Rates of energy consumption and acquisition by lecithotrophic larvae of *Bugula neritina* (Bryozoa: Cheilostomata)

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Abstract Lecithotrophic larvae of the cheilostome bryozoan, *Bugula neritina* (L.), lose metamorphic competence 12 to 24 h after release from the maternal zooid. The high respiration rate of newly released larvae (mean = 306.3 pmol O_2 $larva^{-1}$ h^{-1}, range = 149.3 to 466.6, $n = 18$ trials, 22.5 °C) from adults collected at Link Port, Fort Pierce, Florida during the winter/spring of 1990–1991 reflects their active swimming behavior. The average energy content per larva was 15.24 mJ (range: 13.35 to 20.17 mJ ind^{-1}, $n = 5$ groups). If all cells have an identical energy content and metabolic rate, then 2 and 20% of the total energy content would be consumed by the onset (2 h post-release) and the loss (24 h post-release) of metamorphic competence. Larvae of *B. neritina* are a composite of both larval and juvenile tissues and the loss of metamorphic competence may be due to regional depletion of labile energy stores in transitory "larval" cells, particularly the ciliated cells that comprise the locomotory organ, the corona. Although "nonfeeding", *B. neritina* larvae can acquire nutrients from the environment in the form of dissolved organic materials (DOM) in seawater. Both the amino acid alanine and the fatty acid palmitic acid can be transported from seawater ([S] = 1 μ*M*, 22.5 °C). The rates of alanine influx (appearance of label in tissue) averaged 0.366 pmol $larva^{-1}$ h^{-1} and, based on comparisons between rates of solute transport and metabolism, would contribute little (<1% of required energy) to offset the metabolic demand. The average rate of palmitic acid influx was 4.668 pmol $larva^{-1}$ h^{-1} and, assuming that the measured influx equals the net solute flux, could account for 21 to 72% of energy requirements. These data suggest that the duration of planktonic life of *B. neritina* larvae is principally regulated by the amount of endogenous energy stores, but may be modulated by available DOM in seawater.

Introduction

The length of time that larvae of benthic marine invertebrates remain in the plankton is influenced by such factors as developmental mode (planktotrophy versus lecithotrophy), amount of accumulated energy reserves, the time required to become metamorphically competent, and the presence of an appropriate settlement cue. In the absence of a settlement cue, many larvae can extend their planktonic life after the onset of metamorphic competence, thus delaying settlement and metamorphosis (reviewed by Pechenik 1990). The developmental flexibility that results from the capacity to delay settlement and metamorphosis is thought to increase the probability that larvae will locate benthic habitats suitable for subsequent survival (Thorson 1950; Scheltema 1974; Pechenik 1990). Such an extension of planktonic life is exhibited by larvae that can (e.g. the gastropod *Crepidula fornicata*, Pechenik 1986) and cannot (e.g. the sea star *Mediaster aequalis*, Birkeland et al. 1971) concentrate and clear particles from seawater. The potential duration of the protracted planktonic life is, in general, greater in planktotrophic ("feeding") larvae than in lecithotropic ("nonfeeding") larvae (see Table 1 in Pechenik 1990). However, larvae cannot delay settlement and metamorphosis indefinitely, and there is considerable variability in the duration of the delay period among species. After attaining metamorphic competence, they must complete their developmental program within a finite amount of time (Kempf 1981; Woollacott et al. 1989). The factors regulating the maximum duration of larval life for any particular species remain obscure.

Lecithotrophic larvae of marine invertebrates are structurally incapable of concentrating and clearing particulate

