# Ecological Energetics of the Seaweed Zone in a Marine Bay on the Atlantic Coast of Canada. III. Energy Transformations by Sea Urchins* **

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## Abstract

An energy budget was constructed for a population of the sea urchin *Strongylocentrotus droebachiensis* in the nearshore area of St. Margaret's Bay, Nova Scotia, Canada. Of the 6 age classes identified, ages 1 + and 2 + accounted for about $1/2$ the population energy flow. Population production efficiencies were: production/assimilation = 0.28, production/consumption = 0.04 to 0.13, and production/biomass = 0.80. Although *S. droebachiensis* was the dominant herbivore in the seaweed bed, it utilized only 1 to 7 % of seaweed production. As with other populations of sea urchins, however, it had a proportionately greater influence on seaweed biomass, and also presumably production, by clearing seaweed from large areas of substrate and maintaining it clear. Loss of dissolved organic matter, the only term in the energy budget not measured, was estimated by substracting the other terms in the energy budget from consumption. In laboratory individuals, this ranged from 40 to 80 % of absorption (consumption – faeces). A critical review of energy budgets for 6 other species of marine benthic grazers also revealed large amounts of energy unaccounted for that might be attributed to loss of dissolved organic matter.

## Introduction

The seaweed production in St. Margaret's Bay, Nova Scotia, is very large, 1750 g C/m²/year in the seaweed zone, or 603 g C/m²/year averaged over the entire bay (Mann, 1972b). The fate of the seaweed production must be known if we are to determine its importance to the production of higher trophic levels. In this study, the importance of the dominant grazer in the seaweed zone, the sea urchin *Strongylocentrotus droebachiensis*, was quantified using the methods of ecological energetics.

A second problem considered was the amount of sea urchin production available to predators or to a fishery. This has economic justification because some of the predators — lobster, plaice, and winter flounder — have commercial importance, and *Strongylocentrotus droebachiensis* has potential for export to countries where sea urchin gonads are valued as food.

A third problem, which developed in the course of the study, was the importance of the loss of dissolved

organic matter (DOM) in the population energy budget. Loss of DOM is usually thought to be negligible. However, indirect evidence based on the imbalance of energy budgets of several benthic grazers indicate this term may be quite large.

The population energy equation may be expressed as:

$$C = R + P_r + P_g + F + \text{DOM loss}$$

where $C$ is consumption, $R$ respiration, $P_r$ tissue production as gonads, $P_g$ tissue production as body growth, $F$ faeces, and DOM loss is any net loss of energy in soluble form. DOM loss may result from active excretion, passive loss through body surfaces, loss from the anus with the faeces or leached from the faeces, or loss from material being chewed. $P_r$ is often defined as spawn released (Ricker, 1968; Petrusewicz and Macfadyen, 1970), but this is somewhat lower than the gonad production used here, since some individuals with developing gonads would be lost through mortality before spawning. Absorption ($a$) is C — F and assimilation ($A$) is $R + P_r + P_g$.

## Methods

### Collection and Acclimation

Specimens used in laboratory respiration and feeding experiments were always collected from a single location in St. Margaret's Bay. They were held in the laboratory from 4 to 10 days in flowing sea water within 2 C° and 2‰ salinity of the ambient conditions at the site of collection. The annual ranges of temperature and salinity at the collection site were 0° to 18 °C and 29 to 32‰. Animals were provided with an excess of the kelp *Laminaria longicuris* as food. Lights over the holding tanks provided an intensity of 400 foot candles and were timed to the same day length as in the field.

### Respiration Rates

Respiration rates were measured under a variety of conditions in an attempt to determine the magnitude of possible bias in the rate used in constructing the

population energy budget. All the methods were compared with the routine method which supplied the data for the energy budget.

The routine method was used in the laboratory, and consisted of gently placing a sea urchin in a wide-mouth bottle full of water, without food, capping the bottle and leaving it in a waterbath for about 6 h. Light intensity was 400 foot candles, stirring was provided by a magnetic stirring bar inside each bottle (separated from the sea urchins by a plastic guard), and the drop in $O_2$ concentration was determined by duplicate Winkler titrations (Carpenter, 1965). $O_2$ was controlled within 5 to 20% of the value in control bottles treated identically, but without sea urchins. *Strongylocentrotus droebachiensis* regulates its oxygen consumption independent of environmental oxygen down to 40% of saturation at 10 °C (Johansen and Vadas, 1967).

Three other methods used to measure respiration were similar to that described above, with the following exceptions in each case: (i) experiments were run at night and in the dark; (ii) the stirring was omitted; (iii) experiments were run on the bottom in St. Margaret's Bay, also without stirring. The rates in St. Margaret's Bay were determined by taking wide-mouth jars to the bottom, gently adding sea urchins picked from the bottom and, as before, capping the jars and leaving them undisturbed for about 6 h. At the end of an experiment, the jars were brought to the deck of a support vessel where water samples were taken for DO analysis, and the experimental individuals were weighed.

A fifth method used a flowing system in the laboratory with sea urchins provided with food. The respirometer was a plexiglass tube 10 cm in diameter by 23 cm long, covered on the ends by flat pieces of plexiglass fitted with rubber gaskets to provide a good seal. The inflow was through small holes in one end and the outflow through a siphon of plastic tubing attached to the other end. The apparatus was set on end, siphon up, in a waterbath with a continuous exchange of sea water. Water samples were taken by placing the siphon outlet in a sample bottle beside the waterbath. A similar apparatus used for measuring fish respiration has been described and illustrated by Mann (1965). The respirometers contained several animals of the same size, and pieces of *Laminaria longicruis* for food. There were 2 controls, a respirometer with kelp only, and a respirometer without kelp or animals. The oxygen uptake of sea urchins plus kelp was calculated from the flow rates, and the drop in oxygen concentration relative to the control without sea urchins or kelp. The oxygen consumption per g kelp was calculated from the difference in the oxygen content of water from the two control containers, the weight of kelp in the first control, and the flow rates through both containers. This figure was used to correct for respiration of the average weight of kelp

in the containers with kelp and sea urchins. Flow rates were about 90 ml/min, and experiments were run for 48 h with flow rate and dissolved oxygen measured 2 or 3 times daily.

### Consumption and Absorption Rates

Feeding rates were measured in the laboratory in 1.9 l glass battery jars submerged in a waterbath and provided with a flow of fresh sea water of 0.3 to 0.4 l/min. Lighting was identical to acclimation conditions.

Feeding experiments lasting 6 days with 3 to 10 sea urchins of similar size per experimental container gave acceptable precision. Preliminary feeding experiments, where the daily consumption of each of 4 individuals was monitored for 1 month showed that, over any given 10-day period, the consumption rate of a single sea urchin ranged over an order of magnitude. Use of 3 or more individuals per experimental container and 6 day experiments improved the precision so that 95% confidence limits were usually within 30% of the mean of container replications. Two 6 day experiments with 6 or 7 containers in each were run every 2 months for a year.

Experiments were initiated by adding a known weight (10 to 30 g) of the kelp *Laminaria longicruis* to the battery jars. Food remaining after 3 days was weighed and replaced by new kelp for the final 3 days. The rations provided were at least double the amount eaten, so there was probably no competition among animals for food. Faeces were collected daily when the water temperature was over 8 °C, and every 2 days at lower temperatures. Faeces were collected by siphoning from the bottom of the battery jar onto 0.2 mm mesh netting, then briefly rinsing with distilled water to remove interstitial salt water. The 0.2 mm mesh was adequate, since the sea urchins produced neat globular faeces of at least 1 mm diameter. The brief rinse was not likely to cause significant loss of DOM from faeces, since they had already been washed for hours by sea water while in the feeding container. One battery jar contained kelp only, and was used as a control for any change in kelp weight and any accumulation of sediment that might bias estimates of faeces weights.

The calorific value of kelp and faeces was determined in a Phillipson Microbomb Calorimeter after drying at 60 °C. Duplicate determinations were made on a composite sample of the food remaining in all battery jars after each 3 day period. Variation among determinations of cal/g wet weight was due more to variation of dry:wet weight ratios than to variation of cal/g dry weight. The coefficients of variation were 0.24 and 0.11, respectively. The dry weight of faeces was measured for each experimental container for each 6 day experiment, but cal/g dry weight was measured for only the containers with the largest and

smallest individuals. As there was no difference between determinations for large and small animals ($P > 0.05$) an average cal/g dry weight was used for all animal sizes in each experiment. Averaged over all experiments, calorific values were 0.37 kcal/g wet weight and 2.7 kcal/g dry weight for kelp, and 2.6 kcal/g dry weight for faeces.

