Filtration and respiration rates of the short-necked clam *Paphia undulata* (Born, 1778) (Mollusca, Pelecypoda: Veneridae) under laboratory conditions

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ABSTRACT

The filtration and respiration rates of various size classes (35-39.99, 40-44.99,45-49.99, 50-54.99 and 55-59.99 mm) of the short-necked clam *Paphia undulata* were measured in the laboratory. The effects of three light regimes (0 lux, 172.22 lux and 645.83 lux), three microalgal species (*Isochrysis galbana*, *Tetraselmis tetrahele* and *Chaetoceros calcitrans*) and four microalgal concentrations (10, 25, 50 and 100 x 10^4 cells ml^{-1}) on filtration rates were investigated. Mean filtration rate was highest (0.57 ± 0.04 $Lh^{-1}ind.^{-1}$) under total darkness. This can be attributed to the natural environment of this species which is characterized by silty substrate and low visibility. Filtration was also highest in the microalga *Isochrysis galbana* (0.67 ± 0.05). Rates initially increased from low to moderate microalgal concentrations (25 x 10^4 cells ml^{-1}) and decreased at higher concentrations. Filtration generally decreased with increase in clam size. Light intensity, microalgal species and microalgal concentration showed significant effects on filtration. Respiration of fed clams was higher (0.138 ± 0.026 ml $O_2h^{-1}ind.^{-1}$) than unfed clams (0.053± 0.025 ml O_2h^{-1} $nd.^{-1}$) and increased with clam size.

Key words: Paphia undulata, filtration rate, respiration rate, microalgae

INTRODUCTION

The short-necked clam *Paphia undulata* (Born, 1778) (Fig. 1) is a commercially important bivalve species in the Philippines and neighboring countries such as Thailand and Malaysia. The meat is consumed not only locally but a large quantity goes to the export market (Agasen et al. 1998; Pongthana 1990). It is locally known as "nylon shell" in Western Visayas. Agasen et al. (1998) reported that the species in Negros Occidental is overexploited. Del Norte-Campos & Villarta (2010) showed the worsened state of its exploitation not only based on the higher exploitation rate (E= 0.75) compared to that reported by Agasen et al. (1998) (E= 0.54) 13 years ago, but more importantly the decrease in the sizes of the catch and increase in proportion of immature clams in the catch. *P. undulata* has a moderately inflated and transversely elongate shell. Its outer surface is smooth and glossy, with fine, slightly oblique undulating grooves (FAO 1998). It is usually found in intertidal and sublittoral areas with muddy substrates at a depth of about 30 meters (FAO 1998).

Despite the number of scientific studies on this commercially important clam in the Philippines, there is no published information on its physiology. Knowledge of the feeding habits gained from observations of filtration rates and respiration rates in relation to body size is important in understanding the nutritional biology of this filter feeding bivalve.

The objectives of this study were to 1) determine the light condition, microalgal species and microalgal cell concentration at which filtration rate is highest and 2) compare the respiration rates (R) for unfed and fed clams in relation to body size of the short-necked clam *Paphia undulata*.

Figure 1. The short-necked clam *Paphia undulata*.

MATERIALS AND METHODS

Sample Collection and Laboratory Experiments

Paphia undulata clams were collected from the catches of hired compressor divers in Negros Occidental. The clams were brought to the UPV Institute of Aquaculture Hatchery and Biology laboratory in Miagao, Iloilo. The clams were grouped according to 5 mm size classes: 35-39.99, 40-44.99, 45-49.99, 50-54.99 and 55-59.99 mm to determine the effect of size on filtration and respiration rates. Mean tissue dry weights (g) for each size class were determined. Clams were acclimated in aerated UVFSW (ultraviolet treated 1µm-filtered seawater) at 37-38 ppt inside an air-conditioned laboratory at 26-27 ºC for 3-7 days before the start of the experiments. The salinity and temperature conditions used were similar to the clam's natural environment.

