

OXYGEN CONSUMPTION AND AMMONIA EXCRETION OF LARVAE AND JUVENILES OF THE BAY SCALLOP, *ARGOPECTEN IRRADIANS CONCENTRICUS* (SAY)

YANTIAN T. LU, NORMAN J. BLAKE, AND JOSEPH J. TORRES

Department of Marine Science

University of South Florida

St. Petersburg, Florida 33701

ABSTRACT Rates of oxygen consumption and ammonia excretion were determined at 25 °C for larval and juvenile bay scallops *Argopecten irradians concentricus*. Oxygen consumption rate (Vo_2 , $\mu\text{lO}_2 \text{ h}^{-1}$) varied with body size ash-free dry weight (AFDW, mg) according to the relation $Vo_2 = 7,199 \text{ AFDW}^{0.921}$ for larvae and $Vo_2 = 2,142 \text{ AFDW}^{0.905}$ for juveniles. Mean weight-specific Vo_2 ranged from 14.66 to 15.84 $\mu\text{lO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ for larvae and from 1.80 to 5.28 $\mu\text{lO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ for juveniles. Weight-specific Vo_2 declined with increasing body size at > 2 mm shell height but became independent of body size at > 2 mm shell height. Swimming was estimated to cause 8 to 29% of the total larval oxygen demand. In juveniles of 3.5 to 5.0 mm shell height, Vo_2 increased as temperature increased from 15 to 30 °C, being 1.24 ± 0.35 , 1.77 ± 0.70 , 2.33 ± 0.85 , and $2.74 \pm 0.57 \mu\text{lO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ at 15, 20, 25 and 30 °C, respectively. The Q_{10} was 2.99 at 15 to 20 °C, 1.74 at 20 to 25 °C and 1.37 at 25 to 30 °C. Ammonia excretion rate (U , $\mu\text{gNH}_4\text{-N h}^{-1}$) increased with body size following the equation $U = 0.161 \text{ AFDW}^{0.928}$. Energy loss through ammonia excretion was equal to 1.5 to 3.7% and $13.5 \pm 2.8\%$ of the respiratory energy loss in larvae and juveniles, respectively.

KEY WORDS: Bay scallop larvae, oxygen consumption, ammonia excretion

INTRODUCTION

Metabolism is an important component of physiological energetics, the study of energy gains and losses at the organismal level (Brett and Groves 1979). Metabolic rate is most often estimated as the rate of oxygen consumption, and it represents a major loss of energy in bivalves. Energy loss through ammonia excretion is also very significant (Barber and Blake 1985).

Information on oxygen consumption exists for a variety of adult marine bivalves, but less is known about the respiratory physiology of early developmental stages, with the exception of a few commercially important species (Sprung 1984, MacDonald 1988, Beiras and Camacho 1994). Existing data suggest that, in both larval and adult bivalves, oxygen consumption increases with increasing body size according to the allometric equation $Y = aX^b$, where Y is oxygen consumption, X is body weight, and a and b are fitted parameters (Bayne et al. 1976a). In adult bivalves, b -values range from 0.65 to 0.84, with a mean of 0.7 (Bayne and Newell 1983); whereas, in larval bivalves, b -values are often close to 1 (Riisgård et al. 1981, Gerdes 1983, Beiras and Camacho 1994), demonstrating an isometric relationship between metabolic rate and body size in larvae.

In energy balance studies, energy loss attributable to excretion of nitrogenous products is often overlooked (Bayne and Newell 1983), although it may substantially affect the general estimation of the energy budget. In most marine bivalves, ammonia is the dominant end product of protein catabolism, comprising 41 to 94% of the total nitrogen excretion (reviewed by Bayne et al. 1976b). Very limited data are available on ammonia excretion in pectinids; the only available data were collected by Barber and Blake (1985) on adult *Argopecten irradians concentricus*.

The purpose of this study was to determine the energy loss of larvae and juveniles of the bay scallop *A. irradians concentricus* (Say) by measuring their rates of oxygen consumption and ammonia excretion and to determine the relationships between these physiological rates and body size.

MATERIALS AND METHODS

Bay scallops collected from Homosassa, Florida were spawned at the Department of Marine Science, University of South Florida.

Culture of larvae and juveniles followed the methods described by Lu and Blake (1996). Before each determination of oxygen consumption, larvae and juveniles were filtered onto 35 μm nylon screens, rinsed with, and then released to, 0.45 μm filtered seawater (salinity $26 \pm 1\text{‰}$). Larger juveniles were also cleaned with a small, soft pen brush.

