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Annual Production of Two Nova Scotian Populations of *Nucella lapillus* (L.)

R. N. Hughes

Department of Biology, Dalhousie University,
Halifax, Nova Scotia, Canada

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Summary. One population of *Nucella lapillus*, under conditions of food shortage, decreased in biomass with an annual production of 5.5 kcal per m^2. The second population, with plenty of food, gained biomass and the annual production was 16.7 kcal per m^2.

Individuals grew faster, while attaining sexual maturity and terminating growth at a larger size in the second population. In both populations, energy produced as gametes exceeded the energy produced due to growth. A 2.56 cm female was estimated to produce 46.6 egg capsules (about 1 kcal) a year but the output of males was unknown and assumed to be half that of females. The sex ratio was equal.

Introduction

Nucella lapillus is extremely abundant in Nova Scotia and the easily censused populations provide an opportunity to compare the population energetics of the species in two areas differing in ecological conditions. Most population energy budgets have been expressed per unit area for a specific population, whereas it is evident that populations of a species may vary greatly from place to place. This will be illustrated by comparing the two populations in the present study.

Nucella lapillus is common intertidally on rocky shores on both sides of the North Atlantic. Details of its geographical distribution are given by Cooke (1916). The most northerly record is from the west coast of Novaya Zemlya at 73° 20′ N. On the American shore the northward range of *Nucella* (51° N) is restricted by the Labrador current while the southward range (41° 30′ N) is restricted by warm water current from the Gulf of Mexico. In Europe, owing to the Gulf Stream, the range of *Nucella* is extended from 37° N to 71° N.

Nucella lapillus feeds principally on *Mytilus edulis* L. and barnacles (Moore, 1936, 1938; Largen, 1967).

Materials and Methods

Population Structure

At Purcell's Cove, Halifax, all animals except those less than 0.8 cm long, from a 5 × 10 cm rectangle of beach were counted and their shell lengths measured to the nearest 0.5 mm with vernier calipers in July 1969 and July 1970 (animals were returned to the beach after each census). The 5 m wide zone extended from low water spring to mean high tide level. The beach is one of extreme shelter within Halifax harbour, being composed of angular granite boulders and small stones. Algal cover was restricted to occasional clumps of *Fucus vesiculosus* (L.). Although in 1969, *Nucella, Mytilus edulis* and *Littorina littorea* (L.) were very abundant, the remaining fauna was poor.

A second population of *Nucella* was sampled from the beach below a drumlin bounding the southern end of Lawrencetown Beach, to the north of Halifax. This shore is exposed to heavy wave action at many times in the year. The beach is composed of fairly large, smooth granite boulders among which are numerous tide pools. Large amounts of *Ascophyllum nodosum* (L.) and *Fucus vesiculosus* occurred throughout most of the area, being replaced by *Chondrus crispus* (L.) at low water spring. Compared with Purcell's Cove, the fauna was diverse. Amphipods, isopods, nemerteans, *Acmaea testudinalis* (Muller), *Littorina saxatilis* (Olivi) and *L. littorea* were abundant. *Mytilus edulis* occurred in patches on the boulders. The shore was less steep than at Purcell's Cove so that transects to low water spring were 30 m long. Six contiguous 30 m long and 1 m wide transects were sampled in early April 1969. All animals except those less than 0.8 cm long were counted, measured and returned. Three of the transects were resampled in July 1969 and September 1970. Animals were measured only in the September sample.

Mortality

500 animals from a 3 × 5 m area of beach adjacent to the census area at Purcell's Cove were tagged and released in June 1969. 3/32″ × 3/16″ yellow, numbered fish tags from Howitt Plastics Co., Molalla, Oregon 97038 were glued to the dried *Nucella* shells with epoxy glue which was dried for 6 hours before releasing the animals. Recaptures were made in July, September, November 1969 and June, September 1970 for an estimate of mortality rate and its seasonal fluctuations. Estimates of total annual mortality at Purcell's Cove and for the Lawrencetown population were made from the censuses in 1969 and 1970.