food from seawater. In general, these larvae are provided with greater nutritional investment ("yolk" per egg) than their planktotrophic counterparts (e.g. Turner and Lawrence 1979). It follows then, that energy and nutrients utilized by lecithotrophic larvae during development are supplied solely through the metabolism of these maternally supplied reserves. However, all nonarthropodan embryos and lecithotrophic larvae tested to date have demonstrated a capacity to take up and metabolize certain forms (principally amino acids) of dissolved organic materials (DOM) found in seawater [Bass et al. 1969; Reish and Stephens 1969 (Annelida); Epel 1972 (Echinodermata); Manahan 1983; Jaeckle and Manahan 1989 a; Welborn and Manahan 1990 (Mollusca)]. With two exceptions (Jaeckle and Manahan 1989 a; Welborn and Manahan 1990), these studies evaluated transport as the appearance of a radioactive label in tissue (influx). In order to determine the net solute flux, concurrent determinations of the concentration in the medium of labelled and unlabelled forms of the tested compound must be made. Where those simultaneous measurements have been made for transport by larvae of certain α-amino acids, solute influx equaled the net flux (Davis and Stephens 1984; Jaeckle and Manahan 1989 b, c; Manahan et al. 1989; Manahan 1990). Simultaneous influx and efflux (exchange diffusion, Ussing 1949) has only been reported for the amino acid taurine in larvae of the gastropod mollusc *Haliotis rufescens* and the bivalve mollusc *Crassostrea gigas* (Jaeckle and Manahan 1989 a; Manahan 1989). The ability of lecithotrophic larvae to take up nutrients directly from seawater in the form of DOM, therefore, may provide a quantitatively important mode of energy and nutrient acquisition during larval life.

Larvae of the bryozoan *Bugula neritina* develop within a brood chamber, the ovicell, and at release are 300 to 400 µm (length) × 200 to 300 µm (width) (Woollacott and Zimmer 1971). Following release in the laboratory, larvae of *B. neritina* are active swimmers and soon (ca. 2 h) become competent to settle and metamorphose (Woollacott and Zimmer 1971; Keough 1984, 1989). *B. neritina* larvae are incapable of successful metamorphosis after ca. 12 to 24 h and no longer actively swim after 24+ h in the plankton (Woollacott and Zimmer 1971; personal observations). Examinations of sections (ca. 1 µm thick) of newly released individuals (Woollacott and Zimmer 1971; Jaeckle unpublished) have revealed that *B. neritina* larvae possess substantial stores of lipid and yolk and that the distribution of these materials is not uniform among cells. Those cells that comprise the larval epidermis appear to be nutrient-poor relative to internal parenchymal cells.

Although newly released larvae seem to be provided with substantial endogenous stores, their vigorous swimming and short larval life suggest that the duration of the competent period is dictated by the size of a finite energy store. The goals of the present study were to measure the rates of energy utilization (oxygen consumption), the rates of energy acquisition (DOM transport), and the energy content of larvae of *Bugula neritina*. Together, these data allow an assessment of the relationship between energy loss and the loss of metamorphic competency and an estimate of the potential ecological value of DOM transport in modulating the duration of the competency period.

Materials and methods

Collection of larvae

Colonies of *Bugula neritina* were collected from floating docks and seawalls at the Harbor Branch Oceanographic Institution and the Smithsonian Marine Station at Link Port, Fort Pierce, Florida during the winter and spring of 1990–1991. Colonies were held at temperatures of 22 to 24 °C in unfiltered seawater from the Link Port channel with continuous aeration; the water was changed daily. The release of larvae from adult colonies was induced by a sudden exposure to light after ca. 12 h of complete darkness. Newly released larvae were placed in seawater that had been gently passed through a membrane filter (0.2-µm pore size, hereafter FSW, 22.5 °C). Before experiments, the larvae were washed three to four times with FSW.

Oxygen consumption by larvae

The metabolic rate of larvae was measured as the rate of oxygen consumption at 22.5 ± 0.05 °C. Newly released larvae (4 to 8 trial^{-1}) were transferred to a 100-µl glass respiration chamber (Strathkelvin model # RC 200) that was connected to a recirculating water bath (Lauda/Brinkman model # 132-F). A Clark-type polarographic oxygen electrode (Strathkelvin model # 1302) served as the floor of the respiration chamber and was connected to an oxygen meter (Strathkelvin model # 781). The analog output from the oxygen meter was converted to a digital signal and transferred to an IBM-AT computer using an analog/digital converter and the Datacan computer software package (Sable Systems, Inc.). Larvae were introduced into the respiration chamber and allowed to recover from any handling effects for 10 to 15 min. The larvae were actively swimming after this equilibration period. The chamber was sealed, and the rate of removal of oxygen from the chamber was continuously monitored for 1 h. At the completion of each trial, larvae were removed and counted. For each batch of larvae ($n = 8$), two or three independent trials were completed. After each trial, the chamber was swabbed with 70% ethanol and washed twice each with distilled deionized water and FSW. The rate of oxygen consumption (expressed initially as V larva^{-1} h^{-1}) was calculated as the slope of a regression line for the collected data (V min^{-1}) divided by the number of larvae present and multiplied by 60. After calibrating the measured output voltage for air-saturated FSW with the measured molar concentration of oxygen (determined by the Winkler titration method, Parsons et al. 1984), voltages measured during experiments were converted into amounts of oxygen removed from the respiration chamber. All measured respiration values were corrected for the self-consumption rate of the electrode. The measured rates of oxygen consumption were converted to energy units using an oxyenthalpic equivalent of 480 kJ mol O_2^{-1}, which equals the average oxyenthalpic equivalent for protein, lipid and carbohydrate (527, 441, and 473 kJ mol O_2^{-1}, respectively, all from Gnaiger 1983).