Oxygen consumption rates of various size classes of larvae and juveniles were measured at 25 ± 0.5 °C. Larvae and small juveniles were placed in sealed respiration chambers filled with 0.45 μm filtered seawater at a density of 20 to 80 larvae ml^{-1} or 1 to 10 juveniles ml^{-1} , depending on shell size. Respiration chambers were made from plastic syringes (Torres et al. 1994), whose volume could be adjusted (1-5 ml) according to the number and size of the experimental animals by adjusting the syringe plunger and/or oxygen electrode. Experiments with juveniles larger than 5 mm in shell height were carried out in 25- to 65- ml *Lucite* chambers. Oxygen concentration in the syringes and chambers was measured every 2 minutes using Microcathode oxygen electrodes calibrated with air and nitrogen saturated seawater. Data were recorded using a computer-controlled digital data-logging system. Experiments lasted 4 to 8 hours, during which the oxygen concentration never dropped below 50%.

The effect of temperature on oxygen consumption was determined using juveniles of 3.5 to 5 mm shell height. Experimental procedures were the same as described above, except that experiments were run at four temperatures, 15, 20, 25, and 30 ± 0.2 °C, using circulating water bath to control temperature.

The changing oxygen concentrations recorded for each respiration chamber during the course of a run were regressed against time to obtain a representative slope, a rate. The rate obtained was divided by the number of scallops in the chamber to give the amount of oxygen consumed per individual per hour ($\mu\text{lO}_2 \text{ h}^{-1}$). The oxygen consumption rates were further converted to $\mu\text{lO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ using the weight data (total AFDW) of Lu and Blake (1996). All measured oxygen consumption rates were corrected using control runs without animals.

Ammonia excretion was determined by placing larvae or juveniles in 35- and 50-ml capped glass vials filled with 0.45 μm filtered seawater at 20 to 80 larvae ml^{-1} or 1 to 60 juveniles per vial. Filtered seawater without animals were used as blanks. Ex-

periments lasted 4 to 7 hours at 25 ± 0.2 °C. At the end of each experiment, a 10-ml sample was drawn from each vial and placed in a 20-ml test tube. In experiments with larvae, the samples were passed through a 35- μ m mesh screen to remove the scallops. Ammonia concentrations in the samples and blanks were determined using the indophenol blue method (adapted from Solórzano 1969). To each sample and blank, 0.4 ml of phenol-alcohol reagent, 0.4 ml of nitroprusside reagent, and 1.0 ml of oxidizing reagent were added. The blue color that developed in the dark for 1 hour was read on a Cary spectrophotometer at wavelength of 640 nm. Optical densities were converted to ammonia concentrations using a standard curve determined with a solution of ammonium sulfate.

The following factors were used for converting oxygen consumption and ammonia excretion into energy unit:

$$1 \text{ ml O}_2 = 19.9 \text{ J (Elliott and Davidson 1975)}$$

$$1 \text{ mg NH}_4 - \text{N} = 24.8 \text{ J (Elliott and Davidson 1975)}$$

RESULTS

Table 1 lists the mean oxygen consumption rates of various sizes of larvae and juveniles of the bay scallop. Mean oxygen consumption ranged from 1.35 to $4.10 \times 10^{-3} \mu\text{I O}_2 \text{ h}^{-1}$ for larvae of 120 to 180 μm shell length, and $1.15 \times 10_{-2}$ to $5.15 \mu\text{I O}_2 \text{ h}^{-1}$ for juveniles of 0.5 to 7.0 mm shell height. The oxygen consumption of larvae and juveniles (up to 10 mm height) is closely related to body size according to the following equations:

$$V_{\text{O}_2} (\mu\text{I O}_2 \text{ h}^{-1}) = 0.298L^{2.536} \quad r^2 = 0.718 \text{ (for larvae)}$$

$$V_{\text{O}_2} (\mu\text{I O}_2 \text{ h}^{-1}) = 0.0444H^{2.410} \quad r^2 = 0.956 \text{ (for juveniles)}$$

where L is shell length of larvae in mm, and H is shell height of juveniles in mm. The two equations above can be further transformed to the following using the weight data determined by Lu and Blake (1996):

$$V_{\text{O}_2} (\mu\text{I O}_2 \text{ h}^{-1}) = 7.199 \text{ AFDW}^{0.921} \text{ (for larvae)}$$

$$V_{\text{O}_2} (\mu\text{I O}_2 \text{ h}^{-1}) = 2.142 \text{ AFDW}^{0.905} \text{ (for juveniles)}$$

where AFDW is the total ash free dry weight (including AFDW of the shells) in mg. The measured oxygen consumption rates and the fitted curves are shown in Figure 1 for both larvae and juveniles. Figure 1 was plotted in double logarithmic scales so that oxygen consumption of larvae and small juveniles can be compared on the

