each species has a role in the energy exchange at a given trophic level. The study of physiological energetics is a useful approach to assess the contribution of a species to the strucure, productivity and functioning of a community (1, 2). It also helps in evaluating the potential of a species for aquaculture (3). Additionally, individual budgets of energy flow in trophic structure are necessary for modelling ecosystems energetically (4).

The energy consumed by a gastropod is partitioned in various ways which can be summarized by the equation: C = P$_g$ + P$_r$ + R + M + U + F (After 5, 6, 7), where C = the energy of the food consumed, P$_g$=the energy retained within the population as "growth" and that lost as "mortality", P$_r$=the energy invested in reproduction; R=the energy lost during metabolism (represented by repiration), M=the energy invested in mucus production, U=the energy released as nitrogenous waste, and F=the energy voided as faeces. Despite a knowledge of input and output pathways for energy in a living system, construction of an energy budget is inherently complicated. It is therefore evident that many assumptions are incorporated within most budgets.

There is substantial literature on the energy budgets of intertidal gastropods (4, 8, 9, 10, 11, 12). The lack of field data, however, for subtidal gastropods emphasizes the need for more research.

Buccinum undatum is a common, commercially exploited, subtidal gastropod found on both sides of the northern North Atlantic (13, 14, 15, 16). It is also common around the Isle of Man (personal observation). The common whelk is a predator with a tendency for scavenging (17, 18). In some areas (e.g. Danish waters) they were considered an important enemy of scallops and some other economically important bivalves (13). Cod (*Gadus morrhua*), dogfish (*Scyliorhinus canicula*) and starfish (*Asterias rubens*) are the main predators of adult *Buccinum* (19). Given its wide distribution and abundance, the whelk must be of considerable ecological importance in its ecosystem (16, 17).

The energetic costs of reproduction and mucus production were previously reported for the common

whelk (20, 21). The purpose of the present study is to measure the other parameters of physiological energetics and to construct a complete energy budget for the *Buccinum undatum* population off Douglas, Isle of Man.

Materials and Methods

Growth

Whelks were samples using plastic pots between February 1989 and January 1990 from a population off Douglas (Isle of Man), central northern Irish Sea. The samples were taken within 500-m square centred on 54°8.1'N 4°27.8'W, at a depth of 30 m. Detailed data on sampling are given elsewhere (22).

After sexing and measuring the shell length of each whelk with vernier calipers (to the nearest 0.1 mm), the complete animal was weighed to the nearest 0.01 g. An attempt at ageing individual whelks from the operculum striae with the naked eye (as proposed by Santarelli & Gros, 23) was not satisfactory (24). Therefore, shell length frequency analysis was used to discern age classes. It is interesting to note that out of 12 size frequency histograms, only one sample (January 1990) showed relatively clear modes of possible age classes (24). Therefore this histogram has been used to discriminate age classes of whelks using the mathemathical model MIX (interactive program for fitting mixtures of distributions) developed by Macdonald & Pitcher (25).

The growth parameters obtained from MIX were used to determine growth production. However, since hatching usually occurs in April-May (c.f. 21), the first mode in January represents ~0.75 years of age. The second mode represents ~1.75 years of age, the third mode ~2.75 years of age and so on. Therefore, an adjustment was applied to obtain the mean lengths at ages 1, 2, 3 etc. years using the von Bertalanffy equation:

$$l_t = L_\infty - (1-e^{-K(t-t_o)}) \qquad (26)$$

where l_t is the estimated length at age t, L_∞ is the theoretical maximum length, K is a constant known as the Brody growth coefficient which is related to the rate of approach to length L_∞, t_o is the hypothetical age that the animal would have been at zero length. The parameter t_o was estimated from a least squares regression of ln (L_∞-l_t) on age:

$$t_o = (intercept - \ln L_\infty)/K \qquad (26)$$

l_o, the hypothetical size that the animal would have been

at t=0 (if it had always grown according to the von Bertalanffy equation) was also esimated.

The monthly proportions (% of individuals) of each age class were calculated for the period of February 1989-January 1990. Number of individuals were obtained by multiplying the monthly proportions with corresponding density values of *Buccinum* from the study area estimated by Kideys (22). Specific growth rates (G) for each age class were found using the equation;

$$G = bK(L_\infty-1)/1 \qquad (27)$$

where is the mean length at age, b is the slope of the logarithmic regression for tissue dry weight (or dried organic matter of shell when calculating shell energy) versus shell length, L_∞ and K are from the von Bertalanffy equation.

The dry tissue weight was obtained by extracting the whelk from its shell and after homogenizing by drying at 100°C until a constant weight was reached. The amount of protein in the shell was determined by using dilute hydrochloric acid to dissolve away the mineral contents of a known weight of clean shell taken from live animals (8). The remaining scleroprotein was dried at 60°C in an oven for 48 h. The calorific values of dry tissue (without gonad but with operculum) and shell organic matter were determined using a Philipson microbomb calorimeter for three females and three males sampled in October 1989.

The production of somatic and shell organic matter was then calculated according to Crisp (27). The equation is:

$$\text{Annual Production} = \sum_{t=0}^{t=n} f_i G_i w_i \Delta t$$

were G_i is the weight specific growth rate of size group i, w_i the mean weight of the size group and f_i the number of individuals of this size group existing in the population during the period Δt. The fraction of total standing stock biomass within the size class i is therefore $f_i w_i$.

The loss through mortality was esimated using the equation:

$$E = \sum_{Feb89}^{Jan90} 1/2.(N_i-N_j).(w_i+w_j) \qquad (28)$$

where N_i and N_j are numbers of whelks and w_i and w_j are mean weights, i and j signifying consecutive months.

The annual net production and mortality values (mg dry weight m^{-2} $year^{-1}$) obtained were then converted to energy (kJ $m^{-2}year^{-1}$) using the calorific values of tissue and shell organic matter.

Respiration

Measurement of oxygen uptake for common whelks was conducted in the laboratory at the three different temperatures: namely 10.5°C in May, 15°C in August 1989 and 7.5°C in March 1990. These experimental temperatures were within 1.5°C of the average field temperatures for those months and approximate to the minumum, average and maximum seasonal seawater temperature where these animals occur around the Isle of Man (29).