Growth

Many individuals in both populations showed evidence of growth by a lip of lighter coloured shell extending beyond the old, thicker lip formed after the previous growth season. In December, when animals had completed their annual growth, the shell lengths before and after the new growth were measured to the nearest 0.1 mm with vernier calipers.

A second estimate of growth in the Purcell's Cove population was gained from the animals tagged in June 1969. Recaptured animals were measured every month until December 1969. Only the first 30, easily accessible animals were recaptured each month to avoid undue disturbances which might have affected mortality rates.

Recruitment

Recruitment was estimated from the size of the first peak (animals growing after their first winter after hatching) in the polymodal size-frequency curve for each population.

Spawning

In November 1969, 50 large and therefore assumed to be mature, *Nucella* were enclosed in a 1 × 1 × 0.5 m wire cage. The 5 × 5 mm mesh prevented mature *Nucella* (1.6 cm) from leaving or entering the cage. Large rocks covered with small mussels provided shelter, suitable places for egg laying, and an excess of food for the *Nucella*. The cage was anchored at low tide level near Purcell's Cove where a native population of *Nucella* had been actively spawning. The cage was reopened in October 1970. All surviving *Nucella* were measured, sexed, and the number of egg capsules laid were counted. Most of the egg capsules still contained embryos. Empty capsules adhere to the rocks for several months after hatching so that losses of empty egg capsules would be negligible.

Calorimetry

Samples of 30 males, 30 females, and 30 immature *Nucella* were collected from Lawrencetown each month. After measuring shell lengths to the nearest 0.1 mm, the bodies including the operculum, were dried for 48 hours at 58° C and weighed to the nearest 0.1 mg. Regressions of log dry body weight on log shell length were obtained. Samples of the dried material were soaked, homogenized and redried before igniting in a Phillipson micro-bomb calorimeter, thus giving data for the conversion of monthly biomass into kcal. Dried egg capsules were also combusted. Proportions of ash were measured after roasting the samples in a muffle furnace at 550° C for 24 hours.

Results

Population Structure

The Purcell's Cove population in 1969 (Fig. 1) followed a polymodal frequency distribution with two peaks at about 1.2 cm and 1.4 cm merging into a large peak containing animals of several age groups. The Lawrencetown population in 1969 (Fig. 2) had a similar structure but the peaks at about 1.2 cm and 1.4 cm were less distinct. This type of frequency distribution is typical of invertebrates which live for several years and which have protracted breeding seasons. Because births are not synchronized the age classes become blurred. Nevertheless, the first two age classes of *Nucella* (i.e. animals having passed their first and second winters) were recognized.

Spat collected from Purcell's Cove and Lawrencetown had a model length of 0.40–0.45 cm (Fig. 1).

The density, N, of *Nucella* at Purcell's Cove in July 1969 was 20.5 ± 2.1 per m^2. *Nucella* were noticeably clumped and were associated with patches of small (1–2 cm) mussels. By July 1970 the population had dropped to 4.8 ± 0.4 per m^2. Virtually all the mussels had disappeared

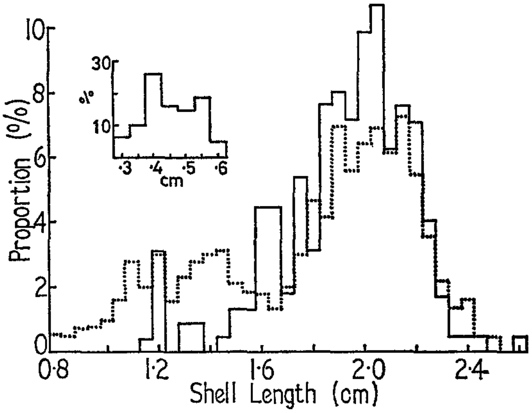

Fig. 1. Dotted histogram: Size-frequency of a sample of 1293 *Nucella* from 50 m^2 at Purcell's Cove in July 1969. Spat (animals less than 0.8 cm long) were not sampled. Solid histogram: Size-frequency of the same population, based on 223 animals in July 1970. Insert: Size-frequency of a sample of spat both from Lawrencetown and Purcell's Cove