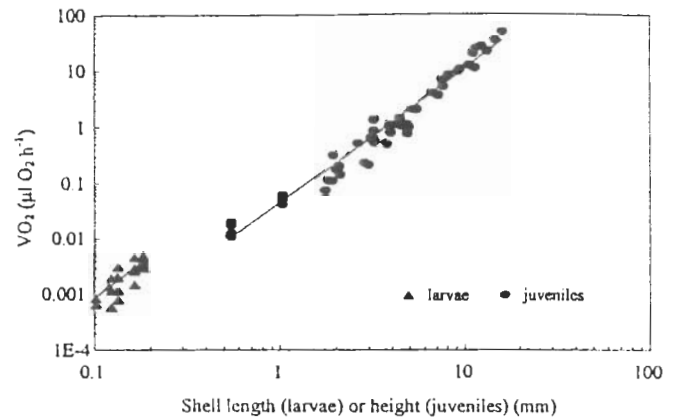


Figure 1. *Argopecten irradians concentricus*. Oxygen consumption rate of larvae and juveniles versus shell size.

same graph. It is clear from Figure 1 that oxygen consumption of larvae is above the extended line fitted to the datapoints of juveniles, suggesting that larvae have higher relative metabolic rates than juveniles.

Weight-specific oxygen consumption decreased with increasing body size at < 2 mm shell height (Fig. 2). Mean values ranged from 14.66 to $15.84 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ for larvae, and from 5.28 to $2.28 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ for juveniles 0.5 to 2 mm shell height. The relationship between weight-specific oxygen consumption rate and body size of juveniles < 2 mm shell height can be best described by the following equation:

$$V_{\text{O}_2} (\mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}) = 3.443H^{-0.648} \quad r^2 = 0.792$$

For juveniles > 2 mm in shell height, weight-specific oxygen consumption rates remained relatively constant, with a mean value of $2.16 \pm 0.20 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$.

In the temperature experiments, oxygen consumption increased with increasing temperature between 15 to 30 °C (Fig. 3). At 15 °C, the mean weight-specific oxygen consumption was $1.24 \pm 0.35 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$, representing 37.5% of the rate of oxygen consumption at 30 °C ($2.74 \pm 0.57 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$). At 20 and 25 °C, mean rates were 1.77 ± 0.70 and $2.33 \pm 0.85 \mu\text{I O}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$, being 64.8 and 85.3% of the rate at 30 °C, respectively. The Q_{10} was 2.99 at 15 to 20 °C, 1.74 at 20 to 25 °C and 1.37 at 25 to 30 °C.

TABLE 1.

Argopecten irradians concentricus. Rates (mean \pm SD) of oxygen consumption and ammonium excretion of larvae and juveniles. n: number of estimates.

Height (mm)	AFDW (mg)	n	O ₂ Consumption Rate		n	Ammonia Excretion Rate	
			$\mu\text{I ind}^{-1} \text{ h}^{-1}$	$\mu\text{I mg AFDW}^{-1} \text{ h}^{-1}$		$\mu\text{g ind}^{-1} \text{ h}^{-1}$	$\mu\text{g mg AFDW}^{-1} \text{ h}^{-1}$
0.12	0.0000915	5	0.00135 \pm 0.00052	14.784 \pm 6.334	6	$(3.51 \pm 0.80) \times 10^{-5}$	0.384 \pm 0.098
0.15	0.0001692	2	0.00268 \pm 0.00074	15.839 \pm 4.034		—	—
0.18	0.0002796	6	0.00410 \pm 0.00077	14.664 \pm 2.801	6	$(4.23 \pm 1.04) \times 10^{-5}$	0.125 \pm 0.035
0.50	0.00217	4	0.0115 \pm 0.0034	5.278 \pm 1.099	5	$(6.35 \pm 1.94) \times 10^{-4}$	0.292 \pm 0.089
1.00	0.0138	4	0.0518 \pm 0.0087	3.754 \pm 0.630	4	0.00304 \pm 0.00063	0.220 \pm 0.045
1.50	0.0406	2	0.0972 \pm 0.0270	2.394 \pm 0.665	5	0.00778 \pm 0.00197	0.192 \pm 0.048
2.00	0.0875	6	0.1994 \pm 0.0733	2.279 \pm 0.838	4	0.01540 \pm 0.00763	0.176 \pm 0.087
3.00	0.2576	2	0.6110 \pm 0.0324	2.372 \pm 0.126	3	0.07604 \pm 0.00505	0.295 \pm 0.019
4.00	0.5543	3	1.2528 \pm 0.2060	2.260 \pm 0.372	4	0.12755 \pm 0.03924	0.230 \pm 0.071
5.00	1.0045	3	1.8100 \pm 0.6429	1.802 \pm 0.640	5	0.18289 \pm 0.02421	0.182 \pm 0.024
7.00	2.4616	2	5.1473 \pm 1.4575	2.088 \pm 0.592	1	0.42635 \pm 0.00000	0.173 \pm 0.000