The following checks were made on possible sources of error in the feeding experiments. By forcing the overflow from the feeding containers to flow through 0.07 mm mesh netting, it was verified that no faeces or food particles were being lost. In one experiment, faeces were collected two or three times a day to reduce possible loss of organic matter by decomposition or solution, but the results (absorption efficiencies) did not differ significantly from those obtained by collecting the faeces every second day. There was no evidence of significant loss of dissolved organics from the kelp during experiments, as there was no weight loss by kelp in the control containers and the dry:wet weight ratios of kelp in the control and experimental containers did not change. Providing individuals with excess food for several days prior to a feeding experiment allowed their guts to reach an equilibrium fullness and insured that faeces egested during a feeding experiment came from the *Laminaria longicuris* supplied. These precautions were necessary for realistic estimates of absorption efficiencies. The assumptions appear to have been met, as color and texture of faeces showed them to be exclusively *L. longicuris*, and rates of defecation showed no consistent trend through the 6 days of an experiment. By dissecting guts of *Strongylocentrotus intermedius*, Fuji (1967) found that they reached an equilibrium fullness in 1 day feeding on *Laminaria japonica*, and in 2 to 3 days feeding on *Ulva pertusa*. He found little difference in results at 5° and 24 °C.

## Body Growth

Annual growth rates were based on analysis of a size-frequency distribution and checked with data from annual growth rings. The seasonal distribution of growth within a year was based on size-frequency analysis of bimonthly collections and growth in aquaria in the laboratory.

An average size-frequency distribution for the entire sea urchin population of the near shore area of St. Margaret's Bay was determined from collections made by SCUBA divers in the summer of 1968. The sampling procedure is described in detail in the first paper of this series (Mann, 1972a) but, in summary, included 165, 0.25 m² quadrats on 24 randomly selected transects laid out at right angles to the shore. The transects averaged 370 m long, and extended from the intertidal to an average maximum depth of 20 m. The size-frequency distribution was constructed from test diameter measurements of 501 individuals mea-

sured to the nearest millimeter, a moving average of 3 was applied to the frequencies, and component "normal" distributions were separated according to the method of Taylor (1965).

Annual growth rings were counted on the plates of the test using the method described by Moore (1935), modified by Jensen (1969). This method was tedious and probably accurate only within ± 1 year, at least for the St. Margaret's Bay population, since the annual rings can be formed over a period of several months (Moore, 1935).

For estimating the seasonal distribution of growth, collections were made approximately bimonthly from December, 1969 through November, 1970 in a 20 × 50 m area on the eastern shore of St. Margaret's Bay. Sea urchins were collected from 40, 0.1 m² randomly located quadrats on each sampling date. The number of specimens in each collection ranged from 300 to 450. Individuals smaller than 9 mm diameter were probably not sampled quantitatively, since they were easily overlooked.

Sea urchins used for growth measurements in the laboratory were maintained in running sea water at near ambient field temperature and salinity. An excess of *Laminaria longicuris* was supplied as food, and sea urchins were weighed monthly.

Growth in diameter of urchins in the natural population was converted to calories using regressions for live weight on diameter and cal/g live weight on live weight. Gonads and stomach contents were removed from specimens used for calorific determinations. Including the gonads and stomach contents in animal live weights did not bias the weights, since changes in volumes of these were offset by changes in the amount of water in the test cavity, and the specific gravity of food and gonads is near that of sea water.

The calorific values of whole sea urchins could not be measured in a calorimeter, because the organic content was too low for the samples to ignite. Adding benzoic acid to the samples permitted ignition, but the results were unreliable; the higher the fraction of benzoic acid in a sample, the lower the estimate of calorific value of the tissue. This was after correction for heat produced by the benzoic acid and correction for endothermy of calcium carbonate (0.14 cal/mg $CaCO_3$) as recommended by Paine (1966).

Because of these problems, the calorific value was calculated as the product of ash-free dry weight, and a constant of 5.9 kcal/g ash-free dry weight. Drying was carried out at 170 °C, and ashing was carried out at 500 °C, in order to overcome the difficulties with calcareous animals discussed by Paine (1964). The value of 5.9 kcal/ash-free g is based on data from Fuji (1967) showing a 7:1 ratio of protein to fat for the organic portion of *Strongylocentrotus intermedius* and values of 5.4 and 9.4 kcal/ash-free g for protein and fat, respectively.

## Gonad Growth

Sea urchins were collected from the same area in St. Margaret's Bay that supplied the specimens used to estimate the seasonal pattern of body growth.

The relationship between gonad size and animal size was determined at bimonthly intervals and expressed as

$$Y = a \, (X - 7)^b$$

where $Y$ is gonad wet weight (g), $X$ animal live weight (g), and 7 g the approximate animal weight at sexual maturity. Gonad weight was measured to the nearest 0.01 g after blotting on paper towelling. Different regressions were calculated for each sex for dates when the gonads were ripe enough to identify eggs and sperm.

Gonads were dried to a constant weight at 60 °C, and two determinations were made on the gonads of each animal using a Phillipson Microbomb Calorimeter.

### Results

#### Respiration

Comparisons of respiration rates from different methods show the highest to be in the laboratory-flow system, the lowest in the field-closed system, and the laboratory-closed system to be intermediate with no effects due to darkness or lack of stirring (Table 1). Comparisons were made by tests of significance (covariance analysis) between the slopes ($b$) and intercepts (log $a$) of two regression equations of the form:

$$\log R = \log a + b \log W$$

where $R$ is the respiration rate (ml $O_2$/urchin/day) and $W$ is animal live weight (g). Laboratory measurements in closed containers were significantly higher than field measurements in closed containers by a factor of 1.4, and rates from the laboratory-flow system averaged 1.5 times rates in the laboratory-closed system. Possible explanations for these differences are that laboratory specimens were better fed

than individuals in the field, and the provision of food and continuous exchange of water in the flow system stimulated respiration. There was no significant difference in the slopes of regressions for any of the comparisons.

The laboratory values from the closed system have been used for calculating population respiration, since they are intermediate in the range of values obtained. If the variables tested produced the maximum possible range of respiration rates, then the largest possible bias caused by using the data from the laboratory-closed system is 1.4 or 0.7 times the true value.

Respiration rates (routine method) showed only a small change with season, and the slopes of log $R$ versus log $W$ regressions showed no trend with season. The experimental conditions and the constants for the regression equations are given in Table 2. A seasonal trend in rates is most easily seen in Fig. 1, where daily respiration rate is given in calories (ml $O_2 \times 4.83$ cal/ml $O_2$, Ivlev, 1934) per 8.3 g urchin, the average size of *Strongylocentrotus droebachiensis* in the St. Margaret's Bay population.

Experiments in both the laboratory and field showed that *Strongylocentrotus droebachiensis'* respiration was not strongly dependent on temperature. A least-squares fit to the points of log respiration versus temperature in Fig. 1 yielded a constant and low $Q_{10}$ of 1.7 over the seasonal range of temperature. Although such a line is a good fit to the points ($r^2 = 0.88$), there are clearly seasonal changes unexplained by temperature. For example the December/January and October/November rates at 7.5° and 8.5 °C are practically the same as the April/May rates at 4 °C, while there is nearly a 50% increase between 2° and 4 °C in the spring. Respiration rates of urchins from above and below the thermocline were measured simultaneously at the site of collection in St. Margaret's Bay (Table 2). Despite a 5 C° difference in temperature, there was no significant difference between the slopes or intercepts of the two regression lines.

Table 1. *Strongylocentrotus droebachiensis*. Comparison of respiration rates obtained by different methods. $R$: oxygen consumption in ml/urchin/day, $W$: animal live weight in g

| Experimental conditions | | | $n$ | $R = aW^b$ $a$ | $b$ | $r^2$ | Level of significance log $a$ | $b$ |
|---|---|---|---|---|---|---|---|---|
| January, 1970 | 2 °C | Day | 7 | 0.592 | 0.708 | 0.88 | P > 0.05 | P > 0.05 |
| January, 1970 | 2 °C | Night | 7 | 0.405 | 0.785 | 0.94 | | |
| July, 1970 | 11.5 °C | Stirring | 9 | 0.775 | 0.815 | 0.96 | P > 0.05 | P > 0.05 |
| July, 1970 | 11.5 °C | No stirring | 9 | 0.865 | 0.791 | 0.98 | | |
| September, 1970 | 17 °C | Laboratory | 20 | 0.788 | 0.866 | 0.98 | P < 0.01 | P > 0.05 |
| August, 1970 | 17 °C | Field | 6 | 0.515 | 0.886 | 0.98 | | |
| September, 1970 | 17 °C | Closed system | 20 | 0.788 | 0.866 | 0.98 | P < 0.01 | P > 0.05 |
| September, 1970 | 15 °C | Flowing system | 8 | 1.245 | 0.850 | 0.98 | | |

*Table 2. Strongylocentrotus droebachiensis. Experimental conditions and results for respiration rate ( R in ml $O_2$/urchin/day) versus animal live weight (W in g) for each 2 month interval, and for above and below the thermocline on August 17, 1970*