A. Filtration Rates

1. Light Intensity Experiment

Three light intensity treatments were used to determine the light condition at which filtration rate is highest: a) 0 lux (total darkness) by using 8L experimental basin covered with black plastic bag; b) 172.22 lux (ambient laboratory room lighting); c) 645.83 lux (using 20 Watts fluorescent illumination placed two feet from the containers). A light meter was used to measure the light intensity for each treatment. The clams were selected at random from the pool of acclimated clams grouped according to the five size classes. For each size class, one set up is composed of three clams and three set ups were used for all experiments. Each set up was placed in separate experimental basins and fed with a mixed microalgal diet in equal proportions of *Chaetoceros calcitrans*, *Isochrysis galbana* and *Tetraselmis tetrahele* with a final concentration of 3 x 10^5 cells ml^{-1}. This concentration corresponds to the levels usually found in aquaculture set ups (Duerr et al. 1998). The mixed microalgal diet was added with ultraviolet filtered seawater to obtain the desired

concentration and volume of the suspension by using the formula:

$$V_1 \times C_1 = V_2 \times C_2 \quad (1)$$

where V_1 is the volume of the undiluted microalgal culture in L; C_1 is the concentration of the undiluted microalgal culture in cells ml^{-1}; V_2 is the desired volume of the final microalgal suspension in L and C_2 is the desired concentration of the final microalgal suspension in cells ml^{-1}.

For each light treatment, control suspensions without clams were made under similar conditions to monitor the reproduction of the microalgae during the experiment. All set ups were aerated to enable proper mixing of the microalgae and to keep them in suspension. The volume of water that each bivalve filtered (F, Lh^{-1}) was determined from the experimental basins with a volume of 8 liters. A 5 ml sample was collected from the center of the experimental basins using a 5 ml syringe every 30 minutes for a period of 3 hours. The samples were stored in plastic canisters and fixed with 2 drops of Lugol's solution. Density of microalgal population in the samples was measured by direct microalgal cell count using a haemacytometer and a microscope. Three replicate counts were made for each sample using one mm^2 block with 16 squares. The filtration rate was determined using the formula used in del Norte-Campos (2004):

$$FR = V \times r \quad (2)$$

where r is the rate constant (h^{-1}) or the negative of the slope obtained from regressing ln C or cell concentration (cells ml^{-1}) against time (h) and V (= 8L) is the set up volume with the diluted microalgal suspension (L) and the clams. Filtration rate was expressed in L h^{-1} ind^{-1}. The light intensity with the highest mean filtration rate was chosen for the succeeding experiments. Two-Way ANOVA with replication was used to examine the effects of size and light intensity on filtration rates.

2. Microalgal Preference Experiment

After the light intensity experiment, microalgal feeding experiment was done. Unialgal cultures of *C. calcitrans* (cell diameter, c.d. = 5.4 ± 0.26 µm), *I. galbana* (c.d. =3.8 ± 0.45 µm) and *T. tetrahele* (c.d. = 10.2 ± 0.70 µm) with a concentration of 1.75 x 10^5 cells ml^{-1} each were used as food. This concentration was set after a series of unialgal feeding trials. These species were chosen because of their nutritive value and they are also considered as excellent food for many bivalves and crustaceans when fed alone or in combination (Kurosawa 1994; FAO 1996; 2004). Feeding was carried out under the preferred light resulting from the light intensity experiment. Procedures and analysis of samples were the same as in the preceding experiment using a different set of clams for each microalgal species set up. Water sampling was done at 45-minute intervals for a period of 4 hours and 30 minutes. The microalgal species with the highest mean filtration rate was chosen for the succeeding experiments. Two-Way ANOVA with replication was used to determine if there is a significant difference in filtration rates between sizes and microalgal species.

