ספרית אורות

המאמרים במערכת הדפים המוגנים על פי חוק זכויות יוצרים

הדפים מאמרים תוקים לטרפי ליםוד והוראה בלבד

אין לעשות כל שימוע מסחרי בנמאמרים.
Lifetime Energy Budget in the Sea Hare Aplysia oculifera

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ABSTRACT. We studied energy budget and resource allocation through the entire postmetamorphic life span, under controlled laboratory conditions, in the sea hare Aplysia oculifera from the Red Sea. Growth of sea hares was according to the Gompertz equation: Body live mass (BLM)t = 105 exp[(- 0.035 × 43.04)]. Maximum postmetamorphic life span was 162 days. Sea hares began to spawn at 8 g BLM. Egg production (Pr) was related to BLM by the equation Pr(egg live mass, g · d⁻¹ · ind⁻¹) = 0.0048(BLM)⁻¹. Oxygen consumption rates of sea hares at 24 ± 0.5°C were related to BLM by the equation VO₂(ml · h⁻¹ · ind⁻¹) = 0.111(BLM)⁻⁰.⁷⁸. Food consumption (C) and feces production (F) were related to BLM by the equations C(g dry mass · d⁻¹ · ind⁻¹) = 0.063(BLM)⁻⁰.⁸⁴ and F(g dry mass · d⁻¹ · ind⁻¹) = 0.047(BLM)⁻⁰.⁴⁴, respectively. The results were transformed to energetic values, and energy budget and resource allocation of the sea hares were calculated. A. oculifera invested 8–16% of the absorbed energy in metabolism (respiration). At BLM < 8 g, all the remaining energy was used for growth. From 8 g BLM on, sea hares began to reproduce and the energy allocated for reproduction increased with BLM, while the energy allocated for growth decreased. Growth stopped at mean BLM of 105 g. Comparison of the results with field data suggest high potential productivity that usually is not utilized in the field. Comp Biochem Physiol 113A:2:205–212, 1996.

KEY WORDS. Aplysia oculifera, energy budget, resource allocation, growth, oxygen consumption, Red Sea

INTRODUCTION

Sea hares of the genus Aplysia (Gastropoda: Opisthobranchia) have short lives, rapid growth rates and high egg production (7). Early postmetamorphic juveniles may grow as much as 13,000% over two-week periods and individual sea hares may produce more than 10⁸ eggs during their life spans (7). Sea hares also show great variability of growth rates and maximum body sizes in different intraspecific populations living at different sites or times, or under various environmental conditions (28,11,12,25). These data suggest that Aplysia spp. have high potential productivity that is utilized variably under different sets of environmental conditions.

An example of these phenomena is the Indo-Pacific sea hare Aplysia oculifera. This species is an important seasonal herbivore, mostly nocturnal, in the inter- and subtidal zones of rocky coasts in the northern Gulf of Eilat (Aqaba), Red Sea. It appears from December to May and feeds on green macroalgae (Enteromorpha intestinalis and Ulva sp.) which bloom seasonally, but in unpredictable temporal and spatial patterns (25). Observations made from 1988 to 1992 at six closely spaced sites showed great differences (more than one order of magnitude) in both body sizes and reproduction intensities among the different populations within a single season and between years (25).

To successfully inhabit unpredictable habitats, sea hares must be able to utilize resources effectively by being highly productive at times when algae are abundant, but also must be able to survive and reproduce when algae are scarce. Sea hares produce offspring in numbers correlated with body size, which in turn is related to food availability (26,7,25). A possible scenario could be that under conditions of high food availability, sea hares, at the beginning of the season, allocate all available resources to somatic growth and delay reproduction until later when their bodies will be larger, allowing production of large numbers of eggs. When food is scarce, they might allocate resources for reproduction at an early stage at small body sizes. This would result in low numbers of offspring, but would ensure the continuity of the population into the next year.