Energy content of larvae

The amount of energy in groups of *Bugula neritina* larvae (5 to 7 ind group^{-1}, $n = 5$ groups; <4 h old) was measured using the dichromate oxidation method (Parsons et al. 1984, as modified by McEdward and Coulter 1987). After respiration trials, larvae were removed from the respiration chamber, washed three times (2 ml wash^{-1}) with cold 3.5% ammonium formate (5 °C), and frozen. The samples were lyophilized for 8 h or placed in a drying oven (80 °C) for 24 h immediately prior to analysis. The measured absorbance ($\lambda = 440$ nm) of each sample was converted to joules of energy using the average standard curve for glucose, glycerol and bovine serum albumin. The mean energy content per larva within each group was calculated by dividing the energy content of the sample by the number of larvae present.

Alanine and palmitic acid transport by larvae

Newly released larvae (<3 h post-release) were transferred to 10 ml of FSW (initial concentration <5 ind ml^{-1}) in an autoclave-sterilized 20-ml scintillation vial. Vials used for experiments with palmitic acid were previously silanized with "Silvue" (SDS Coatings, Inc.) to retard adsorption of palmitic acid to the vial surfaces. All experiments were conducted at an added substrate concentration of 1 μM. After the addition of the label (^{3}H-alanine or ^{3}H-palmitic acid, New England Nuclear, specific activities 70 or 84 Ci $mmol^{-1}$ and 60 Ci $mmol^{-1}$, respectively) and cold carrier, the suspension of larvae was thoroughly mixed and the first sample removed. At every sampling time, 500 µl of the suspension of larvae was removed, layered onto 500 µl of silicone oil (Versilube F-50, General Electric Co.) in a 1.5-ml microcentrifuge tube, and the number of larvae within the sample counted. The larvae were separated from the medium by centrifugation (12 500×g) and collected by cutting off the tip of the microcentrifuge tube. The pellet of larvae was dissolved in tissue solubilizer (Scinti-Gest, Fisher Scientific Co.) for 24 h, and the radioactivity in each sample was measured using a scintillation counter (Beckman Model # 3801) after the addition of scintillation cocktail (Biofluor, New England Nuclear). The measured amount of radioactivity per sample was corrected for quenching and converted to moles of material per individual. The rate of transport was calculated as the slope of the regression line describing the relationship between moles of substrate per larva and time.

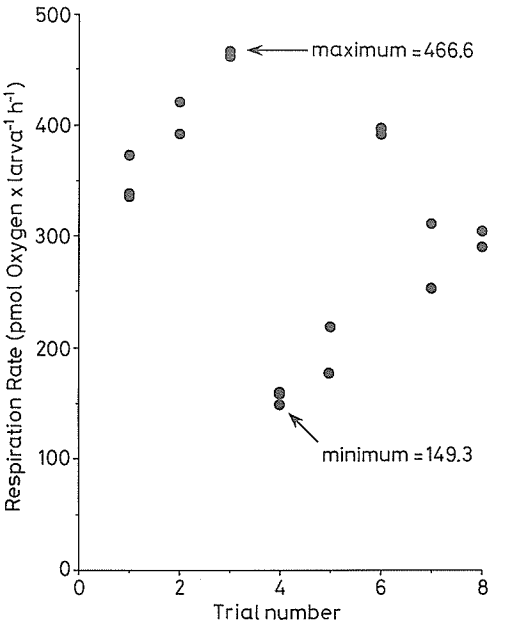


Fig. 1 *Bugula neritina.* Respiration rates of newly released (<3-h old) larvae, expressed as pmol O_2 $larva^{-1}$ h^{-1}, of eight independent batches (n = 18 trials) of larvae