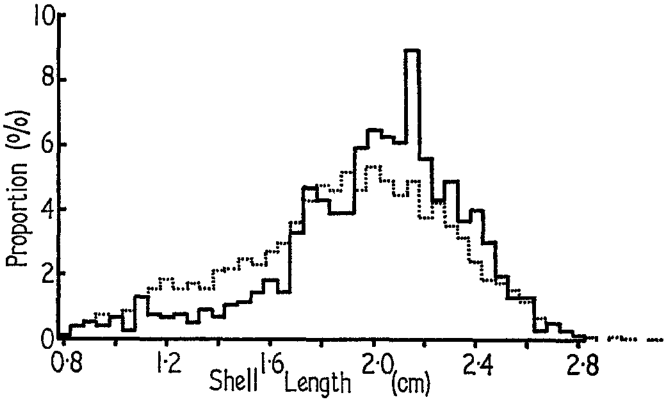

Fig. 2. Dotted histogram: Size frequency of a sample of 4581 *Nucella* from 126 m^2 at Lawrencetown in April 1969. Spat were not sampled. Solid histogram: Size-frequency of the same population in September 1970 (607 animals from 90 m^2)

from the area and the *Nucella* were distributed more evenly, as reflected by the smaller standard error of the 1970 count.

Because of the greater heterogeneity of the Lawrencetown beach, the distribution of *Nucella* was studied in more detail. The average numbers of *Nucella* in each m segment down the length of the shore are plotted in Fig. 3. In early April 1969, very few animals occurred in the

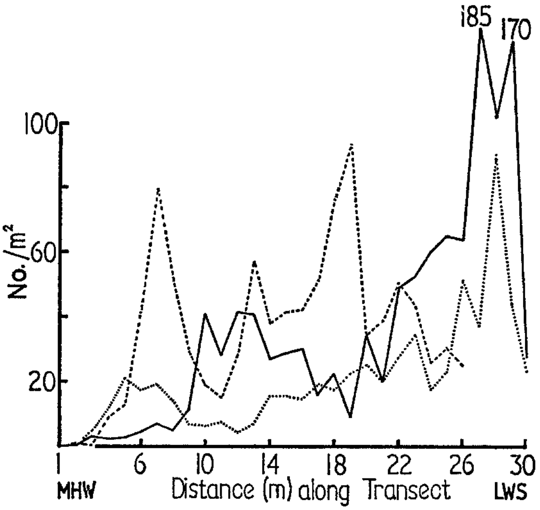

Fig. 3. Mean numbers of *Nucella* per m^2 at successive m intervals from mean high water to low water spring at Lawrencetown. April 1969, mean of 6 contiguous transects; July 1969, mean of 3 contiguous transects; September 1970, mean of 3 contiguous transects

top 9m. Later, in July 1969 and September 1970, animals were more numerous at these levels on the shore, suggesting that there was some seasonal migration at least in the upper levels. In contrast, a few tagged animals at Purcell's Cove made a maximum lateral movement along the beach of 4 m while the majority remained within 2 m of their release point throughout the year. Consequently the influence of immigration or emigration on the population dynamics was probably negligible. Immigration and emigration were also considered negligible in a British population of *Nucella* (Feare, 1970a).

Density increased sharply at low tide level (levels 26–30, Fig. 3) and skin-diving in July 1969 revealed that this approximate density was maintained to a depth of 1.5 m below low spring tide level. With increasing depth, *Nucella* thinned out, only occasional individuals being found at 4 m below low water spring. Whereas at least half the population of *Nucella* at Lawrencetown was sublittoral (and ignored in this study) there was no sublittoral extension at Purcell's Cove, probably because the subtidal mussels were too large for *Nucella* to drill.