A total of 21 whelks from seven representative size groups (30-39, 40-49, 50-59, 60-69, 70-79, 80-89 and ≥90 mm) for the May and August 1989 experiments and 21 whelks from six representative size groups (30-39, 40-49, 50-59, 60-69, 70-79 and ≥80 mm) for the March 1990 experiment were used. Shell surfaces were cleaned of sedentary organisms (e.g. tube worms, barncles etc.). Each animal was then placed in a 1,178 ml capacity respiratory chamber filled with filtered seawater (0.22 μm) previously air-saturated and allowed to stand for 24 h in the controlled temperature room at the temperatures required for the experiment. Each respiratory chamber was then sealed under seawater and incubated for 1-4 h depending on the temperature and size of animals. During all experiments three respiratory chambers containing only seawater were used as controls to correct for any utilization (or production) of oxygen by microorganisms in the seawater. Three samples of seawater were taken prior to the experimental period to calculate the inital oxygen concentration of the seawater.

The dissolved oxygen concentration was determined by the Macro-Winkler technique (30) and the oxygen upake (q) was calculated by;

$$q = v (X_1 - X_2)$$

where v is the volume of the experimental vessel (ml), X_1 and X_2 are the concentration of oxygen (ml l^{-1}) in the water initally and finally. The oxygen concentration was not allowed to fall below 80% of the inital concentration for each respiration chamber (27).

Ingestion

Food consumption and faeces production were measured between October and November 1989 at three different temperatures (10.5°C, 12°C and 14°C). All individuals were acclimated for at least five days prior to the experiment. Twelve whelks from each of six representative size groups (30-39, 40-49, 50-59, 60-69, 70-79 and ≥80 mm) were selected. Each group of 12 was first starved for five days and then allowed to feed on preweighed flesh of dogfish (*Scyliorhinus canicula*, a common dogfish species around the Isle of Man) for 24 hours in a rectangular plastic tank (ca. 15 litre capacity) supplied with flowing seawater. Laboratory experiments have shown that the dogfish is a preferred food (C.J. Gilling, pers. comm., Port Erin Marine Lab., Isle of Man). Seawater was filtered through a net (mesh size 1 mm) fitted on the inflow and outflow. Aeration of the tanks was also provided. The photoperiod was ~12 h dark and ~h light. At the end of the 24 h feeding period the seawater flow was stopped and the remaining uneaten dogfish flesh was weighed. The difference between the uneaten flesh weight and initial weight gave the consumption. Some dogfish flesh was kept under the same conditions in whelk free tanks to determine whether any change in weight of the flesh occurred.

Egestion

In order to determine their faecal production, the animals fed with the dogfish flesh were observed after cessation of feeding for five successive days. Faeces were clearly visible in the bottom of the tank and they were collected daily by filtering all seawater through a fine mesh. Because the feeding experiment was confined to a 24 h period, following a five days starvation period (for complete gut clearance), total weight of faeces collected during the five day experiment were divided by 24 to give the faecal production per hour. After rinsing with distilled water to remove adhering salt, the dry weight of the faeces was determined by drying at 80°C for 24 hours.

At the end of each experiment the shell length of each individual was measured with vernier calipers to the nearest 0.1 m. The whole animal, lightly blotted dry, was first weighed, and the tissue then removed from the shell after breaking it in a vice. The soft tissues (with the operculum) were placed in a preweighed aluminium foil dish and dried in an oven at 100°C until a constant weight was reached. The ash content was obtained by incinerating the dry samples in a muffle furnace at 550° for 4-6 hours.

The energy values of the whelk faeces and dogfish flesh were also determined using a Phillipson microbomb calorimeter.

	Size Group (mm)											
	7.5-28.6		28.7-45.8		45.9-59.9		60.0-71.4		≥71.5			Overall density*
Months	1	f	1	f	1	f	1	f	1	f	n	(indiv. m-2)
Feb. 89	25.7	.004	38.8	.089	53.9	.203	66.1	.255	81.6	.449	1216	0.36
M	26.5	.001	38.4	.032	54.5	.061	66.9	.200	80.3	.705	1371	0.40
A	22.9	.020	38.8	.056	53.7	.130	66.5	.210	82.0	.585	949	0.19
M	24.0	.017	38.7	.127	53.2	.179	65.6	.232	80.6	.445	1146	0.33
J	23.1	.045	38.4	.108	53.4	.152	66.6	.194	81.5	.501	1346	0.20
J	23.6	.012	38.6	.077	52.6	.120	66.6	.200	87.4	.577	574	0.19
A	24.9	.053	37.4	.143	53.0	.061	66.4	.156	80.8	.586	244	0.08
S	23.5	.028	38.7	.121	53.7	.139	66.0	.206	80.7	.506	462	0.14
O	23.0	.046	38.5	.207	53.4	.253	65.8	.278	78.6	.266	909	0.29
N	22.8	.049	38.3	.123	53.6	.165	66.4	.224	79.0	.439	750	0.23
D	24.2	.021	39.1	.088	53.1	.154	66.4	.247	79.5	.490	1145	0.35
Jan. 90	22.0	.091	39.0	.183	53.6	.190	66.6	.237	78.7	.299	705	0.22

Table 1. The mean length (1) and proportion (f) of each size group of *B. undatum* in the samples from February 1989 to January 1990.

*From Kideys (1993).
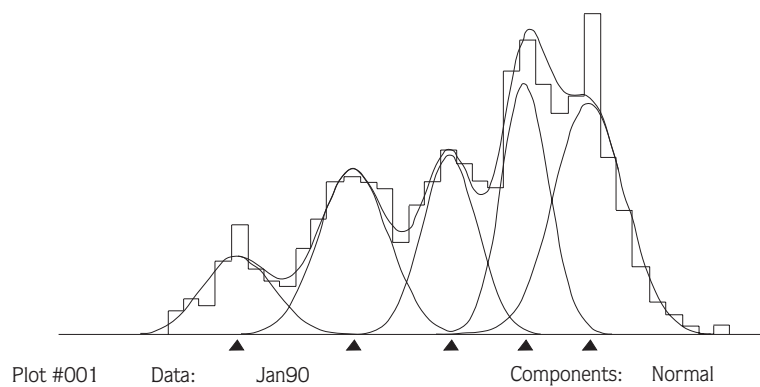

Plot #001   Data: Jan90   Components: Normal

Figure 1. Curve fitting of MIX on legth frequency histogram of *Buccinum undatum* off Douglas (the January 1990 sample, all individuals.