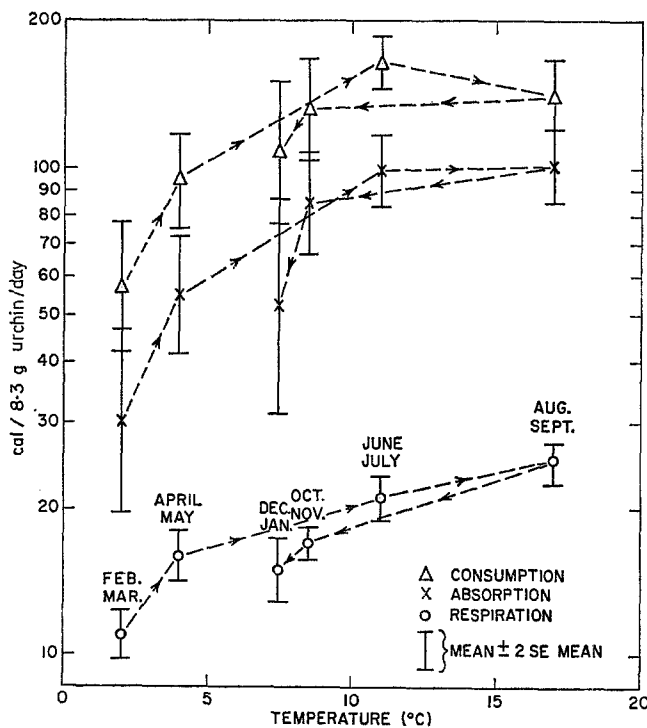| Time interval or location | Temperature (°C) | Range of animal weight (g) | $R = aW^b$ | | | |
|---|---|---|---|---|---|---|
| | | | n | a | b | $r^2$ |
| Feb.—March | 2 | 4.1—63.5 | 18 | 0.437 | 0.795 | 0.96 |
| April—May | 4 | 1.0—50.9 | 20 | 0.647 | 0.772 | 0.94 |
| June—July | 11 | 0.9—42.3 | 18 | 0.772 | 0.823 | 0.97 |
| August—Sept. | 17 | 0.9—39.6 | 20 | 0.793 | 0.877 | 0.98 |
| Oct.—Nov. | 8.5 | 1.0—50.2 | 18 | 0.647 | 0.792 | 0.97 |
| Dec.—Jan. | 7.5 | 1.5—41.7 | 11 | 0.463 | 0.893 | 0.97 |
| Above thermocline | 17 | 0.9—31.9 | 6 | 0.515 | 0.886 | 0.98 |
| Below thermocline | 12 | 0.7—27.4 | 5 | 0.591 | 0.778 | 0.92 |



Fig. 1. *Strongylocentrotus droebachiensis.* Consumption, absorption, and respiration rates in cal/8.3 g urchin/day. SE: Standard error

Table 3. *Strongylocentrotus droebachiensis. Regression equations for consumption (C in cal/urchin/day) versus animal live weight (W in g), and absorption (in cal/urchin/day) versus animal live weight. Also, results of tests for differences between slopes of regressions where $b_C$ is for consumption regression, $b_a$ for absorption regression, and $b_R$ for respiration*

| Time interval | Temperature (°C) | Animal size range (g) | n | $C = aw^b$ | | | Absorption $= aw^b$ | | | $(C - F/C_1)100$ Absorption efficiency | Level of significance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | a | b | $r^2$ | a | b | $r^2$ | | $b_C$ & $b_a$ | $b_C$ & $b_R$ | $b_a$ & $b_R$ |
| Feb.—March | 2 | 1.9—32.1 | 12 | 9.1 | 0.866 | 0.86 | 5.3 | 0.823 | 0.96 | 58 ± 9% | P > 0.05 | P > 0.05 | P > 0.05 |
| April—May | 4 | 1.0—43.8 | 14 | 20.3 | 0.729 | 0.91 | 12.1 | 0.717 | 0.87 | 59 ± 4 | P > 0.05 | P > 0.05 | P > 0.05 |
| June—July | 11 | 1.1—45.3 | 13 | 30.7 | 0.792 | 0.97 | 18.7 | 0.786 | 0.93 | 61 ± 5 | P > 0.05 | P > 0.05 | P > 0.05 |
| August—Sept. | 17 | 0.9—46.4 | 14 | 30.5 | 0.726 | 0.92 | 22.7 | 0.703 | 0.94 | 71 ± 2 | P > 0.05 | P < 0.01 | P < 0.01 |
| Oct.—Nov. | 8.5 | 1.1—47.3 | 12 | 22.7 | 0.833 | 0.92 | 15.8 | 0.794 | 0.92 | 65 ± 3 | P > 0.05 | P > 0.05 | P > 0.05 |
| Dec.—Jan. | 7.5 | 0.9—40.0 | 11 | 20.1 | 0.795 | 0.89 | 8.8 | 0.839 | 0.81 | 49 ± 6 | P > 0.05 | P > 0.05 | P > 0.05 |
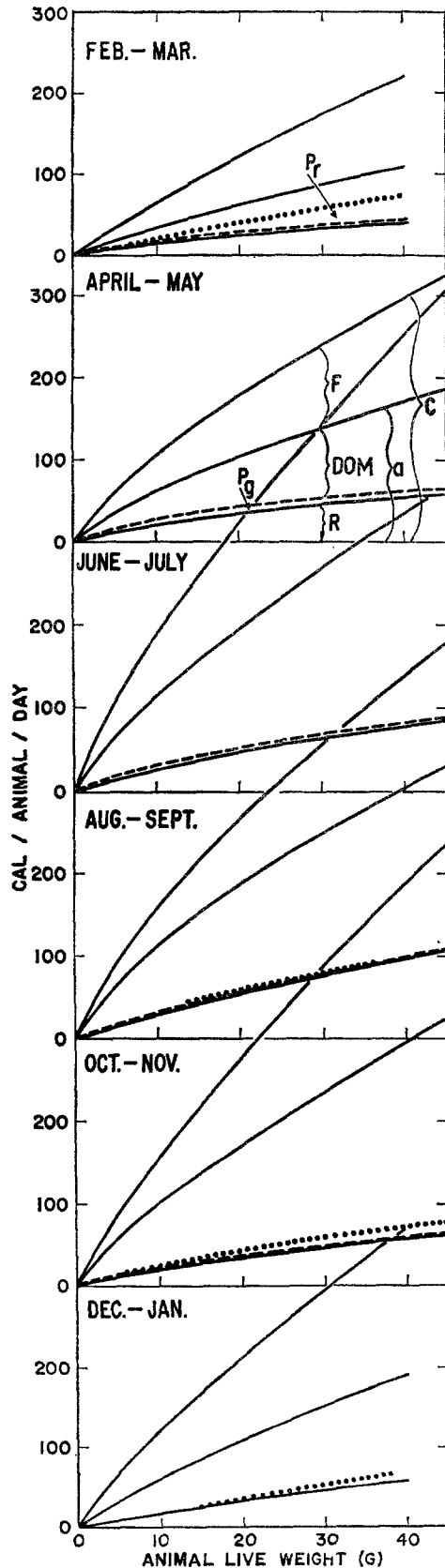
## Consumption and Absorption Rates

Power curves produced good fits to plots of consumption (cal/urchin/day) versus animal weight (g) and absorption versus animal weight. The results for each 2 month interval are given in Table 3. These regressions plus the regressions for respiration versus animal size are shown in Fig. 2.

Comparison of the exponents of the regressions of respiration, consumption, and absorption on animal size for the same dates shows trends of efficiencies with animal size. The lack of differences between the exponents of consumption versus animal size and absorption versus animal size for all 6 time periods ($P > 0.05$) indicates no trend of absorption efficiency with animal size (Table 3). The exponents of both consumption versus animal size and absorption versus animal size differ from the slopes of respiration versus animal size for only one of the 6 time periods (Table 3). For five dates, this indicates no change with animal size for the fraction of consumption or absorption used for respiration. For the sixth period, August/ September, the fraction of consumption and absorption used for respiration increases with animal size ($P < 0.01$). Although statistically significant, the increase is only 9% for the respiration fraction of absorption (23 to 32%), and only 5% for the respiration fraction of consumption (17 to 23%), with an increase in animal size of 1 to 40 g.

The variation of consumption and absorption rates with temperature is not as well explained by a single $Q_{10}$ as is the variation of respiration rate with temperature. Coefficients of determination ($r^2$) for log consumption versus temperature and log absorption versus temperature were 0.65 and 0.73, while log respiration versus temperature had an $r^2$ of 0.87. All three are statistically significant. Consumption and absorption showed greater increases from February/ March to June/July and less change from June/July to October/November than did respiration.

Absorption efficiency was highest at warm temperatures, and ranged from 49% in December/ January to 71% in August/September (Table 3).