3. Microalgal Concentration Experiment

After the microalgal feeding experiment, four concentrations of the preferred microalgal species were tested: 10, 25, 50 and 100 x 10^4 cells ml^{-1} under the preferred light resulting from the light intensity experiment. Three set ups were made for each size class. Water sampling was done every thirty minutes for a period of 3 hours. Procedure and analysis of samples were the same as the preceding experiment using a different set of clams. The microalgal concentration with the highest mean filtration rate was chosen for the succeeding experiment. To show the relationship between filtration rate and size in terms of dry weight, filtration rates (L $h^{-1}ind.^{-1}$) were plotted against dry weights (g) of the organisms. Two-Way ANOVA with replication was used to determine if there is a significant difference in filtration rates between sizes and microalgal concentrations.

B. Respiration Rates

Respiration rates were measured for both unfed (ration = 0; starved for 24 h) and fed clams at 26-27 ºC and 37-38 ppt. The light condition, microalgal species and microalgal concentration used were based from the results of the preceding filtration rate experiments. Fed clams were given *Isochrysis galbana* at 25 x 10^4 cells

ml^{-1} under 0 lux for at least 15 minutes prior to the respiration measurements. For each of the 5 size classes, three set ups were made. The respirometer consisted of an Erlenmeyer flask filled with UVFSW to the brim (1.150 L total volume) with the mouth of the flask covered tightly with a rubber sheath. The YSI DO meter was first calibrated based on the procedure provided by the manufacturer. Preliminary runs with varying intervals and duration were conducted. A 20-min acclimation period following Clausen and Riisgard (1996) and Zhang et al. (2004) was allowed after which oxygen concentration was measured every 3 mins until the oxygen concentration approached 70% of the initial reading. Oxygen concentration was expressed in ml O_2 L^{-1}. A control set up with no clams was first made to test the stability of the chamber or to ensure that there was no leak. Respiration rate (ml O_2 h^{-1} $ind.^{-1}$) was determined as the negative of the slope of ln O_2 concentration versus time (h). To show the relationship between respiration rate and size in terms of dry weight, respiration rates (ml O_2 h^{-1} $ind.^{-1}$) were plotted against dry weights (g) of the organisms. One-Way ANOVA with replication was used to determine if there is a significant difference in respiration rates between sizes.

RESULTS

A. Filtration Rates

1. Light Intensity Experiment

It was observed that the clams opened their valves and extended their siphons when the microalgal suspension was given during the experiment. The filtration rate was highest under 0 lux (total darkness) with a mean value of 0.57 ± 0.04 $Lh^{-1}ind.^{-1}$ Smaller clams had higher filtration rates than bigger ones (Fig. 2).Two-Way ANOVA with replication showed that there was a significant difference in filtration rates between sizes ($F = 59.41$, $P < 0.001$) and light intensities ($F = 734.73$, $P < 0.001$). Interaction between light intensity and size was not significant ($F = 0.3102$, $P = 0.9561$) which suggests that these factors are independent.

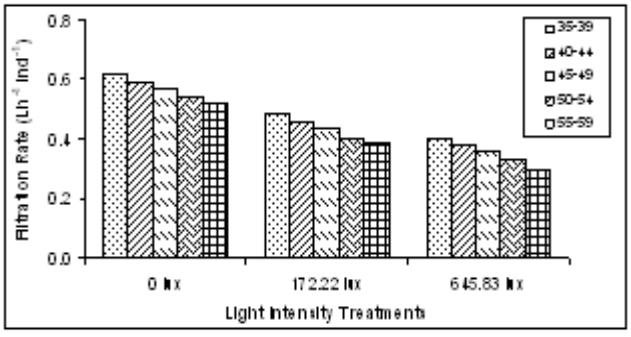

Figure 2. Filtration rates (L h^{-1} ind^{-1}) of various size classes of *P. undulata* under different light intensities (n = 45).

2. Microalgal Preference Experiment

The highest mean filtration rate of 0.67 ± 0.05 $Lh^{-1}ind.^{-1}$ was observed in the microalga *Isochrysis galbana*. Filtration rate also decreased with increasing size (Fig. 3) Two-Way ANOVA with replication showed that there was a significant difference in filtration rates between sizes ($F = 16.46$, $P < 0.001$) and microalgal species ($F = 4.70$, $P < 0.001$). Interaction between microalgal species and clam size was not significant ($F = 0.1845$, $P = 0.9913$) which also suggests that the two factors are independent.