Mean densities for the Lawrencetown population were:

April 1969: 36.4 ± 8.2 per m^2,
July 1969: 35.9 ± 4.7 per m^2,
September 1970: 20.6 ± 3.2 per m^2.

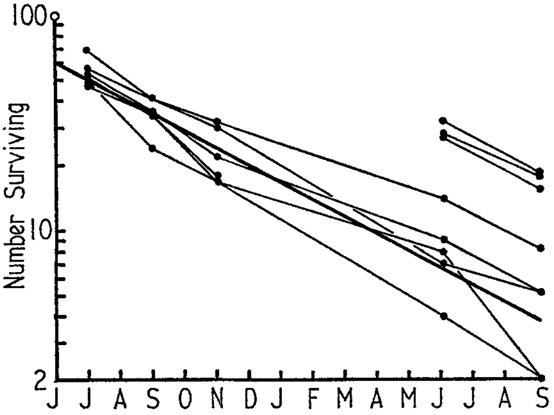

Fig. 4. The numbers of tagged *Nucella* recovered at Purcell's Cove plotted against time on a semilogarithmic scale. Each fine line traces the numbers recaptured from an initial batch of 100 animals. The thick line is the regression fitted to the data. The extra points commencing at June 1970 represent animals released at this time to boost the low numbers of *Nucella* surviving from the previous release. The slope of the regression line fitted to the data (except the animals released in June 1970) gave the monthly mortality rate

Mortality

Numbers of tagged animals recovered at Purcell's Cove are plotted against time on a semilog scale in Fig. 4. The mortality rate per month is given by the regression coefficient of −0.1723 fitted to the data in Fig. 4. Emigration could not account for the negative slope of the recapture curve since tagged animals remained close to their liberation point throughout the study period (maximum lateral migration of 4m); no *Nucella* below low water spring occurred at Purcell's Cove). Tag loss is not thought to have influenced the estimate of mortality rate because many of the dead, empty tagged shells were recovered among the accumulating empty untagged shells. Moreover, occasional tag losses were indicated by a distinct light patch on the shell where the epoxy glue had come away. Initially, the tagging process increased the mortality rate as revealed by the increased slope of the recapture curve when extrapolated back to the ordinate. After the first month the slope decreased and remained fairly constant, suggesting that the tagging process was no longer influencing mortality rate. However, assuming a constant mortality rate, the drop in density between July 1969 and July 1970 revealed by census gave a mortality rate per month of −0.0551.

The drop in density at Lawrencetown between July 1969 and September 1970 gave a mortality rate per month of −0.0292.

Growth

Monthly measurements of tagged animals revealed that growth occurred in spurts. Some animals began growth at the end of April and all had ceased by October. Different animals began and ceased growth at all stages within the growth period, the total annual growth taking anywhere from 1–5 months for completion. Contrary to the findings of Moore (1963), but in agreement with those of Berry and Crothers (1970) and Cowell and Crothers (1970), some tickened individuals put on a spurt of new growth. When computing production, growth rate was assumed to be constant during the growth season, because of the asynchronous and unpredictable seasonal growth pattern of *Nucella*.

Estimates of annual shell growth at Purcell's Cove were obtained from Ford-Walford regressions of length after growth on length before growth (Fig. 5). Regression equations fitted to the data were:

$$\text{tagged animals: } L_{t+1} = 0.4546L_t + 1.1290,$$
$$\text{new shell growth: } L_{t+1} = 0.7575L_t + 0.6498.$$

The mean of these regressions:

$$L_{t+1} = 0.6060L_t + 0.8894$$

was used in computing production.