Consideration of production efficiencies is left for the section on population energy budgets, but it is clear from Fig. 2 that production is small relative to the other parameters. A puzzling feature of the plots in Fig. 2 is the large percentage of absorbed energy not accounted for by respiration and production. This ranges from 40 to 80%, considering all dates and all sized individuals. If the other measurements are assumed reasonable, the missing fraction must be loss

Fig. 2. *Strongylocentrotus droebachiensis.* Consumption ($C$), faeces production ($F$), absorption ($a$), DOM loss, body growth ($P_g$), gonad growth ($P_r$), and respiration ($R$) as function of animal size for each 2 month time interval

of DOM, since this was the only term in the energy budget not measured.

Zooplankton (Leighton, 1968) and sea urchin faeces are possible sources of food energy not measured. Re-ingestion of faeces was not likely, however, as sea urchins normally carried the kelp onto the sides of the container to feed, while faeces collected on the bottom of the container. If feeding on zooplankton was significant, the true fraction of absorption not accounted for was even larger than shown in Fig. 2, since the additional food energy would have been measured as *P*, *R*, and *F*, but not *C*.

### Consumption, Absorption, and Respiration Measurements in a Flow System

Because of the surprisingly large imbalance in the energy equation, experiments were conducted in a flow system where consumption, absorption, and respiration could be measured simultaneously on the same

Table 4. *Strongylocentrotus droebachiensis. Consumption, absorption, and respiration measured in a flow system*

| Experiment | Mean animal size (g) | Consumption | Absorption | Respiration | $\frac{a-R}{a} \times 100$ |
|---|---|---|---|---|---|
| | | (calories/urchin/day) | | | (%) |
| 1 | 7.7 | 88 | 62 | 36 | 42 |
| | 4.0 | 52 | 36 | 18 | 50 |
| 2 | 7.2 | 104 | 69 | 33 | 52 |
| | 3.8 | 57 | 33 | 19 | 43 |
| | 1.8 | 41 | 29 | 11 | 62 |
| 3 | 7.0 | 125 | 86 | 31 | 64 |
| | 3.8 | 68 | 53 | 17 | 60 |
| | 1.8 | 42 | 32 | 10 | 69 |

individuals. Because of the effort required in conducting these experiments, it was not practical to run them long enough to measure growth. However, both laboratory and field experiments had shown that growth was only a small fraction of the absorbed energy.

The apparatus and procedure for measuring respiration are described in the section on respiration methods. Food was weighed at the beginning and end of the experiments, faeces were weighed at the end of experiments, and calorimetry was the same as described in the feeding methods. Experiments were run in September, 1970 at 15 °C. The results of these experiments (Table 4) also show a large fraction of absorbed energy unaccounted for, and the 42 to 69% range is similar to the 40 to 80% range indicated in Fig. 2.

### Body Growth

The fit of normal distributions to a size-frequency plot (Fig. 3) to determine the annual growth rates of the sea urchin population in St. Margaret's Bay was somewhat subjective, but was supported by other data. According to the gonad size and degree of ripeness, the peak spawning period is April, however, 10 of 71 urchins had ripe gonads in November, indicating a second spawning. A modal peak of size frequencies at 8 mm appeared in May, and a second modal peak at 5 mm appeared in July. These are the first two points in Fig. 4. These modes are interpreted as recruitment from November and April spawnings, respectively. Other data dictated that the two modes of a year-class converge for individuals 3 years and older. When comparing the modal peaks for the July, 1968 collections (Fig. 3) with the July results for the biomonthly collections (Fig. 4) and the data from the annual
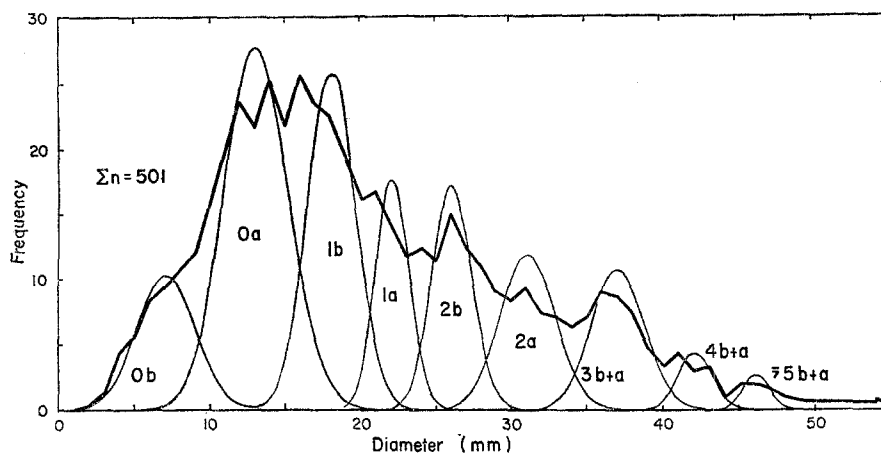


Fig. 3. *Strongylocentrotus droebachiensis.* Size-frequency distribution with fitted normal curves for July, 1968 collections representing the entire St. Margaret's Bay population. Numbers under each curve refer to age class, and subscript distinguishes between animals spawned in November/December (*a*) and April/May (*b*)
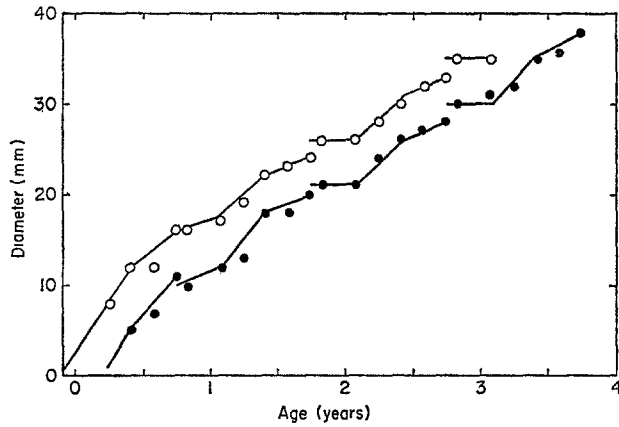
Fig. 4. *Strongylocentrotus droebachiensis*. Composite growth curves for urchins based on size-frequency analyses of bi-monthly collections from one location in St. Margaret's Bay. Open circles: urchins spawned in November; closed circles: urchins spawned in April. Lines are generalized seasonal patterns
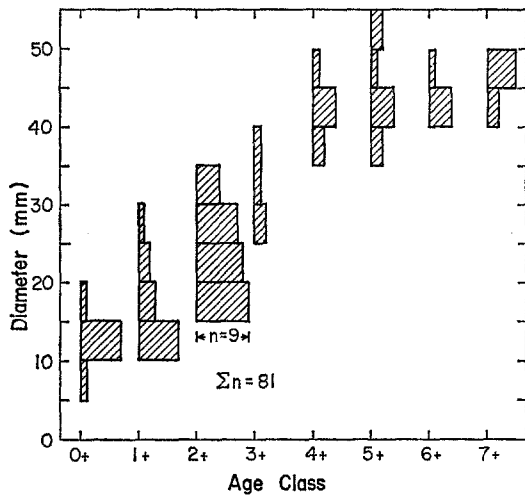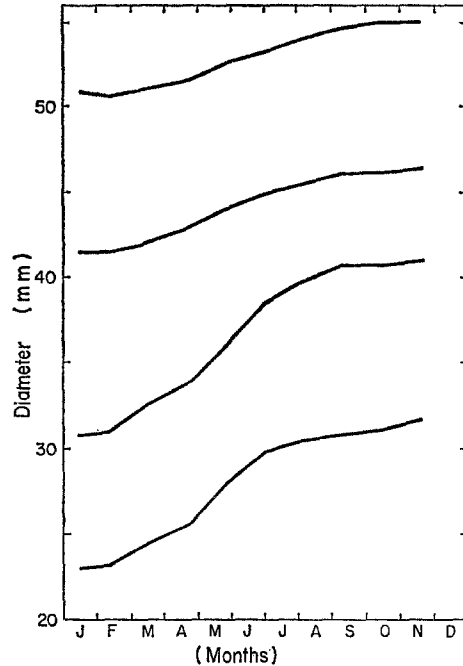


Fig. 6. *Strongylocentrotus droebachiensis*. Diameter increase of 4 sea urchins kept in laboratory at near-ambient field temperature and with excess food
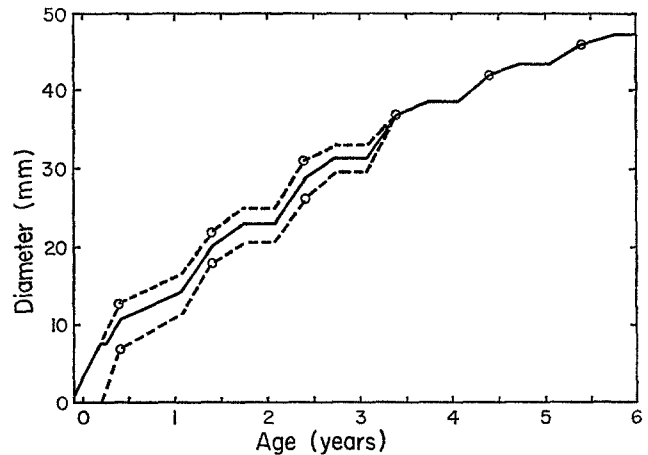


Fig. 5. *Strongylocentrotus droebachiensis*. Diameter at each age based on annual growth rings. Urchins were collected in April, 1970



Fig. 7. *Strongylocentrotus droebachiensis*. Average diameter versus age for sea urchin population in St. Magaret's Bay. Points are modal diameters in Fig. 5. Solid line: average size for urchins from both spawning periods, except before May in the 0 + age group, when only oldest group had been spawned; broken lines: early spawned stock (upper) and late spawned stock (lower)

growth rings (Fig. 5), the age assessment given in Fig. 3 appears the most reasonable.

