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Filtration and Oxygen Consumption in Mussels, *Mytilus edulis*, with and without Pea Crabs, *Pinnotheres maculatus*

ROSINA BIERBAUM[1]
SANDRA E. SHUMWAY[2]
Department of Ecology and Evolution
State University of New York
Stony Brook, New York 11794-5000

ABSTRACT: Filtration rates and oxygen consumption rates were measured in mussels (*Mytilus edulis*) with and without pea crabs (*Pinnotheres maculatus*). Noninfested mussels had a significantly higher rate of oxygen consumption per hour (0.578 ml ± 0.012) than did infested mussels (0.352 ml ± 0.012). There was no significant effect of pea crab size on mussel respiration. Filtration rates of infested mussels were significantly lower than those of uninfested mussels. Assimilation efficiency was not significantly affected by pea crab infestation. The relationship between body size and oxygen consumption in *P. maculatus* is given by the following equation: $\dot{V}O_2 = 0.139\ W^{0.626}$, where $\dot{V}O_2$ is oxygen uptake (ml h^{-1}), and W is dry weight (g). There was no difference between the sexes. It is concluded that the decreased oxygen consumption observed in infested mussels is not due to limitation of oxygen availability, but rather reflects a real metabolic response to the presence of the symbiont and the concomittant deprivation of food to the host. The effect is probably reversible, that is, damage can be compensated for after the symbiont has vacated the mussel, depending upon the period of infestation. Our results indicate that the mussels infested by pea crabs may be at an energetic disadvantage relative to mussels without pea crabs.

Introduction

Pea crabs (Pinnotheridae), considered to be commensals by some (Rathbun 1918; Dales 1957; Barnes 1980) and parasites by others (Orton 1920; Stauber 1945; Pearce 1966; Cheng 1967), are common inhabitants of the mantle cavity of marine molluscs. By clinging to the ctenidial surface with their legs, pea crabs remain positioned on the host's gill where they have access to the food aggregated by the mussel and they remove mucous strings passing toward the mouth (Orton 1920; Stauber 1945). As a result of the symbiont's activities, the gills of the host are often damaged (Christensen and McDermott 1958; Pearce 1966).

Stauber (1945) noted that, at the site where *P. ostreum* clings to its host, *Crassostrea virginica*, the gills become eroded and showed a "marked thickening." Additionally, there was extensive shortening (in height) of one or more demibranchs. Jones (1977) also reported that erosion of the gill demibranchs was common in mussels (*Perna canaliculusi*) inhabited by *P. novaezelandiae*. This damage was most conspicuous in the anterior part of the mussel, just posterior to the labial palps. McDermott (1961) cited gill and palp erosion in *M. edulis* associated with the presence of *P. maculatus* and suggested that demibranch erosion is particularly marked by the pea crab "in the early stages of development." Presumably, he is referring to the hard-shell stages of the male and immature female pea crabs. Whereas males remain of this form for their entire life, females are only hard-shelled for the mating swarm. The hardened carapace of these stages would be more irritating to the tissues of a mussel than the soft-shelled morphs characteristic of mature female pea crabs.

Pregenzer (1979) demonstrated that the presence of *P. hickmani* is associated with decreased pumping rate in *Mytilus edulis*; particles of neutral red dye were removed from the water more slowly by infested mussels than by those without symbionts. In addition to disruption of food strands, by altering the integrity of the gill, the pea crab affects the water current flowing through the mussel and may thereby influence oxygen consumption by the host. Since the gill is one of the major respiratory surfaces of the mussel, damage to individual filaments may result in impaired ability to extract oxygen from the water. However, a variety of responses is available to the mussel to regulate gas exchange at the gill, including an increased pumping (ventilation) rate or increased efficiency of oxygen extraction. Pea crabs may live in a bi-

[1] Present address: Oceans and Environment Program, Office of Technology Assessment, U.S. Congress, Washington, D.C. 20510.

[2] Present address and correspondence: Department of Marine Resources, West Boothbay Harbor, Maine 04575.

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valve for two to three years (Christenson and McDermott 1985; Pearce 1964), and the energetic demand of supporting a pea crab may impair host response to long- or short-term stresses.