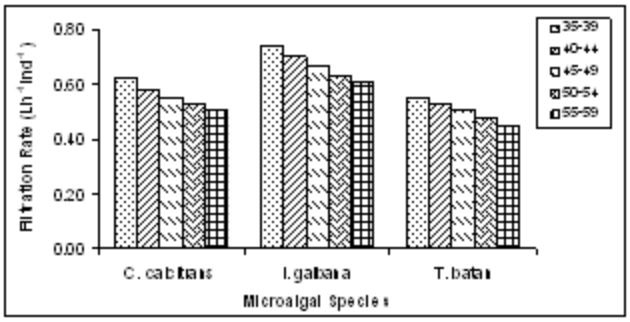

Figure 3. Filtration rates (L h^{-1} ind^{-1}) of various size classes of *P. undulata* at different microalgal species under 0 lux (n = 45).

3. Microalgal Concentration Experiment

The filtration rates of *P. undulata* increased from low to moderate concentrations (100,000 to 250,000 cells ml^{-1}). A decrease in filtration rate was observed at 500,000 cells ml^{-1}, decreasing further at 1,000,000 cells ml^{-1}. When the plastic bag cover was opened after the set up, the clams were observed to have narrow valve gape, their mantle edges were almost invisible, the exhalant siphon was narrow and there was a production of pseudofeces. More pseudofeces were observed at 500,000 and 1,000,000 cells ml^{-1}. The mean filtration

rate values for the different microalgal concentrations ranged from 0.23 ± 0.06 to 0.99 ± 0.07 $Lh^{-1}ind.^{-1}$. Filtration rates initially increased from low to moderate concentrations and decreased at higher concentrations (Fig. 4). Of these concentrations, the highest mean filtration rate of 0.99 ± 0.07 $Lh^{-1}ind.^{-1}$ was observed under 25 x 10^4 cells ml^{-1} thus considered as the optimum concentration of *I. galbana* for feeding. Filtration rates of *P. undulata* plotted against dry weights under the preferred light intensity, microalgal species and microalgal concentration were observed to decrease with an increase in size with a slope of 0.314 (R^2 = 0.692) (Fig. 5). Two-Way ANOVA with replication showed that there was a significant difference in filtration rates between sizes (F = 55.41, P < 0.001) and microalgal concentrations (F = 1794.23, P < 0.001). The interaction between these factors was not significant (F = 0.2538, P = 0.9931) which means that they are also independent.

B. Respiration Rates

Respiration rates of unfed clams were observed to increase with size, i. e. from 0.028 ± 0.002 ml O_2 $h^{-1}ind.^{-1}$ for 35-39.99 mm individuals to 0.089 ± 0.010 ml O_2h^{-1} $ind.^{-1}$ for 55-59.99 mm (Fig. 6). Respiration rates for fed individuals also increased with size. The respiration rate values obtained ranged from 0.099 ± 0.006 ml $O_2h^{-1}ind.^{-1}$ for 35-39.99 mm individuals to 0.166 ± 0.003 ml $O_2h^{-1}ind.^{-1}$ for 55-59.99 mm (Fig. 7). Mean respiration rate for all size classes was observed to be higher (0.138 ± 0.026 ml $O_2h^{-1}ind.^{-1}$) for fed clams than for unfed clams (0.053 ± 0.025 ml $O_2h^{-1}ind.^{-1}$). Respiration rates for fed clams plotted against dry weights (g) were observed to increase with size with a slope of 0.113 (R^2 = 0.825) (Fig. 8). One-Way ANOVA showed that there was a significant difference in respiration rates between sizes for both unfed (F = 31.99, P < 0.001) and fed clams (F = 22.18, P < 0.001).