The growth ring data (Fig. 5) show that some urchins in the population are more than 5 years old. Therefore, the last mode in Fig. 3 probably includes several year-classes. However, since these cannot be separated by size-frequency analysis, and since they are only a small part of the population, they are lumped as a single year-class. The only bias this introduces to the population energy budget is a small overestimate of body growth for 5-year olds.

The size-frequency analysis of bimonthly collections (Fig. 4) and data from 4 laboratory reared ani-

mals (Fig. 6) were used to generate the following assumptions about seasonal growth. The 0 + age group had a linear increase in diameter until July, then grew at about $\frac{1}{3}$ of the early rate for the rest of the year. One-year olds achieved 20% of the year's

growth between November 1 and March 1, 60% between March 1 and July 1, and 20% between July 1 and November 1. Older individuals achieved 0, 68, and 32% of their year's growth in the same periods. These assumptions, combined with annual growth estimates derived from Fig. 3, were used to generate the broken lines in Fig. 7. In calculating the growth component of the energy equation, the average of the two size groups (solid line in Fig. 7) was used.

The same regressions for log live weight on log diameter, and cal/g live weight on live weight were used throughout the year for calculating energy of growth. The log live weight on log diameter relation was determined on 6 dates with more than 100 urchins on each date. As there were no significant differences among slopes or intercepts of these regressions, the data were pooled for a single regression equation of

$$W = 0.0008 \, D^{2.86}$$

where $W$ is in g live weight, and $D$ is in mm diameter. Estimates of cal/g live weight obtained on 4 dates ($\Sigma n = 68$) were pooled for the regression equation of

$$E = 208 - 1.037 \, W$$

where $E$ is cal/g live weight, and $W$ is animal live weight. The negative slope differed significantly from zero ($P < 0.01$) and 95% confidence limits on $\bar{E}$ were $187 \pm 11$ cal/g live weight. There were not sufficient data to speculate on a seasonal variation in this regression.

Growth of an individual of any age class over a 2 month interval was calculated by (i) converting age at the beginning and end of the interval to diameter using Fig. 7; (ii) converting diameters to calories using the above regressions; (iii) obtaining the difference in the two values for growth in calories. This result when divided by 61 gave the average daily growth over 2 month intervals plotted in Fig. 2.

## Gonad Growth

The scatter about the regressions of gonad size versus animal size is large, as indicated by the small $r^2$'s in Table 5. This scatter is a property of the population rather than measurement error, and is probably due to differences in animal rations, size at sexual maturity, and spawning time.

The bimonthly values for gonad energy content (Table 5) were interpolated from measurements on 4 dates. The results were $640 \pm 50$ ($n = 18$), $1038 \pm 139$ ($n = 15$), $1630 \pm 264$ ($n = 9$), and $838 \pm 170$ cal/g wet weight ($n = 8$) for March, June, September, and December, respectively. There was no evidence for a difference in gonad cal/g wet weight with animal size or with sex. The large range of values with season was due primarily to a decrease in the dry weight/wet weight ratio as the gonads ripened, rather than to a change in cal/g dry weight. This ratio ranged from 0.15 in March to 0.30 in September, compared to the range of cal/g dry weight of 4.34 in March to 5.49 in September.

The average daily gonad production of an individual over a 2 month interval ($P_r$/day) is shown in Fig. 2, and was calculated as:

$$P_r/\text{day} = (Y_1 - Y_2) \frac{\text{cal}_1 + \text{cal}_2}{2} \frac{1}{61}$$

where $Y_1$ and $Y_2$ are gonad sizes at the beginning and end of the interval calculated from the appropriate regressions in Table 5 (the regressions were entered with the mean animal size for the interval obtained from Fig. 7), where $(\text{cal}_1 + \text{cal}_2)/2$ is the average calorific value per g of gonad over the interval (from Table 5), and where 1/61 reduces bimonthly to daily growth.

## Population Age Structure

The average population density according to the 1968 samples was 36.8 urchins/m². This value times the relative number in each age class taken from Fig. 3 gave the population density for each age class. A least-squares fit to these densities (Fig. 8, $r^2 = -0.97$) effects a constant logarithmic decrease in number, a situation that would occur if annual recruitment and

Table 5. *Strongylocentrotus droebachiensis. Constants for regressions of gonad wet weight on animal live weight (G = a(W − 7) b plus gonad cal/g wet weight*

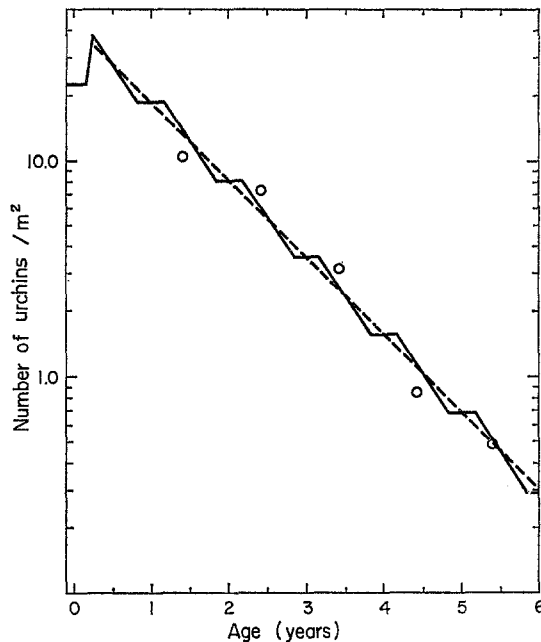| Date | Female | | | | Male | | | | ♀ and ♂ |
| | $n$ | $a$ | $b$ | $r^2$ | $n$ | $a$ | $b$ | $r^2$ | cal/g |
|---|---|---|---|---|---|---|---|---|---|
| Dec. 1 | 21 | 0.082 | 0.856 | 0.51 | 16 | 0.149 | 0.552 | 0.15 | 960 |
| Feb. 1 | 28 | 0.118 | 0.921 | 0.59 | 43 | 1.008 | 0.884 | 0.71 | 760 |
| April 1 | 18 | 0.043 | 1.471 | 0.67 | 18 | 0.116 | 0.963 | 0.67 | 700 |
| | | Female and male | | | | | | | |
| June 1 | 24 | 0.012 | 1.111 | 0.74 | | | | | 970 |
| August 1 | 19 | 0.021 | 0.796 | 0.49 | | | | | 1380 |
| Oct. 1 | 33 | 0.029 | 0.718 | 0.32 | | | | | 1420 |

Fig. 8. *Strongylocentrotus droebachiensis.* Number of urchins/m² in each age class (circles), least squares regression fitted to these points (dotted line), and number of urchins/m² at any age when annual mortality is adjusted for seasonal variation in mortality (solid line)
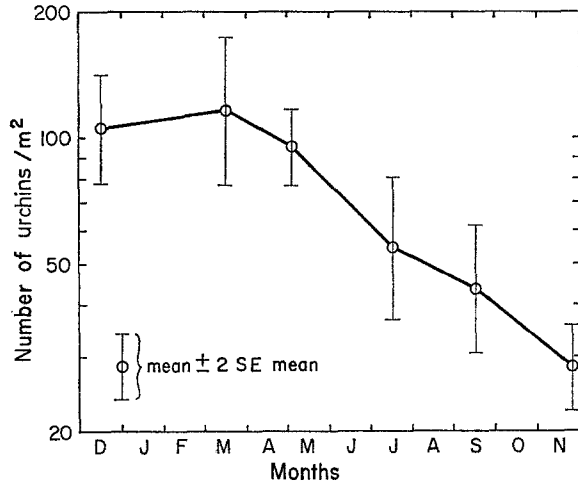


Fig. 9. *Strongylocentrotus droebachiensis.* Density of individuals older than 1 year obtained in bimonthly collections. SE: Standard error

annual mortality were constant. The density of the O + age class was estimated by back extrapolation of the regression line, since the smaller individuals of this age class were too small to be sampled quantitatively.