Results

Oxygen consumption

During all measurements, larvae in the respiration chamber were continually swimming and there was no apparent change in behavior during each trial. However, to ensure that respiration was measured while the larvae were experiencing near normoxic conditions, all experimental trials (n=3) in which the P_{O_2} in the respiration chamber decreased by >10% during the measurement period were excluded from further analysis. For the remaining 18 trials, the average respiration rate of *Bugula neritina* larvae was 306.3±24.9 pmol O_2 $larva^{-1}$ h^{-1} [mean±1 standard error (SE), range = 149.3 to 466.6 pmol O_2 $larva^{-1}$ h^{-1}] (Fig. 1).

Energy content

The energy content of *Bugula neritina* larvae (<4 h post-release), as estimated using the dichromate oxidation assay, ranged for 13.35 to 20.17 mJ $larva^{-1}$. The average energy content was 15.24±1.33 mJ $larva^{-1}$ (mean±1 SE, n=5 groups of larvae).

Alanine and palmitic acid transport

Larvae of *Bugula neritina* transported both alanine and palmitic acid from seawater, but at different rates. For alanine, the average transport rate was 0.366±0.015 pmol $larva^{-1}$ h^{-1} (mean±1 SE, range: 0.337 to 0.386, n=3, Fig. 2). The rate of palmitic acid transport was more than ten times greater, ranging from 4.303 to 5.038 pmol palmitic acid $larva^{-1}$ h^{-1} (mean±1 SE=4.668±0.212, n=3, Fig. 2).

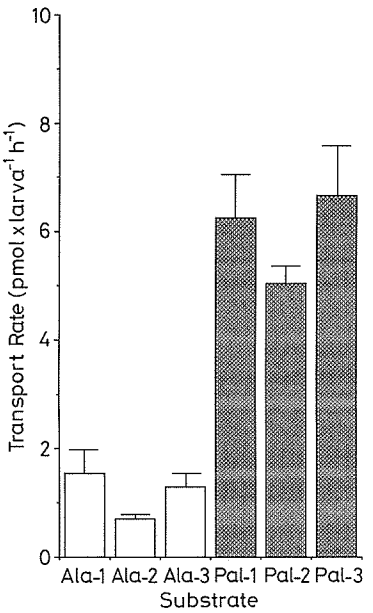


Fig. 2 *Bugula neritina.* Transport rate of alanine (open bar) and palmitic acid (dark, cross-hatched bar), each at an added substrate concentration of 1 μM, from seawater by larvae. Data presented as the measured rate of transport±1 SE of the slope of the regression line between moles of material per larva and time

Discussion

Newly released larvae of *Bugula neritina* are vigorous swimmers and can maintain this active locomotion for at least 12 h. This level of swimming activity indicates that these larvae have a high weight-specific metabolic rate.

Table 1 *Bugula neritina*. Comparison of the weight-specific metabolic rates (μmol O_2 g-larva^{-1} h^{-1}) of soft-bodied (nonarthropodan) invertebrate larvae. All weight values represent dry organic (tissue) weight, and reported respiration rates were adjusted to a temperature of 22.5 °C, assuming a Q_{10} of respiration of 2

Taxa	Weight-specific rate	Source
Bryozoa		
Bugula neritina	204.2	Present study
Bugula neritina	446.4	Crisp (1974)
Mollusca		
Ilyanassa obsoletus	241.0	Pechenik (1980)
Haliotis rufescens	82.0	Jaeckle and Manahan (1989c)
Strombus gigas	153.7–207.0	Erickson (1984)
Bankia gouldi	181.6	Mann and Gallager (1985)
Teredo navalis	198.6	Mann and Gallager (1985)
Mytilus edulis	150.1–269.4	Sprung (1984a, b)