Our objectives in this study were to estimate energy budget and scope for growth with ad libitum feeding throughout the entire postmetamorphic life span of A. oculifera, and to detect changes in resource allocation at different life stages. We estimated energy budget by measuring rates of food consumption (C), somatic growth (Ps), egg production (Pr), maintenance costs (Oxygen consumption, (R)), and feces production (F). We conducted the measurements under laboratory conditions.
TABLE 1. Table of symbols and abbreviations frequently used in text

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>BLM</td>
<td>body live mass (g)</td>
</tr>
<tr>
<td>BLM∞, BLM at time t in Ford-Walford equation (7)</td>
<td></td>
</tr>
<tr>
<td>BLM∞+1, BLM at time t + 1 in Ford-Walford equation (7)</td>
<td></td>
</tr>
<tr>
<td>BLM∞+2, body live mass at age t + 2 (g)</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>food consumption, (g DM · d⁻¹)</td>
</tr>
<tr>
<td>C, food consumption, (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>dry mass, (g)</td>
</tr>
<tr>
<td>F</td>
<td>feces production (g DW · d⁻¹)</td>
</tr>
<tr>
<td>F, feces production (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
<td></td>
</tr>
<tr>
<td>i</td>
<td>initial body size (intercept) in Ford-Walford equation (7)</td>
</tr>
<tr>
<td>K</td>
<td>expression of growth rate at given body size per body size per time, = -ln(m)</td>
</tr>
<tr>
<td>m</td>
<td>growth rate (slope) in Ford-Walford equation (7)</td>
</tr>
<tr>
<td>Pa</td>
<td>Barometric pressure, (mmHg)</td>
</tr>
<tr>
<td>Pr</td>
<td>production of egg clusters, (g DW · d⁻¹)</td>
</tr>
<tr>
<td>Pr, production of egg clusters, (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
<td></td>
</tr>
<tr>
<td>Ps</td>
<td>somatic production, (g BLM · d⁻¹)</td>
</tr>
<tr>
<td>Ps, somatic production, (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>respiration, (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
</tr>
<tr>
<td>R, respiration, (mLO₂ · h⁻¹)</td>
<td></td>
</tr>
<tr>
<td>S₀</td>
<td>oxygen saturation at the beginning of measurement (%)</td>
</tr>
<tr>
<td>S₁</td>
<td>oxygen saturation at the end of measurement (%)</td>
</tr>
<tr>
<td>t</td>
<td>time of measurement (h)</td>
</tr>
<tr>
<td>t₀</td>
<td>postmetamorphic age of sea hare (t₀ = 0 at BLM = 0.006 g) (d)</td>
</tr>
<tr>
<td>U</td>
<td>all unmeasured components of the energy budget (kJ · d⁻¹) or (kJ · 10⁴d⁻¹)</td>
</tr>
<tr>
<td>V</td>
<td>volume of metabolic chamber (l)</td>
</tr>
<tr>
<td>VO₂</td>
<td>oxygen consumption (mLO₂ · h⁻¹)</td>
</tr>
</tbody>
</table>

in order to get an estimate of the highest (potential) productivity. This will permit an estimate of the levels at which A. oculifera utilize their potential productivity in the field.

MATERIALS AND METHODS
Animal Collection and Maintenance

Sea hares used in this study were collected at different sites along the north-western coast of the Gulf of Eilat during the recruitment stage of the populations in December, 1990. The sea hares (0.1–2 g body live mass (BLM)) were kept at the Interuniversity Institute for Marine Sciences of Eilat, in 10–15 l glass aquarium with continuous flow of sand-filtered seawater in an open system (0.3–1.0 l · min⁻¹), at ambient water temperatures (21–26°C) and salinity (40.8 ppt). The aquarium were kept outdoors under shade in natural photoperiod. Each aquarium contained ≤5 sea hares of similar BLM. Sea hares were fed ad libitum with laboratory-reared Ulva sp. The aquarium were monitored twice a day for water flow and food.

Experimental Design

Nine groups, each containing 5 small sea hares at similar sizes (0.06–1.9 g BLM) were placed in aquarium as described above. They were fed ad libitum with measured amounts of Ulva sp. Initial BLM of each specimen was recorded. An individual sea hare within a group could be identified by its color patterns and its relative body size. Measurements were made once every 3 days. They included body and egg masses, and masses of uneaten algae and feces.

Growth and Reproduction

Once every 3 days sea hares were removed from the aquarium, gently dried with blotting paper, and weighed using either a Mettler BasBal Balance (±0.001 g) for small animals or a Sartorius 6100.00 g balance (±0.1 g) for larger animals. Precision was <1% of BLM. They were returned to the seawater immediately after weighing.

Egg clusters were removed from the aquarium once every 3 days, dried on blotting paper for 1–2 min, and weighed. Total wet masses of eggs from each aquarium were divided by total biomasses of sea hares in the aquarium and by 3 days to obtain average spawning rates (g wet mass eggs · d⁻¹ · g BLM⁻¹).