The numbers in the bimonthly collections and observations on the seasonal occurrence of predators

provide evidence that the mortality rate changes seasonally. The total density of individuals older than 1 year in the bimonthly collections (Fig. 9) indicates no mortality from December through March, and approximately a constant mortality rate for the rest of the year, April through November. Again the O + age group was not included, because their vulnerability to sampling increased as they grew. Of the species suspected to be primary predators of sea urchins in the study area, rock crabs, winter flounder, and sculpin were most abundant from June through November, while wolffish were seen mostly in the spring, and lobsters are present the year round. However, lobster walking speed increases by a factor of four between the winter minimum and summer maximum temperature found in St. Margaret's Bay (McLeese and Wilder, 1958) and presumably feeding rate would show a similar range.

In view of the evidence for seasonal variation, the population mortality of each age class was adjusted so that all of the annual mortality occurred in the 8 months from April through November (solid line in Fig. 8). The increase in density of the O + age class between months 2 and 3 represents the recruitment of the individuals spawned in April (group $O_b$ in Fig. 3). Animal density at any age can now be taken from this plot, assuming a logarithmic decrease in numbers with age and that all mortality occurred between April and November.

## Population Energy Budget

Population terms for each 2 month interval of each age class can now be calculated from the product of the daily rates per individual, the number of individuals of each age (Fig. 8), and 61 to convert daily to bimonthly rates. The bimonthly rates were summed to give the annual rates in Table 6. The size of individuals at each age used in calculating the individual rates for consumption, faeces production, and respiration was taken from Fig. 7. These sizes were substituted in equations in Table 2 for respiration, and in equations in Table 3 for consumption. Faeces production was the difference in values for consumption and absorption (Table 3). Calculation of body growth and gonad growth of an individual at each age was explained earlier.

Although consumption (C) and faeces production (F) were calculated from direct measurements in the laboratory, they were also estimated by the common methods of

$$C = \frac{R + P_g + P_r}{AE} \; ; \qquad F = C - (R + P_g + P_r)$$

where R is respiration, $P_g$ is body growth, $P_r$ is gonad growth, and AE is absorption efficiency $[(C - F)/C]$. The second method effects a balanced energy equation (Table 7), whereas the first method leaves a large fraction of consumption unaccounted for by respiration, production and defecation (Table 6).

The large fraction unaccounted for in Table 6 is considered as DOM loss. This is 42% of consumption and 68% of absorption for the total population.

Population production is 49.8 kcal/m²/year with 81% attributable to body growth and 19% to gonad growth. Population gross and net production efficiency with DOM loss are 4.3 and 7.0% (Table 6), without DOM loss 13 and 22% (Table 7).

Ages 1 + and 2 + are responsible for the biggest energy flux for all terms of the energy budget except gonad growth (Table 6). Net and gross production efficiencies decrease moderately with age, but not as much as they would decrease if body growth was the only component of production considered. In ages 4 + and 5 +, for example, gonad growth exceeds body growth.

It is clear that urchins were not concentrated in areas of their greatest potential food supply. 47% of the sea urchin population biomass was in a zone of no seaweeds (Zone 9); a further 38% was in zones with only 17% of the total seaweed biomass (Zones 2 and 8); and only 13% was among the kelps (Zones 5, 6 and 7), which represent 72% of the total seaweed biomass.

### Discussion

#### The Energy Budget and Efficiencies

A large fraction of the energy consumed was unaccounted for in two energy budgets for *Strongylocentrotus droebachiensis* and is presumed to be DOM loss. In the first budget, consumption and defecation were measured separately from respiration, although

Table 6. *Strongylocentrotus droebachiensis. Population energy budgets for each age class in kcal/m²/year, plus production efficiencies, DOM loss included*

| Age class | $C$ | $F$ | $R$ | $P_g$ | $P_r$ | DOM loss $C - (P_r + P_g + R + F)$ | $a$ $(R + P_g + P_r + $ DOM loss$)$ | Efficiencies $\dfrac{P_g + P_r}{C}$ | $\dfrac{P_g + P_r}{a}$ |
|---|---|---|---|---|---|---|---|---|---|
| 0 + | 165.5 | 62.5 | 21.1 | 8.0 | 0 | 73.9 | 103.0 | 0.048 | 0.078 |
| 1 + | 300.9 | 114.8 | 44.3 | 13.4 | 0 | 128.3 | 186.1 | 0.045 | 0.072 |
| 2 + | 284.3 | 108.8 | 45.0 | 10.3 | 2.4 | 117.8 | 175.5 | 0.045 | 0.072 |
| 3 + | 210.5 | 81.1 | 35.1 | 5.8 | 2.9 | 85.6 | 129.4 | 0.041 | 0.067 |
| 4 + | 126.0 | 48.7 | 21.4 | 1.9 | 2.6 | 51.4 | 77.2 | 0.036 | 0.058 |
| 5 + | 65.1 | 23.7 | 11.6 | 0.7 | 1.8 | 27.2 | 41.4 | 0.038 | 0.060 |
| Totals | 1152.2 | 439.6 | 178.5 | 40.1 | 9.7 | 484.2 | 712.6 | | |
| Means | | | | | | | | 0.043 | 0.070 |

Table 7. *Strongylocentrotus droebachiensis. Population energy budget in kcal/m²/year summed over all age classes plus population efficiencies, DOM loss not included*

| $C$ | $F$ | $R$ | $P_g + P_r$ | $\dfrac{A}{(R + P_g + P_r)}$ | $\dfrac{P_g + P_r}{C}$ | $\dfrac{P_g + P_r}{A}$ |
|---|---|---|---|---|---|---|
| 374.4 | 146.1 | 178.5 | 49.8 | 228.4 | 0.13 | 0.22 |

#### Population Distribution

*Strongylocentrotus droebachiensis* distribution in St. Margaret's Bay was determined from the summer 1968 collections representing a strip of bottom averaging 370 m wide around the periphery of the bay. The collection methods are described earlier in this paper and by Mann (1972a). He divided the area into 8 zones, based on seaweed species composition, plus one zone with large sea urchin concentrations, and one zone with neither sea urchins nor seaweeds (Mann's Table 1, 1972a).

on the same specimens and within a few days of each other; in the second budget, respiration, consumption, and defecation were measured simultaneously on the same individuals. Although the body growth and gonad growth terms were estimated from a field population, there is no reason to suspect that this was sufficiently large in laboratory specimens to account for the missing energy. Even using the laboratory growth rates in Fig. 6, net growth efficiency (production/absorption) would not exceed 10%, and a net growth efficiency of over 50% would be required to fill the gap in the energy budgets.

There is abundant evidence in the literature that other benthic grazers have similar gaps in their energy budgets which might be filled by DOM loss (Table 8). In a study of an opisthobranch mollusc, *Aplysia punctata*, Carefoot (1967) found that production plus respiration accounted for only 61% of absorbed energy, and balanced his budget by doubling respiration and by allowing 15% of absorbed energy for excretion and mucus secretion. Although both of these additions are plausible, they are supported only

by the observations that *A. punctata* does secrete mucus, and that some authors have considered laboratory respirometry on certain vertebrates to underestimate respiration by about 50%. In energy budgets for a sea urchin and an abalone (Leighton, 1968), over 65% of the energy estimated to be absorbed could not be accounted for in growth, reproduction, and respiration. For the tropical sea urchins *Tripneustes esculentes* and *Lytechinus variegatus*, large fractions of absorbed energy were unaccounted for in 4 of 5 cases (Moore and McPherson, 1965). Although the authors

ashing material with $CaCO_3$ and found a 42.5% weight loss for pure $CaCO_3$ heated to 600 °C for 19.5 h. The percentage ash was low at 50% dry weight compared to values of about 90% obtained by us and by Pearce et al. (1970) for *Strongylocentrotus purparatus* and *S. franciscanus*. Fuji's (1967) growth data were recalculated, omitting the contribution of carbohydrate in test and lantern. The respiration values, obtained by difference between absorption and growth, appeared too high when the revised growth estimates were used, and a suitable value from Giese et al. (1966,