Table 2 *Bugula neritina*. Comparison of the weight-specific alanine transport rates (μmol alanine g-larva^{-1} h^{-1}) of soft-bodied (nonarthropodan) invertebrate larvae. All weight values used to make the calculations represent dry organic (tissue) weight and the reported respiration rates adjusted to a temperature of 22.5 °C, assuming a Q_{10} of transport of 2

Taxa	Weight-specific rate	Source
Bryozoa		
Bugula neritina	0.24	Present study, Crisp (1974)
Mollusca		
Haliotis rufescens	3.00	Jaeckle and Manahan (1989c), Manahan et al. (1989)
Crassostrea gigas	9.76	Manahan (1989), Gerdes (1983)
Echinodermata		
Strongylocentrotus purpuratus	11.37	Manahan et al. (1989), Shilling and Manahan (1990)

Using Crisp's (1974) value of 1.5 μg as the dry organic weight of a larva of *B. neritina*, the mean weight-specific respiration rate for *B. neritina* larvae is 204.2 μmol O_2 g-larva^{-1} h^{-1}; a value that is among the highest reported for a soft-bodied invertebrate larva (Table 1). Crisp (1974) reported a respiration rate for *B. neritina* larvae (669.6 pmol O_2 larva^{-1} h^{-1}, temperature not given) that was more than two times higher than the mean respiration value presented here. The resulting weight-specific metabolic rate would be 446.4 μmol O_2 g-larva^{-1} h^{-1}, the highest value reported for a nonarthropodan invertebrate larva.

While the measured respiration rates reported here were reasonably consistent within batches of larvae collected on the same day (Fig. 1), there was considerable variability among batches. These results were not caused by instrumentation error because all measured values for air-saturated seawater were within 7% of one another. All larvae, however, were obtained from mixed populations of adults, and batch-to-batch variation was probably not due to different nutritional conditions among parent colonies. Because of the small number of larvae used in each trial, physiological differences among individuals would have a large effect on the respiration rate per trial. The variability in respiration rate per trial may be explained, in part, by differences in the size of newly released larvae (Woollacott and Zimmer 1971; personal observation). The maximum difference in larval volume was calculated to be 67% [size data from Woollacott and Zimmer (1971) and assuming a cylindrical larval shape], a value that is nearly identical to the maximum difference in measured respiration rates (68%).

Although larvae of *Bugula neritina* cannot feed on particulate foods, they may acquire nutrients by assimilating DOM from seawater. The rates of alanine transport measured here were similar to those reported for other soft-bodied invertebrate larvae (Manahan 1990). Using an organic weight of 1.5 μg (Crisp 1974), the average weight-specific transport rate is estimated to be 0.244 μmol alanine g-larva^{-1} h^{-1}, the lowest weight-specific transport rate reported (Table 2). For palmitic acid, the estimated weight-specific rate of transport by *B. neritina* larvae is 3.11 μmol g-larva^{-1} h^{-1}. This weight-specific transport rate compares reasonably well with that found for lecithotrophic larvae of the demosponge *Tedania ignis* (mean = 1.02 μmol g-larva^{-1} h^{-1}; Jaeckle in review).

The transport data reported here represent the rate of influx (appearance of label in tissue), not the net solute flux (Johannes et al. 1969). Exchange diffusion of alanine, however, has not been reported for any nonmolluscan larva tested to date, and it is, therefore, reasonable to assume that the measured influx of alanine is an accurate predictor of the net solute flux. For fatty acid transport systems in larvae, no data on the influx/net flux issue are available. Previous work on fatty acid transport by adult polychaete worms (*Stauronereis rudolphi*) and bivalves (*Crassostrea virginica*), however, has shown that solute influx equaled the net solute flux (Testerman 1972; Bunde and Friede 1978).