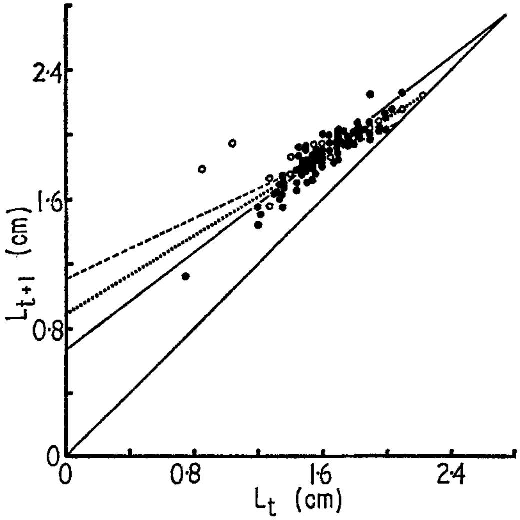

Fig. 5. Ford-Walford plots of length at the end of the growth season (L_{t+1}) against length at the beginning of the growth season (L_t) for Purcell's Cove. • Data from the measurements of new shell growth (see text). ∘ Data from tagged individuals. The mean regression for the two sets of data has been drawn in

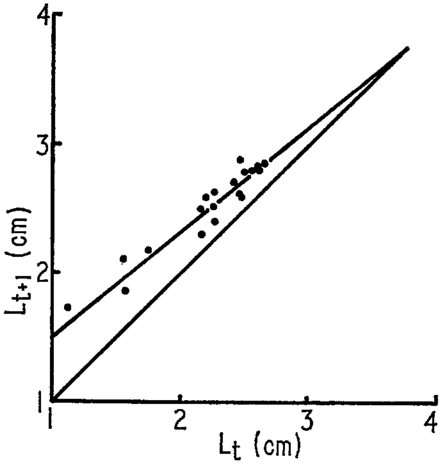

Fig. 6. Ford-Walford plot derived from measurements of new shell growth for the Lawrencetown population of *Nucella*

Fig. 6 displays data from measurements of new shell growth at Lawrencetown. The regression equation fitted to these data and used in the calculations of the production was:

$$L_{t+1} = 0.8270 L_t + 0.6659.$$

Spawning

Nine immatures, 21 females, and 10 males survived in the cage until October 1970. If males are promiscuous the minority of males should not have reduced the fecundity of the females. 978 egg capsules were counted giving a mean of 46.6 egg capsules laid per female, if all mortality accurred before the onset of spawning.

Sexual maturity was attained at about 1.6 cm in the Purcell's Cove population and at about 2.0 cm in the Lawrencetown population. From the size-frequency curves (Figs. 1 and 2) these individuals would be $2^1/_2$–3 years old, similar to the age of $2^1/_2$ years at the onset of sexual maturity in British *Nucella* (Feare, 1970b). Because of the variation in size of mature *Nucella* there was a need to relate egg production to shell length.

The mean length of females in the cage was 2.56 ± 0.18 cm and each was estimated to produce 46.6 egg capsules per year. 12 replicate combustions of single egg capsules gave a mean of 0.0216 ± 0.0021 kcal per capsule. It is reasonable to assume that the weight of the gonad is proportional to the cube of the shell length (Hughes, 1971) so that the calorific output of a female can be related to size by the equation:

$\log_{10}$kcal of output $= 3.\log_{10}$ shell length (cm) $- 1.2217$. The sex ratio was assumed to be equal since $\chi^2 = 2.95$, $P = 0.10$–0.05, for a sample containing 128 males and 157 females. Feare (1970b) found an approximately equal sex ratio in a British population of *Nucella* although there was a suggestion that differential mortality caused females to become predominant among older individuals.