Table 8. *Percentage of absorption (a) not accounted for by respiration (R) and growth (P) for various benthic herbivores. See text for explanation of values*

| Species | Season or age | Food | $a$ | $R$ | $P$ | $\dfrac{a-(P+R)}{a} \times 100$ | Units | Source |
|---|---|---|---|---|---|---|---|---|
| *Tripneustes esculentus* (sea urchin) | Summer | *Thalassia* | 110 | 29 | 0 | 74 | mg carbon | Moore and McPherson |
| | Winter | *Thalassia* | 105 | 19 | 18 | 65 | mg carbon | (1965) |
| *Lytechinus variegatus* (sea urchin) | Summer | *Thalassia* | 77 | 49 | 0 | 36 | mg carbon | Moore and McPherson |
| | | *Thalassia* | 330 | 63 | 0 | 89 | mg carbon | (1965) |
| | Winter | *Thalassia* | 49 | 26 | 30 | −14 | mg carbon | |
| *Aplysia punctata* (sea hare) | Summer | *Procamium* | 15.9 | 4.0 | 5.7 | 39 | kcal/urchin/ 80 days | Carefoot (1967) |
| *Strongylocentrotus intermedius* (sea urchin) | 1 year old | *Laminaria* | 61.8 | 9.0 | 9.8 | 70 | kcal/urchin/ | Fuji (1967) |
| | 2 year old | *Laminaria* | 116.9 | 27.0 | 13.1 | 66 | 342 days | (*P* and *R* |
| | 4 year old | *Laminaria* | 151.2 | 74.8 | 16.0 | 40 | | recalculated) |
| *Strongylocentrotus purpuratus* (sea urchin) | 1 year old | *Macrocystis* | 12.2 | 1.1 | 0.5 | 87 | g organic | Leighton (1968) |
| | 2 year old | *Macrocystis* | 38.3 | 3.3 | 1.7 | 87 | matter/urchin/ | |
| | 3 year old | *Macrycystis* | 66.5 | 6.5 | 2.8 | 86 | year | |
| | 4 year old | *Macrocystis* | 85.0 | 11.0 | 4.1 | 82 | | |
| *Haliotis rufescens* (abalone) | 1 year old | *Macrocystis* | 7.0 | 1.3 | 0.7 | 71 | g organic | Leighton (1968) |
| | 2 year old | *Macrocystis* | 32.1 | 6.4 | 3.8 | 68 | matter/abalone/ | |
| | 3 year old | *Macrocystis* | 73.0 | 16.6 | 8.6 | 65 | year | |
| | 4 year old | *Macrocystis* | 125.4 | 31.2 | 11.6 | 66 | | |
| *Strongylocentrotus droebachiensis* (sea urchin) | 0 year old | *Laminaria* | 103.0 | 21.1 | 8.0 | 72 | kcal/m²/year | Table 7 |
| | 1 year old | *Laminaria* | 186.1 | 44.3 | 13.4 | 69 | kcal/m²/year | (this paper) |
| | 2 year old | *Laminaria* | 175.5 | 45.0 | 12.7 | 67 | kcal/m²/year | |
| | 3 year old | *Laminaria* | 129.4 | 35.1 | 8.7 | 66 | kcal/m²/year | |
| | 4 year old | *Laminaria* | 77.2 | 21.4 | 4.5 | 67 | kcal/m²/year | |
| | 5 year old | *Laminaria* | 41.4 | 11.6 | 2.5 | 66 | kcal/m²/year | |

expressed reservation about constructing budgets because growth data were from the field and other data were from laboratory experiments, growth appeared generally to constitute a small part of the total budget, as with other budgets for benthic herbivores summarized in Tables 8 and 9. These authors also measured phosphorus excretion, and assumed a P:C ratio of 1:106. However, excretion accounted for less than 10% of absorbed carbon in 3 of 4 cases. Fuji (1967, Fig. 35) used a figure of 41% for the carbohydrate content of test and lantern in *Strongylocentrotus intermedius*. This was based on analysis of protein, fat, and ash, and obtaining carbohydrate by difference. This unreasonably high figure was likely due to ashing the animals at 800 C° for 24 h. Paine (1964) suggests 500 °C as an optimum temperature for

3.7 cal/g live weight) was substituted. With these adjustments, Fuji's data also show a large gap in the energy budget (Table 8).

Studies on a benthic filter feeder, a benthic detritus feeder, and recent observations on *Strongylocentrotus droebachiensis*, have demonstrated significant losses of DOM. The grass shrimp *Paleomonetes pugio* fed on diatoms lost 39% of absorbed carbon as DOM (Johannes and Satomi, 1967) and the amphipod *Hyallela azteca* fed on lake sediment lost 31% of absorbed energy as DOM (Hargrave, 1971). Dr. J. G. Field (unpublished MS) placed *S. droebachiensis* in bottles for 50 to 100 min, and noted the increase in dissolved organic carbon compared to control bottles. The loss varied from 2.3 to 0.75 times respiration energy (assuming 1 mg C = 12 cal) at 12° and 3.5 °C,

respectively. The high value would be sufficient to account for the missing energy for 4 of the 6 time periods represented in Fig. 2. As pointed out by the authors of all three studies, these values could be underestimates, as the experimental animals were not feeding and loss from food during ingestion would not have been measured. In the grass shrimp and sea urchin studies, bacterial uptake of DOM may also have contributed to underestimates.

Although it appears wasteful for an animal to lose a large fraction of the energy available to it in probably too high, since the urchins were offered an excess of food at all times, and nearly one-half the St. Margaret's Bay population occurs in areas where macrophytes have been eliminated.

The ecotrophic coefficient, *Strongylocentrotus droebachiensis* consumption/seaweed production, is quite low compared to results for other benthic herbivore populations. With annual seaweed production at 17,500 kcal/m² (Mann, 1972 b) and annual sea urchin consumption between 374 and 1152/kcal/m², the ecotrophic coefficient is 2.1 to 6.6%. However, these

Table 9. *Population production efficiencies for 9 benthic marine herbivores. P: production, R: respiration; A: assimilation ( $=P + R$) B: biomass*

| Species | Common name | Habitat | $P$ (kcal/m²/year) | $\frac{P}{R} \times 100$ | $\frac{P}{A} \times 100$ | $\frac{P}{C} \times 100$ | $P/C$ | Source |
|---|---|---|---|---|---|---|---|---|
| *Littorina irrorata* | Periwinkle | Saltmarsh | 40.6 | 16 | 14 | 6 | 0.81 | Odum and Smalley (1959) |
| *Modiolus demissus* | Mussel | Saltmarsh | 16.7 | 43 | 30 | — | 0.84 | Kuenzler (1961) |
| *Scrobicularia plana* | Clam | Mud flat | 70.8 | 27 | 21 | 13 | 0.59 | Hughes (1970) |
| *Tegula funebralis* | Gastropod | Intertidal rocky shore | 103 | 18 | 15 | 10 | 2.5 | Paine (1971) |
| *Fissurella barbadensis* | Limpet | Intertidal rocky shore | 50.8 | 37 | 27 | 9 | 4.1 | Hughes (1971 a) |
| *Nerita tessellata* | Gastropod | Intertidal rocky shore | 29.3 | 13 | 12 | 5 | 0.78 | Hughes (1971 b) |
| *Nerita versicolor* | Gastropod | Intertidal rocky shore | 7.6 | 15 | 13 | 5 | 0.63 | Hughes (1971 b) |
| *Nerita peloronta* | Gastropod | Intertidal rocky shore | 7.5 | 24 | 19 | 8 | 1.25 | Hughes (1971 b) |
| *Strongylocentrotus droebachiensis* | Sea urchin | Subtidal rocky shore | 49.8 | 28 | 22 | 4—13 | 0.80 | This study |

dissolved form, it is possible that large quantities of carbohydrate have to be processed in order to obtain the necessary amount of protein. Mann (1972a) showed that the carbon:nitrogen ratio of 2 species of *Laminaria* lay between 13.8:1 and 27.2:1, whereas Russell-Hunter (1970) has shown that, excepting ruminants, all animals investigated have a dietary requirement corresponding to a C:N ratio lower than 17:1. The herbivorous abalone *Haliotus discus* showed a strong positive correlation of growth rate with protein content of the diet (Ogino and Kato, 1964).

It is likely that the true consumption and absorption rates for the *Strongylocentrotus droebachiensis* population are higher than the low estimates (Table 7) and lower than high estimates (Table 6); however, since more accurate estimates are not available, these are taken as bounds for the true population parameters. The low estimate of absorption, production plus respiration (i.e., absorption = assimilation), almost certainly underestimates absorption, since there is strong evidence that DOM loss is a significant part of the energy budget. The higher estimate of absorption, based on laboratory measurements (C — F), is

percentages can be halved if seaweed production and sea urchin consumption are considered proportional to their relative biomass. This is because nearly half the sea urchin biomass is in areas of no seaweed, and occasional observations of stomach contents of these animals showed their diet to consist of calcareous algae, filamentous algae, and mud, but rarely contained drift seaweed from nearby beds. Sea urchins that did feed on the seaweed beds fed primarily at the edges. This resulted in reduced size of the beds, and prevented them from utilizing the very large plant production within the bed, hence the low ecotrophic coefficient. Moore and McPherson (1965) estimated that the urchin *Lytechinus variegatus* consumed about 17% of *Thallassia* production as an annual average. The annual consumption of *Strongylocentrotus intermedius* was about half the combined annual production of *Laminaria augustata* and *Ulva pertusa* (Fuji and Kawamura, 1970). The energy needs of the gastropod *Tegula funebralis* equalled the production of seaweeds in its habitat, and drift seaweed was probably essential to support the entire herbivore trophic level (Paine, 1971).