Feeding and Food Consumption

After each growth measurement, fresh, weighed portions of Ulva sp. were added to each aquarium. The algae were gently squeezed by hand, then separated into eleven portions, one for each aquarium and two control portions. Nine food portions were weighed and placed in the populated aquarium. One control portion was weighed and placed in an unpopulated aquarium for 3 days. Then it was weighed again to estimate the changes in wet masses in the periods between measurements due to growth or decomposition of the algae. This portion was then dried and weighed again, and corrections were made in the calculations for food consumption according to the results. The other control portion was weighed, then dried at 60°C for 72 hr and weighed again, to determine the ratio between wet (squeezed) and dry masses of the algae.

Before adding the fresh weighed Ulva sp., all the algae remains were collected from each aquarium, dried at 60°C for 72 hr and weighed. The dry masses of the remains were subtracted from the calculated dry masses of the algae given as food 3 days earlier. The results were divided by the total sea hare biomass in the aquarium and by 3 days to get the food consumption (g dry mass algae · d⁻¹ · g BLM⁻¹).

Feces Production

After the sea hares, egg clusters and algae remains had been removed from the aquarium, the water and feces from each aquarium were siphoned into a clean bucket and the feces were allowed to sink to the bottom. Supernatant water was removed and the feces with the remaining water were filtered through weighed filter papers. The filter papers with the feces were rinsed in fresh water to eliminate sea salts and then dried at 60°C for 72 hr and weighed. The dry masses of the feces were divided by the total biomass of sea hares in the aquarium.
and by 3 days to obtain feces production rates (g dry mass feces \cdot \text{d}^{-1} \cdot \text{g BLM}^{-1})

**Energy Contents of Sea Hare Tissues, Egg Clusters, Algae and Feces**

Energy contents of sea hare tissues, egg clusters, feces and algae were determined using a Gallenkamp Ballistic Bomb Calorimeter. Samples were dried at 60°C until no further mass decreases occurred (48–72 hr). They were then compressed into small pellets, weighed, and combusted in the calorimeter. The calorimeter was calibrated with benzoic acid provided by the manufacturer.

**Oxygen Consumption**

Oxygen consumption rates of sea hares were measured in an 800 ml cylindrical respirometer surrounded by a larger cylinder in which water of constant temperature flowed. Sea hares were starved overnight before measurement to prevent high oxygen consumption due to specific dynamic action (14). Animals were gently placed in the metabolic chamber containing filtered (0.45 μ), aerated seawater, at 24 ± 0.5°C. The chamber was sealed while taking care to eliminate air bubbles, and a magnetic stirrer located under a mesh on the bottom of the respirometer was turned on at moderate speed. Oxygen saturation percentage in the water was measured with a WTW TriOximatic EO 200 electrode fixed in the metabolic chamber cover, a WTW Oxi 530 Oxygenmeter and a Pantos Unirecorder U-228. The electrode was calibrated with N₂ saturated water (0%) and with air aerated water (100%) in addition to vapor calibration recommended by the manufacturer. After correcting by blank runs to eliminate bacterial metabolism and electrode drift, oxygen consumption rates ($V_{O_2}$) were calculated, according to the equation:

$$V_{O_2} (\text{ml} \cdot \text{h}^{-1}) = (S_0 - S_f) \cdot 0.01 \cdot 4.64 \cdot V \cdot t^{-1} \cdot \text{Pa}/760,$$

where $S_0$ and $S_f$ are oxygen content at the beginning and the end of the measurement, in percentages, respectively (calculated from linear segments of at least 15 min of the recorded relation between dissolved oxygen and time, as drawn by the recorder); 4.64 is oxygen concentration in 100% saturated sea water with salinity of 40.5 ppt at 760 mm Hg atmospheric pressure in ml \cdot l^{-1} (13); $V$ is the volume of the metabolic chamber in liters; $t$ is the duration of the measurement (the segment measured on the chart recorder plot) in hours; and Pa is the barometric pressure in mmHg. Measurements began 60–90 min after inserting the animals into the metabolic chamber. Measurement duration was 15–30 min, according to the rate of oxygen decrease. Oxygen level in the respirometer was never allowed to fall below 70% saturation. The value 20.44 J \cdot \text{mlO}_2^{-1} was used to convert oxygen consumption values to energetic values (28).