We have no knowledge of the calorific output of males so half the output of females was assumed. The average output per mature individual may then be expressed as:

$$\log_{10}\text{kcal output} = 3.\log_{10}\text{shell length (cm)} - 1.4085.$$

About 3 % of mature animals both a Purcell's Cove and Lawrence town were infected with rediae of the philophthalmid trematode *Parorchis acanthus* (Nicoll). Although heavily parasitized, the infected *Nucella* contained a few gametes and both males and females were infected. In contrast, Feare (1970a) found that *Nucella* infected with *Parorchis* were castrated. The low incidence of infection would not affect the reproduction of the population significantly.

Calorimetry

Regressions of the $\log_{10}$ dry weight on $\log_{10}$ shell length for each month for males, females and immature *Nucella* are given in Table 1. Apart from October females and November males, the slopes of the regressions were not significantly different from each other. The grand mean slope was 2.9523. Since the October females and the November males gave suspiciously low slopes, probably due to experimental error, they were excluded, and the remaining data had a mean slope of 3.0720. The intercepts of all regressions were adjusted to the fixed slope of 3.0720 while computing production. Using the adjusted regressions, the dry flesh weight of standard males, females and immatures are plotted for each month in Fig. 7. Females tended to be heavier than males but both sexes followed similar seasonal trends. A general decline in body weight occurred throughout the winter, followed by an increase to May, after which there was a temporary decline perhaps associated with the beginning of the spawning season. Immatures followed a more irregular pattern, but again there was a decline in body weight through the winter.

Calorific values per gram of dry tissue and per gram ash free dry tissue are given in Table 2. Fluctuations in calorific value were irregular but males showed a minimum in May followed by females in June. These minimal calorific values of mature animals may have coincided with

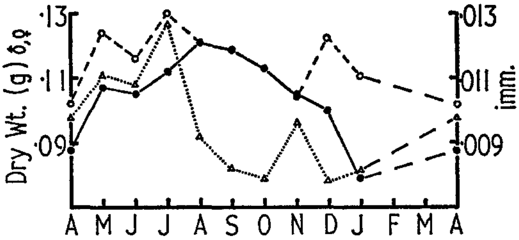

Fig. 7. Seasonal variations in dry flesh weights of standard *Nucella*. Males (•) and females (○) were 2 cm long, and immatures (▵) 1 cm long

Table 1. *Regressions of* $\log_{10}$ *dry flesh weight (g) on* $\log_{10}$ *shell length (cm) with a fixed slope of 3.0720 (see text). The original slopes are in parentheses*

Month	Male		Female		Immature	
	Slope	Intercept	Slope	Intercept	Slope	Intercept
April	3.0720 (3.6482)	−1.9813	3.0720 (3.6803)	−1.9148	3.0720 (2.9677)	−2.0707
May	3.0720 (2.6428)	−1.8937	3.0720 (2.8573)	−1.8314	3.0720 (3.2501)	−1.9452
June	3.0720 (2.7369)	−1.8803	3.0720 (1.9724)	−1.8403	3.0720 (2.7426)	−1.9274
July	3.0720 (2.4345)	−1.8527	3.0720 (3.5023)	−1.7893	3.0720 (2.7407)	−1.8959
Aug.	3.0720 (3.0314)	−1.8205	3.0720 (3.4260)	−1.8199	3.0720 (2.9516)	−2.0871
Sept.	3.0720 (3.2834)	−1.8288	3.0720 (3.4772)	−1.8308	3.0720 (3.3942)	−2.0871
Oct.	3.0720 (3.1084)	−1.8492	3.0720 (1.2883)	−1.8510	3.0720 (3.0292)	−2.1035
Nov.	3.0720 (1.2647)	−1.8741	3.0720 (3.7917)	−1.8855	3.0720 (3.6470)	−2.0161
Dec.	3.0720 (3.0588)	−1.9233	3.0720 (2.2817)	−1.8354	3.0720 (3.1677)	−2.1105
Jan.	3.0720 (2.4176)	−1.9741	3.0720 (3.1562)	−1.8736	3.0720 (3.6140)	−2.0865

spawning at the beginning of the breeding seasons. Calorific values of males, females and immatures were relatively high throughout the summer, decreasing in December and January.