Table 9 lists population production and 4 types of production efficiencies for 9 large benthic herbivores.

The *P/A* and *P/R* ratios for *Strongylocentrotus droebachiensis* will be considered in more detail below, but are near the center of the range of the other values in the table. The *P/C* ratio for *S. droehachiensis* is given as a range because of the uncertainty of the value for *C*, and just spans the range for the other species. The *P/B* ratio of 0.80 is close to 0.86, the value predicted from a regression of log production versus log biomass for long-lived poikilotherms (Mathias, 1967).

### Respiration as an Index of Production

The *P/R* ratio for the *Strongylocentrotus droebachiensis* population is close to the ratio predicted by a regression of log production on log respiration. This regression, modified slightly from that given by McNeill and Lawton (1970), is $P = 0.6440\ R^{0.8517}$ (Miller *et al.*, 1971) where both *P* and *R* are in kcal/m²/year. From a respiration value of 178.5 kcal/m²/year, production is predicted at 53.3 kcal/m²/year and the *P/R* ratio is 30%. These values are close to the 49.9 kcal/m²/year and 28% measured for the *S. droebachiensis* population. The *P/A* ratio, where $A = P + R$, also shows close agreement to the predicted value (22% versus 23%), since the same data are used in its calculation.

Production can be more conveniently predicted from respiration if respiration does not have to be measured through all seasons. It will be demonstrated below that *Strongylocentrotus droebachiensis* respiration for a year could have been predicted from respiration rate at a single temperature, the annual temperature regime in the sea urchin habitat, and a single $Q_{10}$ derived from a respiration-temperature curve representing 14 species of temperate marine poikilotherms (Fig. 10). Annual respiration is 0.77 kcal/g when calculated from the seasonal rates in Table 2. Starting with the seasonal maximum rate at 17 °C, the temperatures for the other 5 time intervals, and a $Q_{10}$ of 2.05 gives an annual rate of 0.81 kcal/g. Starting with the seasonal minimum rate at 2 °C and making the same calculations gives an annual rate of 0.63 kcal/g.

Four restrictions were placed on the choice of data included in the respiration-temperature curve (Fig. 10): all species were north-temperate marine poikilotherms; test temperatures were within the range of environmental temperatures of the experimental animals; some measurements were made at or below 5 °C (in some cases the 5 °C rate had to be interpolated), and animals were acclimated for at least 18 h to the experimental temperature. Laboratory acclimation was usually several days, or experiments were run at the environmental temperature soon after collection. Among 5 equations fitted to the data, an exponential function produced a better fit than either a power curve or first, second, or third degree polynominal. Thus, a constant $Q_{10}$ was indicated and the $Q_{10}$ was 2.05.
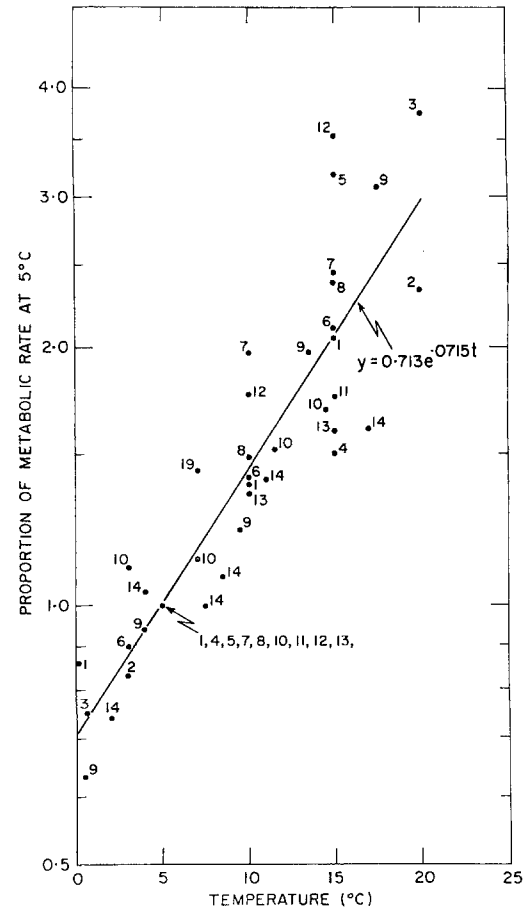


Fig. 10. Respiration as proportion of rate at 5 °C, plotted against temperature for 14 species of temperate marine poikilotherms. 1: *Calanus finmarchicus*, mean for male and female (Marshall *et al.*, 1935); 2: *Emerita talpoida* (Edwards and Irving, 1943); 3: *Tautogolabrus adspersus* (Haugaard and Irving, 1943); 4: *Acartia clausi* (Conover, 1956); 5: *Acartia tonsa* (Conover, 1956); 6: *Gadus macrocephalus*, 430 g fed fish (Saunders, 1963); 7: *Gammarus oceanus*, routine rates (Halcrow and Boyd, 1967); 8: *Euphausia pacifica* (Paranjape, 1967); 9: *Scrobicularia plana* (Hughes, 1970); 10: *Littorina littorea*, mean for active and standard rates (Newell and Pye, 1970); 11: *Mytilus edulis* (Newell and Pye, 1970); 12: *Cottus scorpius* (Edwards *et al.*, 1970); 13: *Pleuronectes platessa* (Edwards *et al.*, 1970); 14: *Strongylocentrotus droebachiensis* (this study)

### Ecological Role of Strongylocentrotus droebachiensis

*Strongylocentrotus droebachiensis* is clearly the most important benthic herbivore in the seaweed zone. Of the 4 most important groups, sea urchins, periwinkles, mussels, and brittle stars, sea urchins are responsible for about 80% of consumption and 70% of production (Miller *et al.*, 1971).

Although the energy needs of sea urchins are large compared to other herbivores in the community, they are less than 7% of seaweed production. Nevertheless, sea urchins are known to have an important influence

on seaweed production by maintaining large areas of substrate free of seaweeds. At 3 sites in St. Margaret's Bay, sea urchins have been observed densely clustered on the edge of a thick bed of *Laminaria* and, in the course of a few months, have caused the edge of the bed to move back 2 to 3 m. They achieve this partly by direct consumption and partly by biting through the stipe so that the plant floats away. Mann and Breen (1972) have reviewed evidence from several sources that sea urchins are capable of denuding large areas of marine macrophytes.

The sea urchin population produced about 50 kcal/m²/year over a large area for consumption by other organisms — either predators or decomposers. Although several higher values have been recorded, they are most commonly for populations of small benthic species and planktonic species with short life histories (see reviews by McNeill and Lawton, 1970; and Dickie, 1972). A production figure of interest, because it is so much greater than any we are aware of for a natural animal population, is for a new set of *Mytilus edulis* in the Irish Sea which grew to a density of 3000 to 6000 kcal/m² within 6 months (P. J. Dare, unpublished manuscript).

## Summary

1. An energy budget was constructed for a population of the sea urchin *Strongylocentrotus droebachiensis* in the nearshore area of St. Margaret's Bay, Nova Scotia, Canada. The terms, in kcal/m²/year, were: body growth = 40, gonad growth = 10, respiration = 179, faeces production = 141 to 440, consumption = 375 to 1152. The range of values for faeces production and consumption account for the possible range of feeding rates in the field.

2. Production efficiencies were: production/assimilation = 0.28, production/consumption = 0.04 to 0.13, production/biomass = 0.80. The first 2 efficiencies decreased with age of the urchins.

3. Of the 6 age classes identified Ages 1 + and 2 + accounted for approximately ¹/₂ the population energy flow for every term except gonad growth.

4. Loss of dissolved organic matter, calculated as consumption minus faeces production, respiration, body growth, and gonad growth may be as high as 484 kcal/m²/year. This unmeasured portion was a large fraction of consumption in each of two laboratory experimental systems. A critical review of energy budgets for 6 other species of marine benthic grazers also revealed large amounts of energy unaccounted for.

5. It was demonstrated that *S. droebachiensis* respiration in kcal/g individual/year could have been approximated from the respiration rate at a single temperature, the annual temperature regime in the sea urchin habitat, and a single $Q_{10}$ of 2.05 derived from a respiration-temperature curve representing 14 species of temperate marine poikilotherms.

6. Although *S. droebachiensis* was the dominant herbivore in the seaweed bed, it utilized only 1 to 7% of seaweed production. As with other populations of sea urchins, however, it had a proportionately greater influence on seaweed biomass, and also presumably production, by clearing seaweed from large areas of substrate and maintaining it clear.

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