**Statistical Procedures**

Rates of physiological processes can be expressed as a power function of body mass (27). For each parameter of the energy balance, the best-fit power curve was calculated in relation to BLM using Systat statistical package Ver. 5.

Energy balance was examined using the equation:

$$C = Ps + Pr + R + F + U,$$

where $C$ is food consumption, $Ps$ is somatic productivity (growth), $Pr$ is reproduction, $R$ is energy used in respiration, and $F$ is feces production. Unmeasured energy lost (activity, urine, mucus, etc.,) was entered as a compensation for imbalance:

$$U = C - (Ps + Pr + R + F).$$

To compare our data with others, we calculated the value $K$, which expresses growth at a given body size per size per time, according to the equation (7):

$$K = -\ln(m),$$

in which $m$ is the regression coefficient (slope) of the relation between the size at time $t = 0$ and at time $t = 1$ in the Ford–Walford equation, converted to mass values (7):

$$BLM_{t+1} = i + m BLM_t.$$  

$BLM_0$ is the BLM at time $t = 0$, $BLM_{t+1}$ is the BLM at the end of the experimental period; $i$ is the intercept. We calculated the value $K$ for *A. oculifera* over a period of 14 days at various BLMs.

**RESULTS**

**Growth**

Under laboratory conditions, fed *ad libitum* with *Ulva* sp., *A. oculifera* grew rapidly. Beginning at 0.06 g BLM, sea hares grew to 10 g in 20 days. At 8–10 g BLM they began to spawn while growth rate gradually decreased. Daily growth, calculated as mass gained per day divided by initial BLM, was inversely related to BLM, and was expressed by the logarithmic growth rate equation in which Growth rate$(BLM_1 - BLM_0) \cdot BLM_0^{-1} = 0.243 - 0.053 \cdot \ln(BLM_0)(R^2 = 0.671, n = 412)$ (Fig. 1).

The decrease of growth rate in relation to BLM was gradual until sea hares gained maximum mean BLM of 105 g. The growth equation indicates that at 0.01 g BLM growth was 49% of BLM per day. Sea hares began to spawn at 8 g BLM, when growth was 13.6% of BLM per day.

According to the relation between growth rate and BLM, growth patterns of sea hares agree with the Gompertz equation (15) which is $BLM_{t_a} = 105 \exp[-\exp(-0.053(t_a - 43.04))]$ (Fig. 2), where $(BLM_{t_a})$ is BLM at time $(t_a)$. $(t_e)$ is the age in days, starting at 0.006 g BLM, the value 105 is maximum BLM according to the logarithmic growth rate equation, and the value −0.053 is the slope in the logarithmic growth rate.
Reproduction

Under the conditions described, *A. oculifera* began to spawn at 8-10 g BLM. Mean quantity of eggs spawned was 1.64 ± 0.62% of BLM per day. The live mass spawned per day (Pr) was related to BLM by the equation $Pr (\text{Eggs live mass} \cdot d^{-1} \cdot g \text{BLM}^{-1}) = 0.0048 (\text{BLM})^{1.323}$ ($R^2 = 0.824$, $n = 58$).

Each individual sea hare spawned once every 2-3 days. The spawn consisted of gelatinous tubes, 0.7-0.9 mm in diameter, containing capsules 0.2-0.3 mm in diameter. Each capsule contained 2-11 eggs. We estimated that each individual sea hare produced about $10^8$ offspring per lifetime under these experimental conditions.

Metabolic Rates

The metabolic rates of sea hares were determined indirectly by measuring oxygen consumption rates ($\dot{V}_{O_2}$). Oxygen consumption rates of *A. oculifera* at rest were correlated to BLM according to the equation $\dot{V}_{O_2} (\text{ml} \cdot \text{ind}^{-1}) = 0.111 (\text{BLM})^{0.778}$ ($R^2 = 0.941$, $n = 59$).

During the oxygen consumption measurements the sea hares were mostly resting on the respirometer walls with no activity.

Food Consumption

Food consumption (C) was related to BLM by the equation $C (\text{g dry mass} \cdot \text{ind}^{-1} \cdot \text{d}^{-1}) = 0.063 (\text{BLM})^{0.839}$ ($R^2 = 0.935$, $n = 87$).

Individual sea hares with BLM < 1 g consumed >90% of their BLM per day (wet mass algae, g), and individual sea hares with BLM > 10 g consumed <63% of their BLM per day (wet mass of algae).