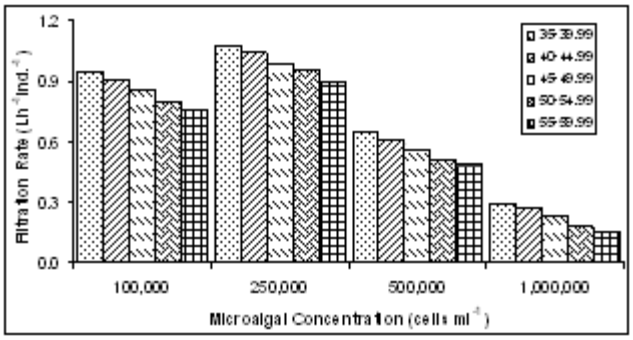

Figure 4. Filtration rates (L h^{-1} ind^{-1}) of various size classes of *P. undulata* at different microalgal concentrations (cells ml^{-1}) of *Isochrysis galbana* (n = 60).

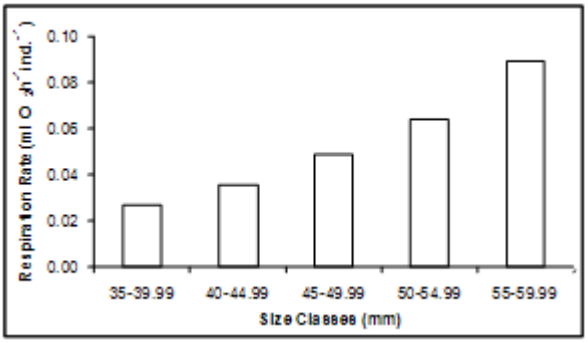

Figure 6. Respiration rates (ml O_2 h^{-1} $ind.^{-1}$) of unfed *P. undulata* versus size classes (mm) (n = 15).

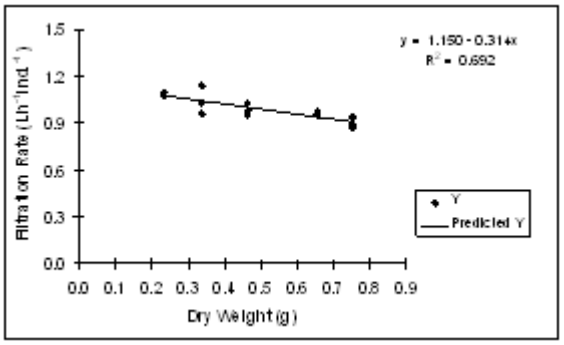

Figure 5. Filtration rates ($Lh^{-1}ind.^{-1}$) of *P. undulata* fed with *Isochrysis galbana* at 25 x 10^4 cells ml^{-1} under 0 lux versus dry weights (g) of 35-39.99, 40-44.99, 45-49.99, 50-54.99 and 55-59.99 mm size classes.

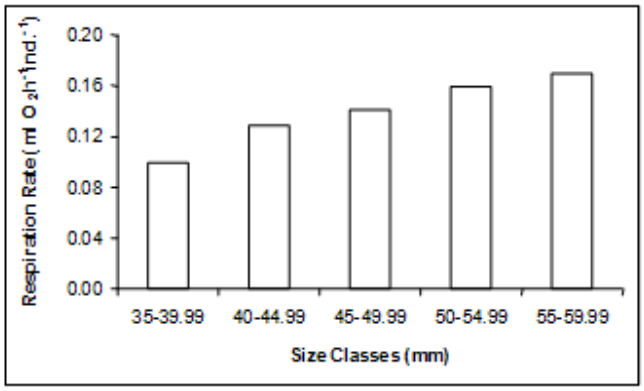

Figure 7. Respiration rates (ml O_2 h^{-1} $ind.^{-1}$) of unfed *P. undulata* versus size classes (mm) (n = 15)