The potential contribution of DOM transport to aerobic metabolism can be estimated by comparing the rate of energy acquisition to the metabolic rate. Alanine transport ([S] = 1 μ*M*) could contribute less than 1% of the measured metabolic rates (Table 3). Assuming that the measured transport rate is equal to the maximal rate (J_{max}) of the transport system, complete compensation of the metabolic rate would be achieved at substrate concentrations ranging from 125 to 500 μ*M*: these concentrations exceed values measured from bulk seawater samples by at least two orders of magnitude (e.g. Mopper and Lindroth 1982; Carlucci et al. 1984). Alanine transport, therefore, probably does not contribute to the energetics of *Bugula neritina* larvae. In contrast, palmitic acid transport could provide a significant metabolic resource for *B. neritina* larvae. The higher rate of palmitic acid transport plus the high catabolic oxygen demand results in potential contributions ranging from 21 to 72% of the metabolic rate (Table 3). The concentration of total fatty acids in seawater, however, is variable among habitats ([S] = n*M* to μ*M*) (Jeffrey 1970; Testerman 1972; Bunde and Friede 1978). If larvae of *B.*

Table 3 *Bugula neritina.* Comparison of the potential contribution of alanine and palmitic acid transport ([S] = 1 μ*M*) to larval metabolism

Transport rate (pmol larva^{-1} h^{-1})	Oxygen equivalent[a] (pmol O_2 larva^{-1} h^{-1})	Respiration rate (pmol O_2 larva^{-1} h^{-1})	% Compensation[b] min.–max.
Alanine transport			
0.386	1.158	149.3–466.6	0.4–0.8
0.375	1.125	149.3–466.6	0.2–0.8
0.337	1.011	149.3–466.6	0.2–0.7
Palmitic acid transport			
4.663	107.249	149.3–466.6	23.0–71.8
5.038	86.894	149.3–466.6	18.6–58.2
4.303	98.969	149.3–466.6	21.2–66.3

[a] Oxygen equivalent to the transport rate calculated by multiplying measured alanine transport rate by 3 (3 mol of O_2 are required for each mol of alanine catabolized). For palmitic acid, the transport rate was multiplied by 23 (23 mol of O_2 are necessary for the complete catabolism of 1 mol of palmitic acid)
[b] The percent compensation calculated by dividing the oxygen equivalent to the transport rate by the rate of respiration and multiplying by 100 for both the maximum (max.) and minimum (min.) measured rates of respiration

neritina do encounter fatty acids in seawater at the upper end of the reported concentrations, they appear to be physiologically capable of transporting these compounds at sufficiently high rates to account for a substantial percentage of the metabolic demand.

Despite the fact that *Bugula neritina* larvae can transport alanine and palmitic acid from seawater, laboratory studies reveal that larvae of *B. neritina*, *B. stolonifera*, and *B. pacifica* cannot successfully undergo settlement and metamorphosis after 12 to 24+ h in the plankton (Woollacott and Zimmer 1971; Young and Chia 1981; Woollacott et al. 1989). Although this loss of competence may be a result of a non-nutritional mechanism, the fact that larvae cease active swimming 24+ h after release from the ovicell suggests that the inability to metamorphose is a result of depletion of labile energy stores, a situation similar to that observed for lecithotrophic cyprid larvae of *Semibalanus balanoides* (Crustacea: Cirripedia, Lucas et al. 1979). Assuming that the metabolic rate of each larva does not change during its planktonic life and knowing the energy content soon after release, the potential maximal duration of the planktonic life of *B. neritina* larvae in the absence of utilizable DOM can be estimated. For the five experiments where both energy content and metabolic rate were measured, the amount of time necessary for the entire larval body to be consumed ranged from 83 to 208 h and the percentage of the larval body consumed in 12 and 24 h varied from 10 to 20% (Table 4).

A more biologically meaningful estimate of "self-consumption" can be made by estimating the percentage of the total larval energy content that serves as a labile energy store and comparing that value to the measured metabolic rate for each group of larvae. There have been no estimates of the partitioning of the energy content of *Bugula neritina* larvae among (1) structural components (2) the cost of metamorphosis and morphogenesis, and (3) the metabolic demands of a planktonic existence. However, Lucas et al. (1979) reported that the fraction of the total energy content available for swimming and searching activities of lecithotrophic *Semibalanus balanoides* cyprid larvae equalled 34%. If it is assumed that 34% of the total energy content of a *B. neritina* larva represents the reserve used to support metabolism during planktonic life, then the energy store would be completely consumed in 29 to 71 h (Table 4) and 34 and 68% of this labile energy store would be consumed after 12 and 24 h in the plankton (4). When larvae of another bugulid species, *B. stolonifera*, remained swimming for ≥6 h in the laboratory, the rate of juvenile colony development was negatively affected (Woollacott et al. 1989). If it is assumed that *B. neritina* larvae respond similarly, then their larval life can be extended 200% (4 h delay to 2 h precompetency = 2) without a negative effect (excluding the increased hazards of remaining in the plankton). During that 6-h planktonic life, a *B. neritina* larva would consume ca. 17% of its labile energy store.