Regression analysis and analysis of covariance of the ingestion and egestion data were carried out. Comparisons of slopes and intercepts of the regression equations were made according to the methods given by Zar (31). The calculations of energy uptake from ingestion (C) and energy losses from egestion (F) and respiration (R) were performed according to the procedure given by Crisp (27).

Results

Growth Production

The relationships between the shell length and tissue, shell and shell organic matter dry weights are presented in the following equations.

Log_{10} Tissue Dry Wt (g) = 3.0875 x Log_{10} Shell Length (mm); R^2 = 0.96, n = 59

Log_{10} Shell Dry Wt (g) = 2.09 x Log_{10} Shell Length (mm); R^2 = 0.96, n = 6.

Log_{10} Shell Organic Matter (g) = 3.205 x Log_{10} Shell Length (mm); R^2 = 0.94, n= 5.

Although the sample sizes are low in the latter two equation, their correlation coefficients were very high.

Unfortunately the calorific values of tissue and shell were obtained only for six animals (three females and three males) sampled in October 1989. The mean energy values of tissues (without shell, operculum and gonad) were 21.40 kJ g^{-1} (SE = 1.03= n=3) and 21.76 kJ g^{-1} (SE = 0.61; n=3) for females and males, respectively. There was no difference between the energy values of female and male tissues (two-sample t-test, F=2.85; P>0,01), therefore an overall mean value of 21.58 kJ g^{-1} was used for the calculation of tissue production of the whelk. A lower energy value was obtained for shell organic matter (mean = 16.17 kJ g^{-1} (SE = 0.54= n=6).

Size frequency analysis showed the existence of at least five age components (Figure 1). After several iterations, MIX calculated a mean, standard deviation and proportion for each component with a goodness-of-fit value (chi squared = 19.745; P = 0.956; df=32). When the means were constrained to lie along a von Bertalanffy

Table 2. Estimation of age-specific growth rate, G+bK[L$_\infty$-1]/1, (Crisp, 1984) of *B. undatum*. The growth parameters are L=123.8 mm, K=0.20. The tissue dry weight-shell length gives the exponent b$_{Tissue}$ =3.088 and shell organic matter dry weight-shell length gives eponent b$_{Shell}$=3.205.

Age (years)	Length (mm)	G$_{Tissue}$ (years)	G$_{shell}$ (years)
0	7.4	9.71	10.08
1	28.5	2.07	2.14
2	45.8	1.05	1.09
3	59.9	0.66	0.68
4	71.5	0.45	0.47

growth curve, a L$_\infty$ value of 123.8 mm (S.E. = 8.58 mm)

and a K value of 0.20 (S.E. = 0.025) were found. The parameter t$_o$ was estimated from least squares regression of In (L$_\infty$-l$_t$) on age. This was: t$_o$ = (intercept-lnL$_\infty$)/K = (4.7567-4.8187)/0.20 = -0.310 By substituting this value in the von Bertalanffy equation, the mean lengths at age 1, 2, 3 years etc. were calculated. The mean length of whelks increased with age. *Buccinum undatum* reached a mean length of 28.5 mm after its first year, 45.8 mm at the end of its second year, 59.9 mm at the end of its third year, 71.5 at the end of its fourth year and 81.0 mm at the end of its fifth year following the hatching. The mean length (l$_o$) of the whelk at age t=0 would be 7.4 mm assuming growth occurred according to the von Bertalanffy equation. The effect of this assumption on the estimation of growth production will be negligible, because of the youngest age group being least abundant in the samples.

The proportion of each size (or age) group was calculated for February 1989 to January 1990 (Table 1). The number of individuals in each age group for each month was calculated by multiplying the density value by the proportion (Table 1). Monthly mean dry tissue weight for each age group was determined using the equation for tissue dry weight and shell length relationship. Whelks older than three years were pooled and assumed to be one age group.

After determining specific growth rates for each age group (Table 2), the total tissue growth production for the population was estimated as 0.69 g m^{-2}year^{-1} for all age groups (Table 3). When this value was multiplied by the calorific value of tissue as a dry weight (21.58 kJ g^{-1}), a growth production value of 14.89 kJ m^{-2} year^{-1} was found.

Age-specific growth rates for shell organic matter were estimated in a similar way to that of tissue growth production (Table 2). The biomass value of shell organic matter amounted to a total of 20.18 mg m^{-2} year^{-1} (Table 4). Multiplying these with the energy value of organic shell material (16.17 kJ g^{-1}), the annual production of shell material of *Buccinum* was estimated as 0.33 kJ m^{-2} year^{-1}.

The sum of tissue and shell growth gives a growth increment value of 15.22 kJ m^{-2} year^{-1}.

Losses of tissue and shell material as a result of mortality in the whelk population were calculated as 0.864 and 0.0242 g m^{-2} year^{-1}, respectively. Using respective tissue and shell organic matter calorific values, the loss of tissue and shell was found to be 18.65 and 0.39 kJ m^{-2}year^{-1}. The sum of energy losses was 19.04 kJ m^{-2} year^{-1}.

Thus, total somatic production for the *Buccinum* population off Douglas during the experimental period was,

Pg = ΔB + E = 15.22+19.04 = 34.26 kJ m^{-2} year^{-1}.

When the reproductive production value of 4.10 kJ m^{-2}year^{-1} obtained by Kideys et al. (1993) is included into this figure, the total production will be 38.36 kJ m^{-2} year^{-1}.

The annual biomass of tissue and shell organic matter of whelks was estimated as 12.24 g dry wt m^{-2} and 0.03 g dry wt m^{-2}, respectively. This gives a total biomass value of 12.27 g dry wt m^{-2} for the year which is equivalent to 27.39 kJ m^{-2} year^{-1}. So, the P/B ratio can be calculated as 38.36/27.39=1.40.