In related studies to assess the effect(s) of pea crab infestation on the physiology of *Mytilus edulis*, Bierbaum (1985) has demonstrated that mussels with long-term resident pea crabs are in poorer physiological condition. These mussels exhibit lower glycogen reserves in gonadal tissue and lower total gonad weight whether measured at quiescent times or at peak gametogenesis. For these animals, lower condition index results in decreased reproductive output. Under some treatments, maximum egg size was less for mussels with large pea crabs. More recently, Bierbaum and Fersun (1986) demonstrated retarded host growth rates under conditions that were otherwise either only periodically suboptimal or optimal.

Many studies have reported detrimental effects of pea crabs on bivalve hosts. Gill lesions, found in infested *Mytilus edulis* (McDermott 1961) and *Crassostrea virginica* (Flower and McDermott 1952; Christensen and McDermott 1958; Haven 1959), were attributed to the crab scraping its chelipeds across the host's soft body parts while feeding. Pearce (1966) mentioned "an indentation in the gonadal mass" of a variety of host clams and mussels. Fibrous lumps or nodules, up to 1 cm in length, have been found on the mantle lips of bivalves harboring pea crabs (Stauber 1945; Dix 1973; Jones 1977). Krucyznski (1972) notes a reduction in dry meat weight of infested scallops when compared with uninfested scallops of the same size. Bivalve meat reduction was greater than the amount corresponding to the physical mass of the pinnotherid. Similarly lowered meat contents were reported for oysters (*C. virginica*) containing *P. ostreum* (Haven 1959), and the California mussel (*M. californianus*) containing *Fabia subquadrata* (Anderson 1975). Notched scallops containing pea crabs grew less over a three-month period than uninfested *Argopecten irradians* of similar size (Krucyznski 1972). Kruczynski (1975) proved that *Pinnotheres maculatus* ingests the food of *Mytilus edulis* by observing accumulation of ^{14}C in pinnotherid tissue after the host was fed labeled diatoms (*Nitzchia closterium* and *Thalassiosira pseudonana*). Pregenzer (1979) demonstrated that particles are cleared from water at a slower rate by mussels that contain pea crabs (*Pinnotheres hickmani*). Silas and Alagarswami (1965) reported that a hermaphroditic species of Indian oyster (*Ostrea cucullata*) normally exhibiting a 1:1 sex ratio becomes significantly skewed toward maleness when infested with pinnotherids.

This investigation was undertaken to determine if the presence of a pea crab, *Pinnotheres maculatus*, affects oxygen consumption and/or filtration rate in the mussel *Mytilus edulis*. The oxygen requirement of pea crabs relative to host oxygen consumption was calculated. Additionally, possible effects of pea crab sex and size on host oxygen uptake were examined.

Materials and Methods

Mytilus edulis from a population known to be heavily infested with pea crabs (69%) were supplied by the Marine Biological Laboratory, Woods Hole. The mussel bed was located near Gay Head, Martha's Vineyard, Massachusetts, at a depth of 40 m in May 1978. The animals were brought to the laboratory and maintained in Instant Ocean Aquaria at their natural ambient temperature (15 °C) and salinity (33‰). The mussels were fed daily with the flagellate *Tetraselmis suecica*. Cell densities were maintained at approximately 10^4 cells ml^{-1}, based on the assumption that mussels are feeding continuously in such a suspension (Willemsen 1952; Theede 1963; Walne 1972; Winter 1973; Thompson and Bayne 1974). The mussels were acclimated for 12 wk prior to experimentation.

Filtration rates were determined on individual mussels at 15 °C and 33‰ salinity. Animals were placed in flow through chambers (1 l) 8 h prior to the first measurement. No algal cells were present during this period. Seawater was pumped continuously through the chambers at a flow rate of 30 to 85 ml min^{-1}; mussel filtration rate does not depend on water flow rate in this range (Hildreth and Crisp 1976). Algal cells were added to the seawater from a concentrated source located upstream of the experimental chambers to maintain a constant food supply. Four measurements of filtration rate were made per mussel, each at 4-h intervals. During a measurement period, three samples were taken per mussel; the outflow water was collected for 3 min per reading and the values were averaged. Each mussel's filtration rate was sampled 12 times over the 16-h experimental period.

The flagellate *Tetraselmis suecica* was the food source, supplied in concentrations of 7,000 to 15,000 cells ml^{-1}. Within this range, mussels can feed continuously without fouling (Winter 1973; Thompson and Bayne 1974) and no pseudofeces were produced. A Coulter Counter was used to count the algal cells.