The analyses above assume that the distribution of energy is uniform among all cells and that the metabolic rate of all cells is identical. Data are currently not available to rigorously evaluate these assumptions. For bugulid larvae, the loss of metamorphic competence after 12 to 24+ h in the plankton (*Bugula neritina*, *B. stolonifera*, *B. pacifica*) and the negative impact of an extended planktonic life (≥6 h) on juvenile growth (*B. stolonifera*) is suggestive of regional depletion of energy reserves. This hypothesis is supported by the fact that the coronate larva of bryozoans is a composite of larval and juvenile tissues (Woollacott and Zimmer 1971; Zimmer and Woollacott 1977 a, b; Reed 1991). Most exterior cells represent larval structures, while internal cells generate the juvenile. The cells of the larval locomotory organ, the corona, are the most likely candidates for energy depletion with increased time in the plankton. These cells are multiciliate and, as their activity propels the larva, they presumably have a high metabolic rate. At metamorphosis, these cells (and other cells of the larval outer epithelium) are involuted and internalized into the preancestrula (Zimmer and Woollacott 1977 b). Once internalized, these cells are degraded and serve as a "significant source of nutrients for growth of the incipient ancestrula" (Zimmer and Woollacott 1977 b). Thus, a protracted larval existence will decrease the energy content of these transitory larval cells, in turn, reducing the energy available for the developing juvenile. This hypothetical scenario is consistent with the report of Nielsen (1981), who noted that postmetamorphic colony development from

Table 4 *Bugula neritina*. Estimated amount of energy consumed and duration of larval life

Trial	Energy content (mJ ind^{-1})	Respiration rate [a] (mJ $larva^{-1}$ h^{-1})	Potential duration [b] (h)	Potential duration (34%) [c] (h)
1	13.35	0.076	175	61
2	13.35	0.16	83	29
3	13.37	0.15	87	31
4	15.97	0.076	208	73
5	20.17	0.13	151	53

[a] Metabolic rate expressed as mJ $larva^{-1}$ h^{-1}. This value calculated by multiplying the measured respiration rate (mol O_2 $larva^{-1}$ h^{-1}) by the average oxyenthalpic equivalent for protein, lipid and carbohydrate (480 kJ mol^{-1}, Gnaiger 1983)

[b] Potential duration calculated by dividing the total energy content by the rate of energy consumption

[c] Time required to consume 34% of the measured energy content of larvae. This assumes that the percentage of their energy content available for swimming and exploring is the same as estimated for nonfeeding cyprid larvae of *Semibalanus balanoides* (from Lucas et al. 1979)

6+ h old larvae of another cheilostome bryozoan, '*Hippodiplosia*' *insculpta*, was slow and produced "unusually small ancestrulae" when compared to colony development from larvae that remained in the plankton for a shorter period of time.

Larvae of *Bugula neritina* are released from the maternal zooid in a fully differentiated morphological condition (Zimmer and Woollacott 1977 a), and these larvae are generally capable of metamorphosing within 2 h of release (Woollacott and Zimmer 1971; Keough 1984, 1989). These "nonfeeding" larvae can transport alanine and palmitic acid from seawater, and palmitic acid transport may be energetically significant. DOM transport, thus, provides the potential to extend the competent period of larval life by serving as an alternate source of energy. Even in the presence of natural DOM in FSW however, 12 to 24+ h post-release from the maternal zooid, larvae of *B. neritina* are incapable of successful settlement and metamorphosis. The high metabolic rate, the mortality after 24 h, and the decrease in either juvenile size or growth rate after an extended planktonic life (6+ h post-release) of larvae from other bryozoan species (*B. stolonifera* and '*Hippodoplosia*' *insculpta*) suggests that the loss of metamorphic competence by larvae of *B. neritina* is ultimately a consequence of depleted labile energy reserves.

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