Respiration

The dissolved oxygen (DO) uptake values [either per whole animal or per g animal dry weight (=weight specific)] are presented in Table 5. Oxygen consumption at 15°C ranged from 0.23 to 4.44 ml h^{-1} between different sized groups of whelks. A slightly narrower margin (0.32-4.44 ml h^{-1}) was found at 10.5°C from that at 15°C. Much lower figures of oxygen uptake were obtained at 7.5°C (range=0.06-2.80 ml h^{-1}). On the other hand, the overall weight specific oxygen uptake by whelks changed from 0.12 to 1.37 ml g dry wt^{-1} h^{-1}at all temperatures (Table 5).

Analysis of covariance (ANCOVA) shows that the slope value at 7.5°C (see Table 4) was different from those at 10.5°C (t=3.50, n=35, P>0.05) and 15°C (t=2.24, n=35, P>0.05) while there were no significant

	Age Group 0			Age Group 1			Age Group 2			Age Group 3			Age Group>3		
Months	w	f	b	w	f	b	w	f	b	w	f	b	w	f	b
Feb 89	.22	.001	<.001	.78	.032	.02	2.15	.073	.16	4.04	.092	.37	7.76	.162	1.25
Mar	.24	<.001	<.001	.76	.013	.01	2.23	.024	.05	4.20	.08	.34	7.38	.282	2.08
Apr	.15	.004	.001	.78	.011	.01	2.13	.025	.05	4.11	.04	.16	7.86	.111	.87
May	.18	.006	.001	.78	.042	.03	2.06	.059	.12	3.95	.077	.30	7.47	.147	1.10
Jun	.16	.009	.001	.75	.022	.02	2.09	.03	.06	4.13	.039	.16	7.72	.100	.77
Jul	.17	.002	<.001	.77	.015	.01	2.00	.023	.05	4.13	.038	.16	9.59	.110	1.05
Aug	.20	.004	.001	.70	.011	.01	2.04	.005	.01	4.10	.012	.05	7.51	.047	.35
Sep	.17	.004	.001	.77	.017	.01	2.13	.019	.04	4.03	.029	.12	7.49	.071	.53
Oct	.15	.013	.002	.76	.060	.05	2.10	.073	.15	3.99	.081	.32	6.91	.077	.53
Nov	.15	.011	.002	.75	.028	.02	2.11	.038	.08	4.10	.052	.21	7.02	.101	.71
Dec	.18	.007	.001	.80	.031	.02	2.05	.054	.11	4.10	.086	.35	7.16	.171	1.23
Jan 90	.14	.020	.003	.80	.04	.03	2.12	.042	.09	4.14	.052	.22	6.92	.066	.46
Average biomass		.001			.021			.08			.23			.91	
Specific Growth Rate (year^{-1})		9.71			2.07			1.05			.66			.45	
Production		.01			.04			.08			.15			.41	

Total = 0.69 g dry weight tissue m^{-2} year^{-1} = 14.89 kJ m^{-2} year^{-1}

Table 3. Computation of tissue production of *B. undatum* off Douglas. w (mean tissue dry weight in grams) was calculated from relationship Log w=-5.014+3.088 Log Shell Length. f (individual m^{-2}) was found by multiplying proportions with respective density values from Table 1. b (biomass - g m^{-2}) was w x f.

	Age Group 0			Age Group 1			Age Group 2			Age Group 3			Age Group>3		
Months	w	f	b	w	f	b	w	f	b	w	f	b	w	f	b
Feb 89	5.37	.001	.008	20.10	.032	.64	57.64	.073	4.21	111.00	0.92	10.19	218.51	.162	35.32
Mar	5.94	<.001	.002	19.50	.013	.25	59.86	.024	1.46	115.48	.080	9.24	207.56	.282	58.53
Apr	3.73	.004	.014	20.13	.011	.21	57.19	.025	1.41	113.11	.040	4.51	221.53	.111	24.62
May	4.30	.006	.024	20.03	.042	.84	55.24	.059	3.26	108.33	.077	8.29	210.05	.147	30.85
Jun	3.81	.009	.034	19.41	.022	.42	55.91	.030	1.70	113.55	.039	4.41	217.31	.100	21.77
Jul	4.09	.002	.009	19.83	.015	.29	53.52	.023	1.22	113.55	.038	4.31	272.28	.110	29.85
Aug	4.84	.004	.021	17.95	.011	.21	54.71	.005	.27	112.68	.012	1.41	211.14	.047	9.90
Sep	4.03	.004	.016	20.00	.017	.34	57.06	.019	1.11	110.62	.029	3.19	210.80	.071	14.93
Oct	3.75	.013	.050	19.72	.060	1.18	56.18	.073	4.12	109.61	.081	8.84	193.65	.077	14.94
Nov	3.65	.011	.041	19.29	.028	.55	56.58	.038	2.15	112.84	.052	5.81	196.98	.101	19.89
Dec	4.44	.007	.033	20.63	.031	.64	54.97	.054	2.96	112.62	.086	9.74	201.08	.171	34.49
Jan 90	3.28	.020	.066	20.55	.040	.83	56.72	.042	2.37	113.99	0.52	5.94	194.12	.066	12.77
Average biomass		.03			.53			2.19			6.32			25.66	
Specific Growth Rate (year^{-1})		10.08			2.14			1.09			.68			.47	
Production		.30			1.13			2.39			4.30			12.06	

Total = 20.18 mg dry weight tissue m^{-2} year^{-1} = 0.33 kJ m^{-2} year^{-1}

Table 4. Computation of shell organic matter production of *B. undatum* off Douglas. w (mean organic matter dry weight in mg) was calculated from relationship Log w=-6.788+3.205 Log Shell Length. f (individual m^{-2}) was found by multiplying proportions with respective density values from Table 1. b (biomass-mg m^{-2}) was w x f.

differences between the slopes at 10.5^{o}C and 15°C (t=1.54, n=38; P<0.05).