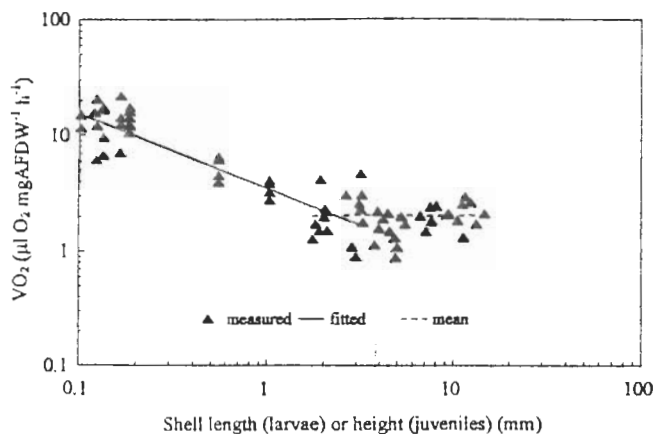


Figure 2. *Argopecten irradians concentricus*. Weight-specific oxygen consumption rate of larvae and juveniles versus shell size.

Mean ammonia excretion rates are also summarized in Table 1. In larvae, ammonia excretion was similar for young and old larvae; whereas, in juveniles, it was an increasing function of body size. The relationship between ammonia excretion rate (U) and body size of juveniles can be described by the following equations:

$$U (\mu\text{gNH}_4 - \text{N h}^{-1}) = 0.00302H^{2.472} (r^2 = 0.875)$$

$$U (\mu\text{gNH}_4 - \text{N h}^{-1}) = 0.161\text{AFDW}^{0.928}$$

The measured ammonia excretion rates and the fitted U to H curve are shown in Figure 4.

Mean weight-specific ammonia excretion decreased from 0.384 $\mu\text{gN mg AFDW}^{-1} \text{h}^{-1}$ in 120 μm larvae to 0.125 $\mu\text{gN mg AFDW}^{-1} \text{h}^{-1}$ in 180 μm larvae. Energy loss through ammonia excretion was equivalent to 1.5 to 3.7% of the larval respiratory energy loss. In juveniles, mean weight-specific ammonia excretion was relatively constant, ranging from 0.173 to 0.295 $\mu\text{gN mg AFDW}^{-1} \text{h}^{-1}$ with a mean of $0.220 \pm 0.046 \mu\text{gN mg AFDW}^{-1} \text{h}^{-1}$. Energy loss through juvenile ammonia excretion equaled $13.5 \pm 2.8\%$ of the respiratory energy loss.

DISCUSSION

Allometric exponents determined for the relationship between oxygen consumption and body size of larval and juvenile bay

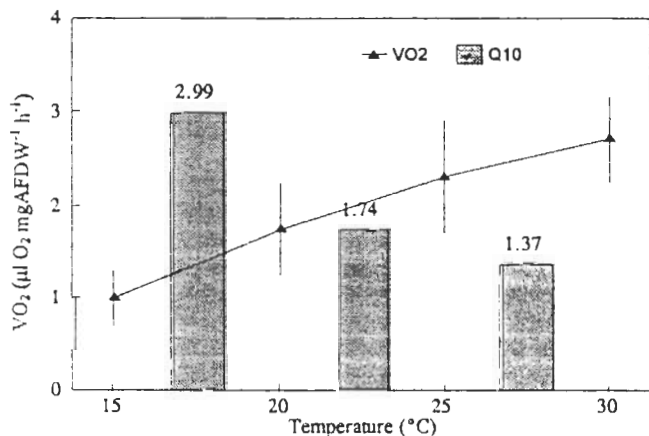


Figure 3. *Argopecten irradians concentricus*. Weight-specific oxygen consumption rate and Q_{10} values of juveniles versus temperature.