Feces Production

Measuring feces production (F) of sea hares is difficult because the feces dispersed in the seawater and some portion of them dissolved. On the other hand, materials like pieces of leftover algae or sediment might have been added. These problems can cause over-estimation, especially when dealing with individuals of small body sizes. The amounts of feces (g dry mass) produced by individual sea hares per day were related to BLM by the equation $F (\text{g dry mass} \cdot \text{ind}^{-1} \cdot \text{d}^{-1}) = 0.047 (\text{BLM})^{0.443}$ ($R^2 = 0.714$, $n = 84$).

Energy Balance

To convert the values of growth, egg production, food consumption and feces production to energetic values, the energy contents of all the components of the energy budget, including sea hare tissue, egg clusters, feces and *Ulva* spp., were measured using a bomb calorimeter. The percentage dry mass
TABLE 2. Growth coefficient (K) for the sea hare Aplysia oculifera under laboratory conditions at different initial body live mass (BLM) and for other Aplysia spp. fed with Ulva spp. K = −ln(m/i) (m) calculated from Ford–Walford growth equation BLM(t+1) = i + m BLM(t) (7). [See text for details.]

<table>
<thead>
<tr>
<th>Species</th>
<th>Starting BLM (g)</th>
<th>Temp. (°C)</th>
<th>K growth coefficient</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. oculifera</td>
<td>0.01</td>
<td>24</td>
<td>−5.58</td>
<td>This paper</td>
</tr>
<tr>
<td></td>
<td>0.1</td>
<td>24</td>
<td>−4.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>24</td>
<td>−3.08</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>24</td>
<td>−1.64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>24</td>
<td>−0.03</td>
<td></td>
</tr>
<tr>
<td>A. dactylo melata</td>
<td>52</td>
<td>28</td>
<td>0.01</td>
<td>5</td>
</tr>
<tr>
<td>A. juliana</td>
<td>29.3</td>
<td>28</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.01*</td>
<td>25</td>
<td>−5.84</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>0.01*</td>
<td>25</td>
<td>−5.49</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.01*</td>
<td>25</td>
<td>−5.08</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>23.5</td>
<td>−1.66</td>
<td>Vitalis, 1981†</td>
</tr>
<tr>
<td></td>
<td>1.2</td>
<td>23.5</td>
<td>−2.11</td>
<td></td>
</tr>
<tr>
<td>A. punctata</td>
<td>6.1</td>
<td>15</td>
<td>0.16</td>
<td>3</td>
</tr>
</tbody>
</table>

* Sea hares fed with three different species of Ulva spp.
† See reference in 7.

(g dry mass per 100 g live mass × 100 ± SD) was 10.0 ± 1.2% (n = 17) for sea hare tissue, 11.2 ± 1.9% (n = 26) for egg clusters, and 14.0 ± 2.3% (n = 32) for Ulva sp. No wet mass was measured in feces. The energy contents of these components were 12.1 ± 0.6 kJ · g dry mass⁻¹ (DM) for sea hare tissue, 14.3 ± 0.8 kJ · g DM⁻¹ for egg clusters, 11.5 ± 0.5 kJ · g DM⁻¹ for feces and 8.7 ± 0.4 kJ · g DM⁻¹ for Ulva sp.

Converting the data into energetic values made possible the presentation of the energy balance of A. oculifera at various body sizes (Fig. 3). As body size increased, sea hares consumed and assimilated more food, produced more feces and invested different amounts of energy in the various energetic pathways. The relations amongst the various pathways, as part of the total energy absorbed (C−F), changed as the sea hares grew and aged (Fig. 4). At any given body size, 8−16% of the absorbed energy was allocated to standard metabolism (R). Until reaching BLM of ~8 g, A. oculifera allocated 52−62% of absorbed energy to somatic growth (Ps). From ~8 g BLM on, sea hares began to allocate resources to reproduction (Pr). From this stage on, investment in somatic growth decreased gradually and stopped at mean size of 105 g BLM, while investment in eggs increased and reached a maximum of 15.9% of the total absorbed energy.

FIG. 3. Energy budget of the sea hare Aplysia oculifera in relation to body live mass (BLM). Energy consumed (C) and energy allocated to somatic growth (Ps), reproduction (Pr), metabolism (R), and feces (F), in the sea hare under experimental laboratory conditions, fed ad lib with Ulva sp.