Filtration rate was calculated from the difference in particle concentration per unit time between inflow (sampled from control) and outflow (sampled from each mussel chamber) according to the following:

$$R_f = F(C_1 - C_2)/C_1$$

where R_f is filtration rate, F is water flow through

the vessel, C_1 is the concentration of particles in the inflow water, and C_2 is the concentration in the outflow water. If a mussel cleared less than the equivalent of 0.4 l h^{-1} during any 3 min test period, the measurement was discarded; such a low value indicates that the animal had temporarily ceased filtering.

Following the experiment, animals were removed from the chambers and sacrificed. Feces produced during the 16-h period were collected for each individual mussel and washed three times with 3% ammonium formate to remove salt. The samples were oven-dried in pre-ashed aluminum boats at 65°C for 12 h and weighed to the nearest μg on a Cahn microbalance packed with desiccant. Feces were then ashed at 430°C for 4 h in a muffle furnace and reweighed. Assimilation efficiency was calculated as the difference between the organic content of the food (*Tetraselmis suecica*, determined to be 88% by ashing) and the sample.

The equation describing the assimilation efficiency was defined (Conover 1966) as:

$$\text{Assimilation efficiency} = \frac{(F - E)}{(1 - E)(F)} \times 100$$

where F is the ratio of ash-free dry weight of the food to the total dry weight of the food and E is the same ratio in the feces. A total of 99 laboratory acclimated mussels were used in the experiments.

Oxygen consumption rate ($\mathring{V}O_2$; ml O_2 h^{-1}) was monitored in a closed system using a Radiometer PO_2 electrode as described by Crisp et al. (1978). Individual mussels were used in experiments and oxygen concentrations were never allowed to drop below 70% saturation. Mussels were placed in experimental chambers for 1 h prior to measurements, and chambers were aerated during this acclimation period. Animals were not fed during either the 1 h acclimation period or the experiment. All experiments were carried out at 15 °C and salinity of 33‰ and lasted approximately 2 h.

Mussels in the size range of 45 to 90 mm (approximately 0.8–1.6 g dry tissue weight) were taken at random for measurement. After measurement, the mussel was sacrificed. If a pea crab was present, $\mathring{V}O_2$ was immediately determined for the isolated crab by repeating the technique described above for mussel respiration. Both mussels and crabs were oven-dried at 60°C for 24 h to obtain dry weights. Oxygen consumption rates for mussels containing pea crabs were calculated by subtracting the $\mathring{V}O_2$ (crab) from the initial reading which actually represented the combined oxygen uptake for the mussel and crab. Crabs were sexed and no females were gravid.

Attempts were made to control host-switching by small pea crabs and to examine the reversibility or persistence of a pea crab effect on mussel metabolism. Efforts to cage individual animals in the laboratory prior to experimentation were unsuccessful. Fine mesh cages (1 mm) fouled quickly, and mussel mortality greatly increased under these conditions. Wider mesh cages (3 mm) allowed immature female and male pea crabs to escape. We were therefore unable to determine length of residence for small pea crabs before oxygen consumption measurements were made. However, field studies allowed us to estimate the frequency of pea crab movement between hosts. Suspending mussels 1 m above the sediment for 3 months resulted in a loss of 89% of those pea crabs less than 6 mm across the carapace. It appears that symbionts attempting to change hosts in this situation fall to the substrate and are lost from the population. (Switching attempts made on the benthos would be more successful; while pea crabs can maneuver somewhat, they cannot swim back up to a suspended population of hosts.) Large pea crabs (>6 mm, i.e., mature females) are physically unable to leave their hosts because the mussel gape is not large enough (Wells 1940; Irvine and Coffin 1960).

A multivariate analysis of variance was performed on the oxygen consumption of mussels with pea crab size as classes. Absence of a pea crab was designated size "0." Immature female and all male pea crabs (corresponding to a carapace width of less than 6 mm and an age of less than one year) were termed size "1." Female pea crabs greater than 6 mm in size with a globose body form characteristic of maturity (at least one year old) were classified as size "2."