In order to calculate energy losses due to respiration for the whelk population, values of oxygen consumption (ml h^{-1}) were converted to energy (J h^{-1}) assuming 1 ml of oxygen is equivalent to 20.2 Joules (Ivlev, 1934 cited in 27). Since a significant difference was observed between the slope values, it was impossible to calculate a common slope value (b$_c$). Therefore, the regression coefficients obtained for 10.5°C were assumed to reflect the annual respiration rate and used for the total energy losses calculation. This temperature value is very close to the average field temperature (11.1°C) during the experimental period (February 1989 - January 1990). The regression equation when combined with the data on population density estimates over the entire weight range enabled the estimation of the respiratory energy losses of *Buccinum undatum* at different temperatures for the whole year. The energy loss of *Buccinum undatum* through respiration was estimated as 66.73 kJ m^{-2} year^{-1}. However, it sould be noted that the laboratory method of measuring oxygen consumption of animals suffers from the defect that these animals are smoewhat constrained in an unnatural situation over the measurement period. The respiration rate obtained in respiratory chambers will probably be different from that which takes place in the field. Several investigators have measured respiration rates of animals at rest and found it

Temperature	7.5°C		10.5°C		15°C	
Size Group	Dry Wt	DO Cons.	Dry Wt	DO Cons.	Dry Wt	DO Cons
(mm)	(g)	(ml h-1)	(g)	(ml h-1)	(g)	(ml h-1)
≥90	-	-	13.61	4.44 (0.33)	14.49	4.13 (0.29)
≥90	-	-	9.66	2.84 (0.29)	10.30	3.55 (0.34)
≥90	-	-	9.98	3.45 (0.35)	13.14	4.44 (0.34)
80-89	12.28	2.80 (0.23)	7.24	2.34 (0.32)	9.51	2.43 (0.26)
80-89	7.67	2.29 (0.30)	7.09	1.87 (0.26)	6.95	2.20 (0.32)
80-89	10.66	2.16 (0.20)	11.92	2.37 (0.20)	6.67	2.33 (0.35)
70-79	11.35	1.32 (0.12)	9.65	2.59 (0.27)	6.09	1.87 (0.31)
70-79	10.18	1.91 (0.19)	9.87	2.46 (0.25)	4.37	0.88 (0.20)
70-79	10.67	0.90 (0.08)	7.24	2.46 (0.34)	6.16	2.18 (0.35)
60-69	4.95	1.35 (0.27)	8.19	1.64 (0.20)	3.93	1.89 (0.48)
60-69	3.47	1.00 (0.29)	4.14	0.97 (0.23)	3.39	1.53 (0.45)
60.69	4.33	0.72 (0.17)	2.24	1.45 (0.65)	3.05	1.34 (0.44)
50-59	3.41	0.77 (0.23)	2.31	0.87 (0.38)	1.76	0.66 (0.38)
50-59	4.13	0.80 (0.19)	2.65	1.23 (0.46)	1.94	1.22 (0.63)
50-59	2.19	0.60 (0.27)	2.07	0.76 (0.37)	1.79	0.97 (0.54)
40-49	1.74	0.41 (0.24)	1.61	0.72 (0.45)	1.31	0.82 (0.63)
40-49	0.94	0.30 (0.32)	1.17	0.66 (0.56)	1.00	0.64 (0.64)
40-49	0.51	0.70 (1.37)	0.62	0.41 (0.66)	0.82	0.52 (0.63)
30-39	1.01	0.29 (0.29)	0.77	0.43 (0.56)	0.71	0.46 (0.65)
30-39	0.75	0.10 (0.13)	0.49	0.51 (1.04)	0.64	0.26 (0.41)
30-39	0.50	0.06 (0.12)	0.60	0.32 (0.53)	0.52	0.23 (0.44)

Table 5. Respiration data for *B. uhdatum* at three temperatures. [Weight-specific Uptake (ml g dry wt^{-1} h^{-1}) given in parent-hesis].

DO Cons. = Dissolved oxygen consumption.

Metabolic Process (Y)	Temperature (°C)	Equation	df	F	r	P
Food consumption	10.5	Log Y=0.763+0.637xLog W	5	20.9	0.84	0.010
Food consumption	12	Log Y=0.809+0.771xLog W	5	46.4	0.96	0.002
Food consumption	14	Log Y=0.780+0.729xLog W	5	40.7	0.95	0.03
Faecal production	10.5	Log Y=-1.075+0.522xLog W	5	62.3	0.97	0.001
Faecal production	12	Log Y=-0.806+0.612xLog W	5	101.0	0.98	0.001
Faecal production	14	Log Y=-0.788+0.773xLog W	5	74.1	0.97	0.001
Oxygen consumption**	7.5	Log Y=-0.704+0.994xLog W	17	131.0	0.94	0.000
Oxygen consumption**	10.5	Log Y=-0.248+0.668xLog W	20	208.2	0.96	0.000
Oxygen consumption**	15	Log Y=-0.281+0.775xLog W	20	226.9	0.96	0.000
Pedal Mucus production*	8	Log Y=-0.207+0.063xW	16	4.3	0.47	0.055
Pedal Mucus production*	10.5	Log Y=-0.063xW	17	8.2	0.58	0.000
Pedal Mucus production	15	Log Y=-0.015+0.090xW	17	8.2	0.58	0.011
Hypobranchial Mucus production*	8	Log Y=0.880+0.031xW	17	5.5	0.51	0.032
Hypobranchial Mucus production*	10.5	Log Y=0.277+0.096xW	16	17.7	0.72	0.001
Hypobranchial Mucus production*	15	Log Y=0.629+0.094xW	17	19.5	0.74	0.000

Table 6. Results of the relationship betwenn several metabolic processes (as mg dry weight h^{-1}) and tissue dry weight (W, ingrams) for *B undatum* at different temperatures.

* from Kideys Hartnoll (1991),

** ml oxygen h^{-1}

necessary to double the respiration rates to account for activity in the natural environment (12, 32, 33, 34). *Buccinum undatum* was always observed to be active in the field (personal observations from underwater television and diving). According to Himmelman (35) common whelks are able to crawl 50 m a day. The constraining of animals in a glass jar (just over 1 litre in volume) during this experiment very likely caused inhibition of normal activity compared to that observed in the field. However, instead of an arbitrary doubling of the energy value of respiration rates, Engelmann's (36)

method was employed to correct this value for activity. Engelmann (36) noted a positive correlation between log_{10} respiration and log_{10} total production of molluscs. The relationship is given by the equation:

log_{10} Respiration = 0.86 (log_{10} Total production) + 0.62.