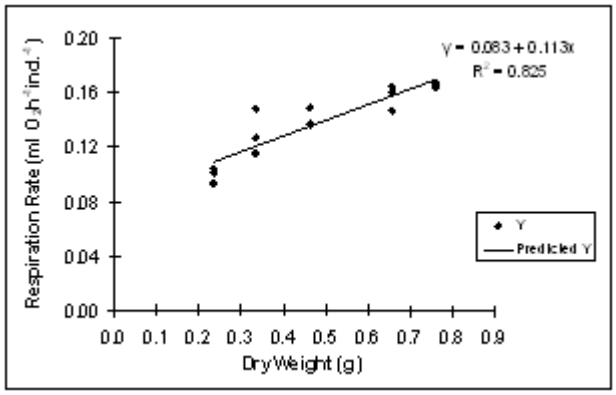

Figure 8. Respiration rates (ml O_2 h^{-1}ind.$^{-1}$) of fed *P. undulata* versus dry weights (g) of 35-39.99, 40-44.99, 45-49.99, 50-54.99 and 55-59.99 mm size classes.

DISCUSSION

Jørgensen (1990) reported that a relaxed and unrestrained bivalve fully opens its valves and extends its siphons. These conditions result to an efficient food uptake and maximum filtration rates. The highest filtration rate was observed under 0 lux (total darkness) treatment for all size classes used. *Paphia undulata* is a mud burrower adapted to dark conditions thus it may be sensitive to direct light. Similar results were observed by Corda & del Norte-Campos (1998) for the angelwing clam *Pholas orientalis* which is also a mud burrower. The high filtration rate of *P. undulata* under dark condition can be attributed to its natural environment which is characterized by a silty substrate and low visibility.

The difference in the filtration rates between microalgal species was significant. Although *I. galbana* may not be in the clam's natural habitat, the highest filtration rate (0.67 $Lh^{-1}ind.^{-1}$) of *P. undulata* to this microalga can be due to its smaller size (3.8 ± 0.45 µm, the smallest among the three microalgal species) which makes it much easier to ingest and faster to digest than *C. calcitrans* (5.4 ± 0.26 µm) and *T. tetrahele* (10.2 ± 0.70 µm). The results also suggest that algal size and quality (not availability) are the determining factors in food selection if the clam is given a variety of choices such as the three species used in the experiment. In addition, *I. galbana* has a higher nutritive value specifically its carbohydrate and lipid content which makes it an excellent food for many bivalves and crustaceans (FAO 1996; Taylor et al. 1997; Brown et al. 1999; Phatarpekar et al. 2000; FAO 2004). In bivalves, particle size and quality play a major role in filtration. Those that are too large are not utilized as food so they are rejected and those that are too small may pass through the filter (Dame 1996). The feeding mechanism of bivalves is said to be a process of actively sorting particles of different sizes prior to ingesting them (Jørgensen 1996). The result of this study agrees with that of Epifanio & Ewart (1977) wherein the oyster *Crassostrea virginica* had higher filtration rates for the smaller algae *Isochrysis* and *Thalassiosira* than the larger *Croomonas* and *Carteria*. This was also observed in the mussel *Limnoperna fortunei* which filter faster when fed with the smaller microalga *Scenedesmus sp*. than *Schizochytrium sp*. which is twice its size (Pestana et al. 2009).

The filtration rates of *P. undulata* initially increased from low to moderate concentrations and decreased at higher concentrations. A decrease in filtration rates at high concentrations were also observed in the surf clam *Paphies donacina* (Marsden 1999), the yellow clam *Paphia malabarica,* the mussel *Perna viridis,* the oysters *Crassostrea madrasensis* (Rajesh et al. 2001) and *Crassostrea gigas* (Gerdes 1983), the clam *Tapes decussatus* (Khalil 1996) and the mussel *Mytilus chilensis* (Navarro & Winter 1982). Low algal concentrations stimulate valve opening and filtration activity thus filtration rate is increased whereas high algal concentrations cause an overloading of the alimentary canal which in turn results to valve closure thereby reducing filtration rate (Riisgard 1988; Jørgensen 1990). In all the microalgal concentration set ups [in this present work], the clams were fully open and siphons extended during the experiment. It was also observed that filtration rate was reduced and more pseudofaeces were produced at higher microalgal concentrations of 500,000 and 1,000,000 cells ml^{-1}. These results showed that there is an inverse relationship between filtration rate and pseudofaeces production. Production of pseudofaeces or undigested food particles in mucus form implies that bivalves maximize energy gain during feeding by rejecting excess particles filtered by the gills (instead of utilizing more energy to metabolize excess particles). It also allows bivalves to regulate ingestion rate and prevent saturation of the alimentary system. Foster-Smith (1975) also