Results

An analysis of variance showed a highly significant effect of size of pea crab ($F = 9.05$; $df = 2$; $p < 0.0009$) on oxygen consumption ($\mathring{V}O_2$) (Fig. 1). Crab-infested mussels had a significantly lower rate ($p < 0.001$) of oxygen consumption ($\mathring{V}O_2$; ml h^{-1}) ($\mathring{V}O_2 = 0.352$ ml $\pm$ 0.012) than did noninfested mussels ($\mathring{V}O_2 = 0.578$ ml $\pm$ 0.012) (Fig. 2). There was also a significant effect of mussel weight on weight-specific oxygen consumption (QO_2: ml O_2 h^{-1} g^{-1}) ($p < 0.0001$), but no interaction between size of pea crab and mussel body weight ($F = 2.2$; $df = 2$; $p < 0.13$). Contrasts of factor level means of QO_2 for (1) mussels with and without pea crabs and (2) mussels with small (<6 mm) vs. large (>6 mm) pea crabs were calculated (Neter and Wasserman 1974). Results indicate (Table 1) that the apparent size effect in the ANOVA on $\mathring{V}O_2$ resulted from the marked difference in means between all mussels with pea crabs and all mussels without pea crabs. The "presence/absence" of a pea crab is highly significant to mussel respiration

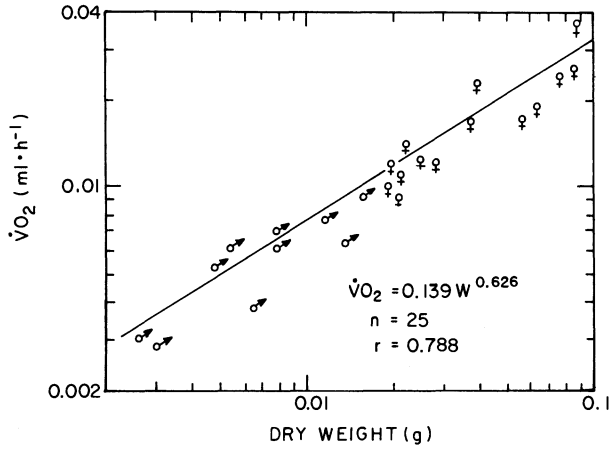

Fig. 1. Respiration rates of pea crabs, *Pinnotheres maculatus*.

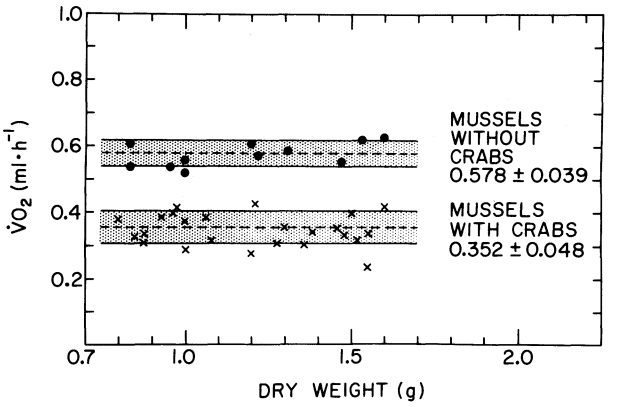

Fig. 2. Oxygen consumption by mussels with (×) and without (●) pea crabs.

(F = 15.95; df = 1; p < 0.0004) but there is no difference in oxygen uptake in mussels related to the actual size (and therefore, sex) of the symbiont (F = 2.59; df = 1; p < 0.12).

Table 1 presents the means and standard errors of QO_2 and body weight for mussels without pea crabs (0), with small crabs (1), and with large female pea crabs (2). Values for a Studentized Maximum Modulus Test show that "0" is significantly different from both "1" and "2"; whereas "1" and "2" are not detectably different from each other. The relationship between body size and oxygen consumption rate for *P. maculatus* is shown in Fig. 1. Although female pea crabs tend to be larger than males, there was no significant difference in slope for sexes treated separately and the data were subsequently combined.

The mean filtration rates decrease with increases in pea crab size: mussels with no pea crab average 2.66 ± 0.21 l h^{-1}; with small pea crabs, 2.11 ± 0.22 l h^{-1}; and with large pea crabs, 1.54 ± 0.20 l h^{-1}. Analysis of covariance for filtration rates of mussels maintained with and without pea crabs indicates that the presence of any size pea crab significantly decreases the filtration rate of the mussel and that large pea crabs have a more pronounced effect on filtration rate than do small crabs (F = 3.47; df = 2; p < 0.04). Pea crabs had no significant effect on assimilation efficiency (F = 1.31; df = 2; p < 0.27).