FIG. 4. Energy resource allocation in the sea hare Aplysia oculifera in relation to body live mass (BLM) and to postmetamorphic age (small frame, at t BL, BLM = 0.006 g). Resource allocation calculated as percentage of absorbed energy (C−F), allocated to somatic growth (Ps), reproduction (Pr), and metabolism (R) in sea hares under experimental laboratory conditions, fed ad lib with Ulva sp.
Out of a life span of 160 days, approximately the first 23 days (14.3%) were dedicated to somatic growth only. For the rest of its life, an average sea hare produced large amounts of eggs due to its large body size.

**DISCUSSION**

**Growth, Reproduction, Food Consumption, Feces Production and Metabolism**

Under laboratory conditions *A. oculifera* reached a maximum BLM (mean 105 g, maximum 210 g) up to two orders of magnitude higher than maximum mean BLM in several populations observed in the field (25). In nature, during four years of observations and out of more than 5000 specimens sampled, only three individuals with BLM > 100 g were found, and in many populations the maximum mean BLM was less than 4 g (25). Hence, the growth potential of *A. oculifera* is far greater than that usually found in natural populations. Since the reproductive rate is directly related to body size, we assume that reproductive potential is also much higher than that existing in nature.

*A. oculifera* from the Gulf of Eilat grew in the laboratory faster than all the other *Aplysia* species previously studied (3,4,5,16,17,28,29,34,24,26). Comparison of K values for *A. oculifera* and other *Aplysia* spp. fed with *Ulva* spp. (Table 2) shows that the only similar K values are of *A. juliana* during initial postmetamorphic stages (28,29). In all the other species growth rates were lower than that found for *A. oculifera*, including other species fed on other algae (7, Table X, pp. 232–233). These differences might be related to the genotypic maximum BLM of each species.

Rapid growth in the initial postmetamorphic stages is an important advantage for sea hares. In the early stages, sea hares are exposed to higher mortality due to physical conditions and predation (28,29,7,20,21,22,23). Rapid growth helps sea hares to escape this vulnerable stage, and is akin to refuge in size for sessile species. In addition, in the northern Gulf of Eilat the algae used as food exist only for a short duration of about 5 months each year and quite often the algae are destroyed by unpredictable storms several times within a season (25). Rapid growth enables *A. oculifera* to effectively utilize the resources present for a limited time and to become reproductive shortly after recruitment.

Under experimental conditions, *A. oculifera* produced eggs at rates of 1.6 ± 0.6% of BLM per day, or 10^8 eggs per life span. This value is similar to those found for other species (*A. juliana* from Japan, 1.02 × 10^8, 32; *A. juliana* and *A. dactylomela* from Hawaii, 6.7 × 10^7 and 2.7 × 10^8, respectively, 31).

The allometric relation between oxygen consumption (V_{O_2}) and body mass (BLM) in animals takes the form V_{O_2} = a(BLM)^b. The universal value of the exponent (b) is 0.75 for poikilotherms (30,2). The value found for *A. oculifera* (b = 0.778) agree with this and with similar data reported for other *Aplysia* spp. (28,6,8,18).

**Energy Budget**

In our measurements the energy budget (Eq. 2) did not balance. Complete balance is rarely found when measuring energy balance, that is, intake and losses of materials or energy (33). Imbalances can be a result of failure to measure with sufficient accuracy urinary and other losses such as mucus and dissolved organic molecules (7), but can also result from several other reasons (19,33). In *Aplysia*, large imbalances in the energy budget are apparent (e.g., −3 to +155% for *A. punctata* (7,8); −46% for *A. juliana* (28)). Several energy loss pathways in *Aplysia* have never been measured. These include urinary and ink secretion, radula teeth lost during feeding, sperm (7), and mucus loss from the skin during crawling (10,11). In Table 3 we used the component U as an expression of all these pathways combined with the imbalance. We measured resting (standard) metabolic rates, not routine metabolic rates. Carefoot (9) found more than a two-fold increase in oxygen consumption during feeding, locomotion, and possibly after spawning, compared with standard metabolic rates in two species of tropical *Aplysia*. Thus, our results may represent only about half of the actual value. The difference between resting metabolic rate and routine metabolic rate was also added to the value U. In spite of the imbalance of the energy budget, the results still give a significant picture of the physiological characteristics of *A. oculifera*. This will permit analysis of physiological strategies found in the field and comparison with other species of *Aplysia*.