reported a decrease in filtration rates and increase in pseudofaeces production with increasing concentrations of the diatom *Phaeodactylum* in the mussel *Mytilus edulis*, the cockle *Cerastoderma edule* and the clam *Venerupis pullastra*.

Results of this study showed that filtration rates of *P. undulata* decreased with an increase in size in terms of dry weight. This implies that there is a higher energetic cost on filtration rate for larger clams than smaller ones. This is also supported by the results on the respiration rate experiment in this study which showed an increase in respiration rate with size. The higher filtration rates of smaller sized *P. undulata* can support its faster growth rate with K = 1.0-1.2 yr^{-1} (Agasen et al 1998; del Norte-Campos & Villarta, 2010) compared to subtropical bivalve species such as the pearl oyster *Pinctada maxima* with K = 0.72-0.79 yr^{-1} (Hart & Joll 2006). The observed higher growth rates of *P. undulata* before they reach sexual maturity (Agasen et al. 1998) around 40-50 mm confirms the need for smaller individuals to filter faster in order to support the energetic demands of growth and development. Filtration rates of the hard clam *Meretrix lusoria* also decrease with size (Chien & Hsu 2006). In contrast, the filtration rates of *Paphia malabarica, Perna viridis* and *Crassostrea madrasensis* (Rajesh et al. 2001), *Crassostrea gigas* (Ren et al. 2000, Gerdes 1983), *Pinctada margaritifera , Pinctada maxima* (Yukihira et al. 1998), *Chlamys farreri* (Kuang et al. 1997),*Tapes decussatus* (Khalil 1996) and *Mytilus chilensis* (Navarro & Winter 1982) increase with size. Filtration rate in general is said to increase with increasing body size (in W) and this is represented by an allometric equation $F = aW^b$ (Bayne et al. 1976; Winter 1978).

The respiration rate of *P. undulata* was lower (0.053 ± 0.025 ml $O_2 h^{-1} ind.^{-1}$) when starved and increased (0.138 ± 0.026 ml $O_2 h^{-1} ind.^{-1}$) with feeding. Similar results were obtained in the study of del Norte-Campos (2004) for the sunset clam *Gari elongata*. When a bivalve is starved, the rate of oxygen consumption declines to a standard rate or steady state due to a decreased filtration and ventilation activity. When a bivalve is fed, the oxygen consumption is in the active rate which is marked by an increased uptake of oxygen and ventilation activity (Navarro & Winter 1982). Feeding results to an increase in respiration rate two to three times compared to the standard rate of an organism at rest (Jørgensen 1990). There was an increase in the respiration rate of *P. undulata* by 0.085 ml $O_2 h^{-1} ind^{-1}$ with feeding. The respiration rates increased with size and this observation was also reported in the pearl oysters *Pinctada margaritifera* and *Pinctada maxima* (Yukihira et al. 1998) and the mussel *Mytilus chilensis* (Navarro & Winter 1982). Oxygen consumption increases with bivalve size according to the power function $R = aW^b$ (Bayne et al. 1976; Winter 1978; Dame 1996).

Based on the results of the study, filtration rate of *P. undulata* was highest under 0 lux (total darkness) treatment, microalga *Isochrysis galbana* and 25 x 10^4 cells ml^{-1} concentration of *I. galbana* under laboratory conditions. Filtration rates of *P. undulata* also decreased with an increase in clam size. Light intensity, microalgal species and microalgal concentration have significant effect on filtration rate. Respiration rate of fed clams was higher than unfed ones. Respiration rate also increased with an increase in clam size.

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