By substituting the total production value with 38.36 kJ m^{-2} year^{-1}, Engelmann's equation predicts an annual respiration value of 95.97 kJ m^{-2} year^{-1} for the estimated population of *Buccinum*. This value is 30% higher than

Table 7.   Laboratory ingestion rates (mg dry wt food h^{-1}) for *B. undatum* feeding on dogfish (*Scyliorhinus canicula*) flesh at different temperatures.

Mean Dry Wt	Temperature (^{O}C)		
(g) of animal	10.5	12	14
0.50	2.7	3.5	3.0
1.37	11.1	7.8	8.7
3.39	11.4	18.9	18.1
5.31	19.1	32.0	23.0
7.08	23.8	32.3	29.1
9.31	16.8	23.6	20.1

the laboratory measurement.

Ingestion

The food consumption rates determined at each of the

experimental temperatures are presented in Table 7. The ingestion rate at 10.5℃ ranged from 2.7 to 23.8 mg dry wt h^{-1} ind^{-1} for the different size group of whelks. The range of values obtained at higher temperatures (12℃ and 14℃) was greater from that at 10.5℃ (3.5-32.3 mg dry wt h^{-1} ind^{-1} and 3.0-29.0 mg dry wt h^{-1} ind^{-1}, respectively). Whelks measuring 70-79 mm in shell length (mean weight 7.08 g) always consumed much more food than other size groups at all temperatures.

The relationships between log animal dry weight (g) and log food consumption (mg dry wt h^{-1}) for each temperature are given in Table 6. ANCOVA (31) demonstrated that temperature had no significant effect on either the slope or the elevation of the equation for food consumption (F_{slopes}=0.31, $F_{elevations}$=1.17,

F_{table}[0.05,(1),2,12=3.89, df=12).

Since temperature did not show any significant effect on the ingestion rates of *Buccinum undatum*, the ingestion values at all temperatures were pooled. Values of food consumption (mg dry wt h^{-1}) were converted to energy (j h^{-1}) using the energy value of dogfish flesh which was determined calorimetrically from three replicate samples to be 19.80±1.14 kJ g^{-1} dry wt. Using a similar procedure to that employed to calculate respiration cost, the total amount of energy gained via feeding between February 1989 and January 1990 was estimated as 752.65 kJ m^{-2} year^{-1}.

Ammonia and Mucus Excretion

In this study no attempt has been made to quantify energy losses via ammonia excretion which rarely exceed 1% of the ingested energy vaule in the energy budget of gastropods (11, 28). Assuming this ratio of 1% in the present study, the energy losses via ammonia excretion would be approximately 8 kJ m^{-2}year^{-1}.

Kideys & Hartnoll (20) found that the energy alllocated to mucus (pedal + hypobranchial) was about 29% of the total energy uptake. This corresponds to a 218 kJ m^{-2}year^{-1} for the whelk population off Douglas.

Egestion

The dry weights obtained from daily faeces collections are tabulated in Table 8. Highest defaecation generally occurred on the third day following feeding. There were only negligible amounts of faeces on the first and last (fifth) days of the collection period. Faeces production at 14℃ ranged from 0.109 to 1.236 mg dry wt h^{-1} for

Table 8.   Daily faeces production (mg dry wt day^{-1} indv.$^{-1}$) of *B. undatum* at different temperatures

Size Group	Mean Dry Wt	Temperature														
		*14°C				12°C					10.5^{O}C					
(mg)	(g)	48h	72h	96h	110h	24h	48h	72h	96h	11h	24h	48h	72h	96h	110h	136h
30-39	0.5	21.8	7.3	2.3	0	8.5	6.4	15.8	2.4	0.7	0.9	0.4	5.2	7.7	1.4	0
40-49	1.4	17.4	30.4	10.0	0	1.0	9.7	25.0	6.1	0.4	5.3	0	8.0	19.8	4.3	0
50.59	3.4	28.5	37.7	26.5	5.7	10.9	15.8	50.6	16.3	8.2	0	0	1.9	27.5	6.8	7.0
60-69	5.3	42.9	23.5	48.0	22.9	4.4	35.1	69.4	10.6	10.2	8.1	0	13.0	20.7	11.3	4.1
70-79	7.1	73.6	31.9	84.4	27.1	9.3	20.3	69.5	39.3	12.0	0	5.7	16.3	40.9	13.7	3.7
80-89	9.3	87.6	149.4	55.3	34.3	17.2	14.7	63.7	41.1	26.0	0	31.0	0	33.4	9.1	0

*no faeces collection was made in the first 24 h at 14°C as there were no visible faeces.

Table 9.   Ecological efficiencies (%) of marine molluscs. [* indicates reproduction (Pr) was not included as part of assimilation (A)]. (C=Consumption, R=Respiration, P=Production, M=Mucus production).

Species	A/C	R/A	P/A	M/A	M/C	P/C	Reference
Marine polyplacophore							
Chiton pelliserpentis Low	88.1	29.5	4.5	66.0	58.2	4.0	Horn, 1986
Chiton pelliserpentis High	93.4	19.4	4.8	74.5	69.5	4.3	Horn, 1986
Marine gastropods							
Baccinum undatum	47.7	26.7	10.7	60.5	28.8	5.1	This study
Haliotis tuberculata	78.4-82.3	21.6-31.1	22.0-45.6	28.3-37.1	23.3-37.1	17.3-37.5	Peck et al., 1987
Ilyanassa obsoleata	38.1	15.7	2.5	80.3	30.6	1.0	Edwards & Welsh, 1982
Navanax inermis *	62	47	45			28	Paine, 1965
Nerita peloronta	41-43	81-88	5-8			4-7	Hughes, 1971
N. versicolor	39	87	13			5	Hughes, 1971
N. tessellata	40	88.2	12			4.8	Hughes, 1971
Patella vulgata	41.2	75.2	24.8		23.0**	10.2	Wright & Hartnoll, 1981
Polinices duplicatus *	79	57	43			35	Huebner & Edwards, 1981
Tegula funebralis	70.3	76.5	13.6	9.9	7.0	9.6	Paine, 1971
Marina bivalves							
Corbula gibba	50.0	79.1	21.0			10.4	Lauretta, 1986
Nucula turgida *	6.4	64.0	36.0			2.3	Davis & Wilson, 1985
Scrobicularia plana	60.7	78.9	21.1			12.8	Hughes, 1970

**from Davies et al. (1990).

different size groups of whelks. Faeces production rates decrease with decreasing temperature (0.117-0.617 mg dry wt h^{-1} at 12°C and 0.054-0.255 mg dry wt h^{-1} at 10.5°C).