The pattern of energy allocation in *A. oculifera* changed in relation to body size. Only the energy invested in metabolism, measured as oxygen consumption, was an approximately constant part of the absorbed energy through the entire life span. During postmetamorphic and juvenile stages all the energy allocated to production was used for somatic growth, as in other species of *Aplysia* (*A. dactylomela*: 5,34; *A. juliana*: 28; and *A. punctata*: 3,4). When the sea hares became reproductive, the relative resource allocation for growth decreased and that for reproduction increased. In other *Aplysia* spp. the relative allocation for reproduction ranged from 3 to 11% of the total absorbed energy (3,4). *A. oculifera* invested a similar share, up to 16% of the absorbed energy.

In all the studies in which energy allocation of *Aplysia* was measured, no separate data were reported for different body sizes. Sarver (28) measured energy allocation of *A. juliana* under laboratory conditions during a period of 104 days, starting from 2.5 g BLM. Comparison of our data for *A. oculifera* with his (Table 3, taking into account the differences in maximum BLM between the species: ~250 g for *A. juliana* and ~100 g for *A. oculifera*) suggests general similarity between the two species. The main difference is in the feces energy content: 4.0 kJ · g⁻¹ and 11.5 ± 0.5 kJ · g⁻¹ for *A. juliana* and *A. oculifera*, respectively. This is probably due to different measuring methods. However, our results are similar to those for *A. punctata*: 8.8 kJ · g⁻¹ (3). Energy content of other components reported by Sarver (28) was lower than, but similar to our findings. In both species respiration required a con-
Energy Budget of Aplysia oculifera

TABLE 3. Energy budgets of Aplysia juliana (data from 28) and A. oculifera.

<table>
<thead>
<tr>
<th>Energy pathway</th>
<th>A. oculifera</th>
<th>A. juliana</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>kJ · ind⁻¹</td>
<td>% of C</td>
</tr>
<tr>
<td>Food consumption (C)</td>
<td>1473.7</td>
<td>100.00</td>
</tr>
<tr>
<td>Metabolism (R)</td>
<td>113.7</td>
<td>7.7</td>
</tr>
<tr>
<td>Somatic growth (Ps)</td>
<td>122.2</td>
<td>8.3</td>
</tr>
<tr>
<td>Reproduction (Pr)</td>
<td>167.1</td>
<td>11.3</td>
</tr>
<tr>
<td>Feces production (F)</td>
<td>280.0</td>
<td>19.0</td>
</tr>
<tr>
<td>Unaccounted energy (U)</td>
<td>790.7</td>
<td>53.7</td>
</tr>
</tbody>
</table>

Measurements started at 2.5 g and 0.01 g body live mass for A. juliana and A. oculifera, respectively, and continued for 104 days. Values of U calculated from the balance equation, C = Ps + Pr + R + F + U and include all unmeasured energy.

A considerable part of the energy budget, and more energy was invested during the period of 104 days in reproduction than in growth.

In other species of Aplysia in which energy allocation has been studied (A. punctata: 3,4; A. dactylomela: 6) the methods of measurements and body sizes of the animals do not allow direct comparison with our data. The values reported ranged for somatic growth (Ps) from 8 to 25%, for reproduction (Pr) from 3 to 11%, for metabolism (R) from 13 to 54%, and for feces production (F) from 25 to 49% of the consumed energy (C) (data from 7, Table XI, pp. 240). Although these data are not directly comparable with ours, they indicate that the energy investment of A. oculifera in productivity, including growth and reproduction, is within the range to other Aplysia spp.

CONCLUSIONS

Potential for high productivity is essential for sea hares in order to grow rapidly through the vulnerable small size stages and to become large, protected and highly reproductive adults (28,29,7,20,21,22,23). The danger of predation for A. oculifera in the northern Gulf of Eilat is low (25). However, the algae eaten by A. oculifera in the Gulf of Eilat are available for only 5 months during the year, and in unpredictable patterns of occurrence (25). Rapid growth and high reproductive capacity are therefore necessary for the sea hares in the Gulf of Eilat to complete their life cycle in time, and to produce sufficient numbers of offspring in a limited time that might end unpredictably.

Data presented elsewhere (25) suggest that A. oculifera do not utilize their whole productivity potential (scope for productivity) in their natural habitat in the northern Gulf of Eilat. This is probably due to the influence of environmental conditions. The effects of environmental conditions on A. oculifera productivity are demonstrated and discussed in Plaut (25).

References


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