Discussion

Bayne et al. (1973) describe three levels of oxygen consumption in *M. edulis*: standard, routine, and active. The standard rate is associated with negligible filtration activity representing a low steady-state, for example, under starvation conditions. Maximum oxygen consumption—active—is a short-term response (6 h to several days) and is concommitant with high filtration rates when food is supplied to a starved animal. Respiration eventually declines to a steady state level intermediate between the standard and active levels (see Bayne et al. 1973, Fig. 1, p. 183). This routine level reflects acclimation to current conditions and occurs for example, within 2 wk following a large temperature change (Widdows and Bayne 1971), and within 10 d of normal feeding following a 2-wk period of starvation (Thompson and Bayne 1974). Whereas the standard and maximum levels represent responses to changed conditions, the routine level is established and maintained as long as ambient conditions are above the maintenance requirement. Measurements of oxygen consumption in this study were of animals that had been maintained in the laboratory under constant tempera-

TABLE 1. Effect of pea crabs on QO_2 (ml O_2 h^{-1} g body wt^{-1}) in mussels, *M. edulis*. 0 = pea crab absent; 1 = immature female or male pea crab (<6 mm); 2 = mature female pea crab (6 mm or larger).

		Means			
Size crab	N	QO_2	Std. Error	Body Weight	Std. Error
0	11	0.50	0.032	1.18	0.082
1	14	0.29	0.025	1.25	0.069
2	10	0.33	0.021	1.13	0.084

Studentized Maximum Modulus (GT_2) Test for Variable: QO_2
Alpha = 0.05
Confidence = 0.95 df = 29 MSE = 0.0018061
Critical Value of Studentized Maximum Modulus = 2.527

Comparisons Significant at the 0.05 Level are Indicated by '***'

Size Pea Crab Comparison		Confidence Limit	Between Means	Confidence Limit	
0	−2	0.13	0.18	0.23	***
0	−1	0.17	0.21	0.26	***
2	−0	−0.22	−0.18	−0.13	***
2	−1	−0.01	0.04	0.08	
1	−0	−0.26	−0.21	−0.17	***
1	−2	−0.08	−0.04	0.01	

ture (15°C), constant salinity (33‰), and high food conditions. Our data and that of Bierbaum (1985) suggest that the presence of a pea crab deprives the mussels of sufficient food, and it is therefore likely that maintenance requirements are not met for infested mussels. Because the hosts were confined during oxygen measurements, rates reflect primarily ciliary action as well as some residual expenditure related to food processing. Locomotion and byssus production did not occur during measurement.

The experimental mussels were sacrificed just prior to spawning. Gametogenesis is a time of particularly high energetic demand, usually corresponding to high levels of oxygen consumption. Thus the rates measured here reflect the routine respiration rates for uninfested mussels for an energetically demanding time of the year. Differences in metabolic rate between infested and uninfested mussels thus represents the energetic "cost" of harboring a pea crab.

There are several possible explanations for the observed decrease in rate of oxygen uptake in crab-infested mussels. 1. Lowered oxygen availability due to respiration of the crab. 2. Reduced "effective" gill area in the mussel due to pea crab damage. 3. Slower metabolism in mussels with pea crabs reflecting a generally weakened condition from continual stress of supporting a symbiont. 4. Starvation of mussels infested with pea crabs.

Seawater at 15°C, 33‰ salinity contains approximately 5.8 ml O_2 l^{-1} (100% saturation). A mussel of 1 g dry weight pumps approximately 2 l h^{-1} of water (Bayne 1976) and uses approximately 0.6 ml O_2 h^{-1}, which should allow sufficient oxygen for metabolic requirements. The rate of oxygen consumption of an average crab (0.02 g) with respect to that of its host mussel (1.0 g) is inconsequential in that it only amounts to about 2% of that of the mussel. Data on the respiratory rates of pea crabs are scant. Craig (1974) reported on the effects of temperature on oxygen consumption of two species of commensal crabs, *Pinnixa chaetopterna* and *Polyonyx gibbesi.* These species are commonly associated with tube-forming polychaetes.

Elliot (1981) published a detailed study of the respiration rates for pea crabs, *Pinnotheres hickmani,* during various developmental stages and on the effects of temperature and light on those rates. The rates reported here for *P. maculatus* are similar to those reported previously for the other three species. Elliot (1981) reached a similar conclusion in the case of mussels infested by pea crab, *P. hickmani.* We conclude that the decreased oxygen consumption observed in infested mussels is not due to any limitation of oxygen in the water, but reflects a real metabolic response to the presence of a pea crab, such as starvation and/or a generally weakened condition.