The relationships between log animal weight (g) and log faeces production (mg dry wt h^{-1}) are given in Table 6 for all temperatures. While there were no significant differences between the slopes, the elevation value at 10.5°C differed from that at 14°C and 12°C (ANCOVA, $F_{elevations}$=38.11, F_{table} [0.05,(1),2,12=3.89, df=12, P>0.05).

The energy value of the feaces of *Buccinum undatum* was determined as 12.98±0.71 (n=3) kJ g^{-1} dry wt. Values of faeces production (mg dry wt h^{-1}) were first converted to energy (j h^{-1}) using a determined energy value of faeces. The total amount of energy lost via defaecation between February 1989 and January 1990 was estimated as 7.59 kJ m^{-2} $year^{-1}$.

The annual faeces production value of 7.59 kJ m^{-2} $year^{-1}$ found in this study was much lower than found for other gastropods. For example, while Peck et al. (3) reported a value of 15.3 kJ $m^{-2}year^{-1}$ for 1 g dry weight of the ormer, *Haliotis tuberculata*, Horn (37) estimated a range of 34 to 132 kJ m^{-2} $year^{-1}$ for polyplacophore *Chiton pelliserpentis*. Together with the density of the animals in the study area, there may be several other

reasons for the low faeces production value in this study. A 24 h feeding period followed by a prolonged starvation period (five days) may force the whelk to use its food more economically and hence lead to reduced defaecation in comparison to the continuous feeding conditions in the field. Given the feeding biology of *Buccinum*, there is also a possibility that whelks may reingest their faeces in the absence of food. Unfortunately, no attempt could be made to observe this type of feeding behaviour in this study. Reingesting the faeces has been reported for other gastropods. Carriker (1946, cited in 38) reports that, in addition to employing a prolonged digestive period, *Lymnaea stagnalis (appressa)* frequently eats faecal material even in the presence of fresh food. Bleakney (38) also suggests that some helicid snails may obtain some nutritive benefit from their own faeces. *Hydrobia ulvae* may also reingest its faeces (39). In molluscs a substantial amount of energy is lost via defaecation (see A/C ratio in Table 9). Yet, in the present study the percentage of faecal energy was undoubtly underestimated to be only 1% the ingested energy. Therefore, a correction factor for faecal energy losses is necessary. Taking into account ammonia excretion losses, faecal energy loss can therefore be recalculated as:

$$F = C - (A)$$

Since,

$A = P_g + P_r + M + R + U = 34 + 4 + 218 + 96 + 8 = 360$ kJ m^{-2} year^{-1}.

$F = 753 - (360) = 393$ kJ m^{-2} year^{-1}.

Thus, energy losses via egestion comprised 52% of the ingested energy.

Discussion

The growth production (P_g) value of 34.26 kJ m^{-2} year^{-1} obtained for *Buccinum undatum* is comparable with the results obtained for other molluscs. For example Hughes (9) found growth production values of 87, 28.5 and 28 kJ m^{-2}year^{-1} for herbivorous gastropods *Nerita tessellata, N. peloronta* and *N. versicolor,* respectively. Davis & Wilson (40) reported a Pg value of 3 kJ m^{-2} year^{-1} for detritus feeder *Nucula turgida*. A range of 63-103 kJ m^{-2} year^{-1} for different age groups was obtained for a carnivorous gastropod, *Polinices duplicatus* (4).

There appears to have been only one attempt to measure oxygen consumption of the common whelk reported in the literature (41). In this study, oxygen consumption of unfed whelks was approximately half that of fed whelks. However, the authors pointed out that the increase may reflect a seasonal change in metabolism rather than short-term fluctuations after feeding as the fed animals sampled a few weeks apart from the starved ones. In the present experiment, whelks were given food daily, which, it is assumed, resembles the behaviour in the field. Mean specific oxygen uptake (0.169±0.016 g dry wt^{-1} h^{-1} for fed animals) obtained by Crisp et al. (41) are much lower than the value (0.414±0.044 g dry wt^{-1}h^{-1}) of this study. This may be simply caused by the differences in sizes of whelks (or by the season which experiments were conducted) in both studies. It is well known that weight specific oygen uptake decreases with increasing animal size. The weight range of whelks in the present study was 0.49-14.49 g dry wt, but unfortunately the size range of whelks in Crisp et al. (41)'s study was not given.

The consumption rate increased with increasing body size except for the >80 mm (mean weight 9.31 g) size group at all temperatures. Metabolic rate is approximately proportional to body weight (42) and food requirement might be expected to follow suit. The mean slope value (0.713) obtained here between body size and ingestion rate was higher from that of another carnivorous gastropod, *Nucella lapillus* (b=0.54; 1911) and some herbivorous gastropods, i.e. 0.56-0.62 for *Nerita* spp. (9). The range of consumption rates found in this study (2.74-32.27 mg dry wt h^{-1}animal^{-1}) is different from that of a herbivorous gastropod, *Haliotis*

tuberculata (0.01-11.08 mg dry wt h^{-1}animal^{-1}; 3). The mean ingestion index value of 11.8 was higher than most of the values for other gastropods. For example Hughes (9) reports a value of 4.5 for *Nerita tessellata,* 4.0 for *N. versicolor* and 5.6 for *N. peloranta*. A range of 6.2-9.5 has been reported for a carnivorous gastropod, *Navanax inermis* (43). The reason for the high ingestion rate was probably the prolonged starvation period (five days) prior to the experiment in this study. The effect of starvation period on the ingestion rate of gastropods has been reported (44, 45). For *Nucella lapillus*, daily ingestion rate after 16 days of starvation was twice that after 4 days (45). Teherefore, it is possible that the feeding experiment overestimated the actual ingestion rate.