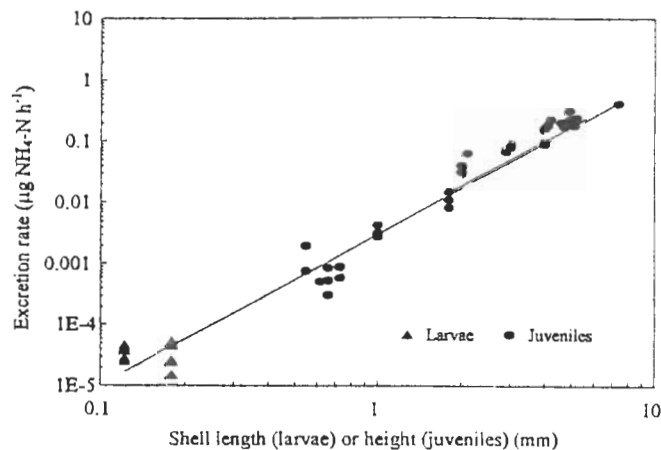


Figure 4. *Argopecten irradians concentricus*. Ammonia excretion rate of larvae and juveniles versus shell size.

scallops are very similar, being 0.921 and 0.905, respectively. These values are higher than those determined for adult bivalves, which range from 0.65 to 0.84, with a mean of 0.72 (Bayne and Newell 1983). A similar trend was found for the Japanese scallop *Patinopecten yessoensis*, in which a b -value of 0.81 was found for adults (Fuji and Hashizume 1974); whereas, a b -value of 1.39 was found for larvae (MacDonald 1988). High values of b were also reported for early stages of other bivalves; for example, 0.90 for *Mytilus edulis* larvae (Riisgård et al. 1981) and 1.09 for *Ostrea edulis* larvae (Beiras and Camacho 1994).

Weight-specific oxygen consumption of bay scallop larvae determined in the present study ranged from 3.0 to 0.6 $\mu\text{lO}_2 \text{ mg DW}^{-1} \text{h}^{-1}$ (6.2 to 20.5 $\mu\text{lO}_2 \text{ mg AFDW}^{-1} \text{h}^{-1}$). These values fell at the lower end of the range 4.6 to 15.2 $\mu\text{lO}_2 \text{ mg DW}^{-1} \text{h}^{-1}$ determined for larval *Argopecten irradians* (Siddall 1987) but were similar to the values of 1.6 to 10.0 $\mu\text{lO}_2 \text{ mg DW}^{-1} \text{h}^{-1}$ determined for larvae of other bivalves (reviewed by Holland 1978; Sprung 1984). Similar oxygen consumption was found for larvae of the Japanese scallop *P. yessoensis*, with a range of 5.2 to 11.6 $\mu\text{lO}_2 \text{ mg DW}^{-1} \text{h}^{-1}$ (calculated from MacDonald 1988).

Despite the similar values of b for larvae and juveniles of the bay scallop, the weight-specific oxygen consumption of larvae is 3 to 9 times higher than that determined for juveniles. High metabolic rates observed for larvae are likely a reflection of the energy expended in swimming during this planktonic stage. Swimming activity of bivalve larvae generally represents 8 to 50% of respiration loss (Zeuthen 1947). Sprung (1984) assumed that the energy expenditure of swimming larvae of *Mytilus edulis* was twice the amount needed to overcome the force of sinking (assuming the horizontal component equals the vertical component) and calculated that the energy used in locomotion was less than 2% of the respiration loss. He pointed out that his values were low, because metabolic effort is transferred to the action of motion with certain efficiencies (Klyashtorin and Yarzhombek 1973), and the cost of swimming could be much higher.