Table 2. *Calorific values per gram of dry* Nucella *tissue (including operculum) with standard errors. Calorific values per ash-free gram are in parentheses*

Month	Male	Female	Immature
April	5.38 ± 0.14 (6.42)	5.63 ± 0.27 (6.68)	5.12 ± 0.18 (5.58)
May	4.88 ± 0.08 (5.42)	5.93 ± 0.14 (6.50)	4.73 ± 0.17 (5.17)
June	5.16 ± 0.06 (5.75)	5.00 ± 0.18 (5.50)	5.42 ± 0.18 (5.83)
July	5.79 ± 0.13 (6.22)	5.53 ± 0.03 (5.94)	5.43 ± 0.07 (6.02)
Aug.	5.32 ± 0.08 (5.68)	5.46 ± 0.09 (5.94)	5.44 ± 0.12 (5.93)
Sept.	5.77 ± 0.10 (6.25)	5.60 ± 0.15 (6.14)	5.57 ± 0.31 (5.83)
Oct.	5.57 ± 0.15 (6.10)	5.39 ± 0.14 (5.94)	5.50 ± 0.13 (5.81)
Nov.	5.53 ± 0.03 (6.03)	5.66 ± 0.09 (6.19)	5.55 ± 0.50 (6.03)
Dec.	5.66 ± 0.21 (6.25)	6.04 ± 0.11 (6.62)	5.40 ± 0.30 (5.83)
Jan.	5.67 ± 0.10 (6.20)	5.33 ± 0.22 (5.76)	4.30 ± 0.11 (5.34)

Production

For the purpose of computing population production (Table 3), the animals were divided into 0.05 cm size-classes. Starting with the numbers present in each size-class at Purcell's Cove in July 1969 and at Lawrencetown in April 1970, the numbers surviving in each month of the year were generated by successive multiplication by the appropriate monthly survival rate (1-mortality rate). The lengths of each size group at the end of each month were derived from the appropriate Ford-Walford equations on the assumption that an equal proportion of annual growth occurred in each month of the growing season. The shell lengths in each month were converted to biomass using the adjusted regressions in Table 1. Biomass was converted to kcal using the data in Table 2. Production due to growth (*Pg*) was obtained by summing for each monthly interval the change in biomass (kcal) of survivors including additions due to recruitment. The numbers and the sizes of mature animals occurring each month during the spawning season were substituted into the equation relating calorific output to shell size (see " Spawning ") to yield production due to gamete release (*Pr*). Summation of *Pg* and *Pr* gave total production (*P*).

The equation $Pg = E + \Delta B$, where E = energy eleminated via mortality, and ΔB = net annual change in biomass, affords a second method of calculating *Pg*. *E* was derived from the numbers dying and the mean weight of each size-class per monthly interval.

Discussion

The crash in numbers of *Nucella* at Purcell's Cove between July 1969 and July 1970 was possibly associated with the early depletion of mussels, which were the main food supply in the area. Barnacles were rare and the large numbers of *Littorina littorea* persisting in the area did not seem to be preyed upon by *Nucella*. A few small *Littorina* were found partly drilled by *Nucella* but the shell seemed so be too thick for complete penetration.

Berry and Crothers (1970) suggested that the reduced and varying salinity of the Bristol Channel caused periodic shortages of food leading to localized extinction and disruptions of growth among populations of *Nucella*. Many *Nucella* at Purcell's Cove showed evidence of disrupted growth accompanied by a thickening of the shell lip, a feature which Cowell and Crothers (1970b) attributed to starvation. However, members of the Muricidae are able to withstand long periods of starvation. Murdoch (1970) showed that *Thais emarginata* (Deshayes) could survive at least 6 months without food. Consequently, if starvation was important at Purcell's Cove, mortality rate would be expected to have increased towards the end of the study period.