There were no significant effects of temperature on the ingestion rates of whelks. There are some reports in the literature which indicate a relationship between temperature and ingestion rates for marine gastropods. For example Sawyer (46) showed that a single carnivorous gastropod, *Polinices duplicata*, from 9 to 12 mm across the maximum dimension, could destroy an average of 0.67 clams (*Mya arenaria*) day^{-1} at summer temperature (21°C), but about 0.13 clams day^{-1} when the temperature lowered to 10°C. Huebner & Edwards (4) also reported, for the same species, that feeding by the snails varied directly with temperature and ceased for 4 months in winter. Feeding rate was also temperature dependent for the *Littorina littoralis* (11). On the other hand, changes in the temperature may not affect the feeding rate of some marine gastropods, (*Patella vulgata, Nucella lapillus,* 11; *Crepidula fornicata, Littorina littorea,* Newell & Branch, 1980 cited in 42). There are no previous attempts to measure the feeding rates of *B. undatum* at different temperatures. However, in the laboratory, Hancock (47) observed that the feeding rate of *B. undatum* was lowest in summer and greater during the spring. Martel *et al.* (48) reported similar results. *B. undatum* is an opportunistic feeder and makes use of readily available food sources even when their feeding activity is low (49). In the laboratory I observed a decrease in the feeding rate only in February and March over two years. This decrease was probably related with the reproductive biology of whelks as February and March are the "nursing" period for eggs at least by some of the females. The digestive gland size of females from field also showed decreases during these months. The feeding experiments for all temperatures have been carried out between October and November, and the experimental temperatures tested (10.5, 12 and 14°C) did not show any effect on the feeding rates of *Buccinum* in this study. However in the field especially during the

"nursing" period, decreases in feeding rates of female whelks could be expected.

In this study, the relationship between body weight and faecal production was experessed better as a log-log regression than a linear one, similar to other reports in the literature (8, 9, 37, 44). This means that younger whelks are better assimilators of energy input when compared to older specimens.

In the literature, the energy content of faeces are measured generally for herbivorous gastropods. This is perhaps because carnivorous gastropods feed upon animal prey lacking skeletal material, or avoid their prey's skeletal tests, and thus produce soft faeces. This may make faeces collection difficult for subsequent calorimetric analysis. There is a great difference between the energy contents of faeces from various marine gastropods (based on kJ g^{-1} dry wt, 2.34 for *Tegula funebralis (10), 5.09 for Littorina littorea* (49), 11.79 for *Haliotis tuberculata* (3). It is not surprising to find a calorific value of 12.98 kJ g^{-1} dry wt for *Buccinum* faeces in this study as the food (dogfish flesh) should have higher energy content (per dry weight) than seaweed which was used as food for herbivorous gastropods. Ritz & Crisp (1970, cited in 49) reports a higher calorific value (15.69 kJ g^{-1} dry wt) for the crustacean *Balanus balanoides* faeces feeding on animal prey, *Artemia.*

In contrast to the ingestion, egestion rates of *Buccinum* were temperature-dependent. The significant differences in the elevation values of regression lines between temperature and faeces production denote that increase in temperature from 10.5°C to 12°C and 14°C caused significant increases in the faeces production of whelks. There has not been much direct measurement of the effect of temperature on faeces production of marine gastropods. However, it has been reported that temperature affected assimilation in the sea urchin *Stronglylocentrotus droebachiensis* (Miller & Mann, 1973, cited in 50).

Components of the energy budget of *Buccinum* are compared with those found in the literature (Table 9). It should be pointed out that there is a lot of systematic, morphological and environmental heterogeneity in the animals presented in this table. The net growth efficiency or net production efficiency (P/A) is an index of the extent to which the energy assimilated by a species is converted into material available for higher trophic levels. *Buccinum* had a net growth efficiency of 10.7% which is lower than most of the values estimated for molluscs (Table 9). This is partly caused by a low mortality rate as the population is dominated by older whelks.

In this study, the assimilation efficiency of *Buccinum undatum* was found to be 47.7% of the ingested energy. This value falls within the range of 38 to 93% reported for other molluscs in the literature. The highest values of assimilation efficiencies were recorded for a marine polyplacophore, *Chiton pelliserpentis,* at 88 and 93% (for low and high shore populations respectively; 37) and for an intertidal scraper, *Haliotis tuberculata,* at a range of 78-82% (3), and the lowest for a detritus feeder bivalve, *Nucula turgida* at 6% (40). The value for *B. undatum* is mid-range for marine molluscs. Welch (51) states that the lower the assimilation efficiency of an animal the higher is its net growth efficiency. However, this statement is not valid for *Buccinum* which uses most (60.5%) of the assimilated energy for mucus production, leaving only a small percentage for net growth efficiency (P/A). Wright (11) also refuted such a general statement on the ground that most of the molluscs did not fall close to the plotted line for the assumed relationships between net growth efficiency and assimilation efficiency. The line which Welch computed using a variety of marine and freshwater animals, included only one molluscan species, *Aplysia punctata.* Therefore Wright (11) concluded that molluscs appear to show no relationship at all between assimilation efficiency and net growth efficiency.

Respiration accounted for only 26.7% of assimilated energy with mucus production being the major component. This finding is contrary to the commonly held view that respiration accounts for the bulk of assimilated energy in animal energetics (5, 52).

The P/B ratio (or turnover rate) of 1.40 found in the present study is close to the value of 1.25 for *Nerita peloronta* (9). The range of P/B values in marine molluscan literature is 0.28 to 5.54 with the majority around 1.0 (for review see 6 and 11). P/B ratio is an indication of the general metabolic activity of a population (11). The P/B ratio is high for short-lived species, and low for long-lived ones where the bulk of the populations is comprised of older slow-growing individuals. This trend is clearly indicated for molluscs (6, 12, 53). Therefore, the P/B value of 1.40 found for *Buccinum* represents an intermediate life span for this species. According to Santarelli and Gros (23) *Buccinum* lives maximum 9 years in the northern France.

Buccinum undatum is highly efficient in both predation of live animals and scavenging on freshly dead animals. In both ways, it plays an important role in the processing of organic matter (16). The population energy budget for *Buccinum* shows clearly their importance as energy transformers in the ecosystem off Douglas.

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