Projected oxygen consumption rates of bay scallop larvae were calculated by extrapolation using the allometric equation for small juvenile bay scallops of 0.5 to 2 mm shell height. If the calculated rates are assumed to be equivalent to the metabolic rates of non-swimming larvae, by comparing them with the metabolic rates measured for swimming larvae, we can estimate that the energy expended in swimming is 8.0% and 27.8% of the total metabolism

of larvae 120 μm and 180 μm in shell length, respectively. Larger larvae spend a greater proportion of energy on swimming than smaller ones, a trend that was also found in *Mytilus edulis* larvae (Sprung 1984). The estimation is in accordance with the observation that in *Crassostrea virginica* and *C. gigas*, oxygen consumption of larvae dropped approximately 40% when exposed to epinephrine, a metamorphosis inducer, probably because of the cessation of swimming activity (Haws et al. 1993).

Although weight-specific oxygen consumption decreases with increasing body size in small juveniles (< 2 mm shell height), it is independent of body size in larger juveniles (2–16 mm shell height), with a mean of 2.16 $\mu\text{LO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$. This value is higher than the mean rate of 1.11 $\mu\text{LO}_2 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ determined for adult *Argopecten irradians concentricus* (calculated from Barber and Blake 1985, assuming 85% of tissue dry weight is AFDW), consistent with the general trend that larger animals have lower weight-specific metabolic rates.

Juvenile bay scallops are well adapted to temperatures between 20–30 °C, as indicated by the low Q_{10} values over this temperature range (1.73, 20–25 °C; 1.37, 25–30 °C). This is in contrast with the case at low temperatures, where Q_{10} is much higher (2.99 at 15–20 °C). In adult bay scallops, a Q_{10} of 1.38 was obtained from VO_2 values published by Barber and Blake (1985) over a temperature range of 21–31 °C (calculated by Bricelj et al. 1987). This value is very close to the Q_{10} found for juveniles over 20–30 °C in this study. Thus, respiration of juvenile bay scallops responds to temperature in a manner similar to adults.

As compared to oxygen consumption, ammonia excretion has been a neglected area in the study of the physiological energetics of marine bivalves. In the present study, energy loss through ammonia excretion represented about 12% of the total energy loss (respiration + ammonia excretion) in juvenile bay scallops, making a significant contribution to the energy budget. Adult bay scallops *A. i. concentricus* were found to lose a similar percentage (7–15.5%) of energy through ammonia excretion (calculated from Barber and Blake 1985). In contrast, the energy loss in bay scallop larvae attributable to ammonia excretion is much less, comprising only 1.5–3.6% of the total energy loss. This may be a result of the high oxygen consumption rate, because weight-specific ammonia excretion of larvae is comparable with that of juveniles; whereas, weight-specific oxygen consumption is much higher.

The highest weight-specific rate of ammonia excretion was

found for 120 μm larvae. Bay scallop life history begins with a brief lecithotrophic stage, during which energy metabolism is supported by the energy reserve of eggs. As determined by Lu and Blake (1997), larvae of 120 μm shell length have started to feed on phytoplankton. The observed high ammonia excretion rate may indicate that these larvae cannot assimilate sufficient energy for their metabolic demand and still must partially depend on the energy reserves from the eggs, which consist mainly of protein (Lu 1996). In eyed larvae, protein metabolism is dramatically reduced, as shown by the low weight-specific ammonia excretion of larvae at this stage. Heavy utilization of protein occurs during metamorphosis, and, thus, a high rate of ammonia excretion would be expected for metamorphosing larvae. Data from the present study show that the smallest juveniles tested (500 μm shell height) did not display significantly higher rates of ammonia excretion than larger ones as expected, probably because they had finished metamorphosis and already lost the characteristics of metamorphosing larvae. Direct measurements on metamorphosing larvae may provide some evidence on this matter.

Weight-specific ammonia excretion found for juvenile bay scallops in the present study (146–250 $\text{ngN mg DW}^{-1} \text{ h}^{-1}$) is higher than that found for adults (72 to 140 $\text{ngN mg DW}^{-1} \text{ h}^{-1}$). This is consistent with the findings that weight-specific physiological rates (feeding and respiration) are higher in juveniles than in adults.

Oxygen consumption measured for larvae and juveniles of the bay scallop is comparable to that found for other bivalve larvae and juveniles (reviewed by Sprung 1984; Beiras and Camacho 1994), despite the fact that our measurements were made at a higher temperature (25 °C). Because metabolic rates are often determined at the optimum temperature range for each species, this may simply indicate that the bay scallop is adapted to the temperature encountered in its natural environment. Our data show that weight-specific ammonia excretion of larvae and juveniles is slightly higher but comparable to those determined for adult bay scallops, following the general trend that weight-specific physiological rates decrease as animals develop.

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