Another possible cause of mortality at Purcell's Cove was predation. Potential predators were *Tautoglabrus adspersus* (Walbaum), *Cancer irroratus* Say and *Larus argentatus* Pontoppidan. Gibson (1970) and Kitching *et al.* (1966) have shown that shore crabs *Carcinus maenas* (L.), are able to kill and eat *Nucella* without cracking the shell.

Feare (1970) revealed the importance of predation by *Cancer pagurus* (L.) on a British population of *Nucella* at low levels on the beach during the summer months. However, it is unlikely that *Cancer irroratus* was a significant predator at Purcell's Cove since it migrates offshore during the winter and could not maintain the steady mortality rate observed.

At Lawrencetown there was always an excess of food (small mussels). Recruitment was higher than at Purcell's Cove but there was a drop in numbers of *Nucella* between April 1969 and April 1970. However, the growth of the survivors was sufficient to produce a net annual increase in biomass (ΔB).

Table 3. *Population parameters*

Location	Monthly mortality rate	Mortality (E)	Recruitment	Net annual change in biomass (ΔB)
Pucell's Cove				
Mark-recapture	−0.1723	11.95	0.03	−12.37
Census	−0.0551	6.90	0.03	− 5.31
Mean	−0.1137	10.36	0.03	−10.09
Lawrencetown	−0.0292	6.73	0.28	1.43

As shown in Figs. 5 and 6, *Nucella* at Lawrencetown grew faster and to a larger size than those at Purcell's Cove. Also, sexual maturity occurred at a greater shell length (about 2.0 cm at Lawrencetown and 1.6 cm at Purcell's Cove). Availability of prey probably accounted for these differences in growth pattern.

Direct estimates of production due to growth (Pg) agreed closely with the indirect estimates from summing mortality (E) and the net annual change in biomass (ΔB). The indirect estimate for Lawrencetown exceeded the direct estimate by about 5%. Larger proportional differences in these estimates for Purcell's Cove were due to the small values of Pg involved.

Estimates of the energy released as spawned gametes (Pr) greatly exceed Pg for the Purcell's Cove population. The difference is less for the Lawrencetown population where higher growth rates led to a greater estimate of Pg. Although the estimate of egg production per female is probably reliable, that for the calorific output of males, which was arbitrarily assumed to be half that of the females, may be erroneous.

McNeill and Lawton (1970) have shown that a first order regression predicts $\log_{10}$ annual population respiration from $\log_{10}$ annual population production fairly well, especially if species are grouped into those living less than, and those living more than, one year. The expected annual respiration of the two *Nucella* populations (Table 3) was calculated using the equation appropriate to poikilotherms living more than one year (McNeill and Lawton, 1970). Summation of annual production and expected annual respiration gave the expected annual assimilation, or energy flow for each population (Table 3). From the expected values of assimilation, net population growth efficiencies (P/A) ranged from about 25–27% (Table 3).

The large differences between the structure and dynamics of the two *Nucella* populations led to different estimates of annual production per unit area, although these differences were less than an order of magni-

of Nucella lapillus *from 2 localities*

$\Delta B+E$	Growth (Pg)	Spawning (Pr)	Production (P)	Expected respiration (R')	Assimilation ($P+R'$)	$\frac{P}{P+R'}$
−0.42	0.24	3.69	3.93	10.32	14.25	0.28
1.59	1.49	5.85	7.34	20.18	27.50	0.27
0.27	0.60	4.91	5.51	14.84	20.35	0.27
8.16	7.77	8.89	16.66	48.63	65.29	0.26

tude. Spatial and temporal heterogeneity is typical of many invertebrate species (Hughes, 1971; Paine, 1965; Sutherland, 1970) so that estimates of energy parameters for populations at a specific site are only useful for order of magnitude predictions about other populations.

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Zoology Department
University College of North Wales
Bangor
Caerns, United Kingdom