Bierbaum (1985) and Bierbaum and Ferson (1986) stated that gill lesions occur in mussels infested with pea crabs. Distinguishing which of the two proposed mechanisms (gill damage or decreased metabolic rate) is responsible for observed differences in mussels with and without pea crabs is difficult; the physiological result will be effectively the same in either case. Bayne et al. (1976) note that cilial movement bears an exponential relationship with oxygen consumption; therefore, small changes in gill movement cause large changes in respiration rate. This is consistent with gill damage cited by several researchers in conjunction with the presence of pea crabs. Reduced ciliary activity due to tearing of the gills or disruption of water currents would result in a reduction in oxygen consumption for a routine ventilation rate. This is analogous to the response of mussel respiration under poor nutrient conditions where part of the gill is inactive. Dral (1968) demonstrated that under conditions of low food, *Mytilus* may actually use less than half of the gill area to move water through the mantle cavity. Such a decrease in surface area would diminish gas exchange and the effectiveness of oxygen extraction, thereby decreasing respiration.

Many other studies have found reduced respiration rates to be a likely response to varying nutrition. Bayne et al. (1975, Table 1, p. 678) showed that under low food rations, oxygen consumption of mussels is less than at high ration. Similarly, under artificially imposed conditions of low oxygen, feeding rate is depressed. Bayne et al. (1976) note that under normal circumstances, PO_2 is high but, teleologically speaking, food input must be maximized. The strategy adopted is the development of a large surface area with a high ventilation rate and a low oxygen utilization efficiency. During regulation to low PO_2, adjustments to provide an adequate oxygen supply are essential, and a reduction in food intake is inevitable.

However, Bayne et al. (1973) found that over a range of temperatures from 5° to 25 °C, normally fed *Mytilus* showed a remarkable capacity to adjust its rate of oxygen consumption to constant or routine levels. Presumably, such perturbations as low food and temperature changes, produce predictable but reversible changes in oxygen consumption; if the perturbation is continual, metabolic rate may equilibrate at a lower level.

Because mussels with pea crabs have reduced oxygen consumption levels relative to uninfested mussels maintained under the same conditions, the symbionts must be considered a detriment. If damage to the mussels is reversible, respiration rates

would be expected to return to routine levels following the cessation of the stress, that is, if a pea crab vacates the bivalve.

Based on this estimate of a high rate of switching by male and immature female pea crabs, several of the mussels measured for oxygen uptake should have recently acquired or lost a small pea crab. Figure 3 shows the oxygen consumption for mussels without pea crabs (upper line) and with pea crabs (lower line). On the latter, mussels with large pea crabs (>6 mm) are marked by closed circles, and those with small pea crabs by open circles. The open circles could represent recently invaded hosts; likewise, mussels without pea crabs plotted on the upper line may have just been vacated. Because these points do not grade into each other or overlap, it appears that mussels adjust to the presence or absence of a pea crab very quickly. This suggests that the effects of a pea crab on host respiration are reversible, and that once a crab is removed, feeding rates can return to high levels and any residual gill damage may be compensated.

While a pea crab is resident, however, the average rate of oxygen consumption for a mussel is 0.30 ml O_2 h^{-1} g dry wt^{-1} (QO_2). This is very close to the QO_2 measurements of 0.27 for the standard respiration rate of *Mytilus* at 15 °C, measured by Bayne et al. (1973), and lends further evidence to suggest nutritive stress in infested mussels. Bayne et al. (1975) showed that during starvation, oxygen uptake of *M. edulis* decreases metabolism to a standard rate (a maintenance level) and similar reductions have been found in *M. californianus*. Levels of oxygen uptake for mussels with symbionts average 60% that of uninfested mussels. Such a marked reduction in oxygen consumption summed over a long period of time should be reflected in several other physiological parameters, for example, growth rates and gonadal development. Bayne et al. (1975) noted that starved, inactive animals are unable to acclimate to temperature changes over the long-term. Apparently, adaptiveness to additional stresses is contingent on the energetic status of the animal.

We have shown that both small and large pea crabs decrease a mussel's metabolic rate; these effects are immediate, but potentially reversible if a small crab vacates the host. Continued depression of respiration and filtration rates results in decreased energy reserves and reduction of gonadal material (Bierbaum 1985). Ultimately, the effects of reduced metabolism and depleted energy reserves become irreversible. When the strain of supporting a pea crab is exacerbated by environmental perturbations (e.g., low salinity or poor nutrient conditions), some negative effects are detected sooner. For example, mussels in a low nutrient lo-

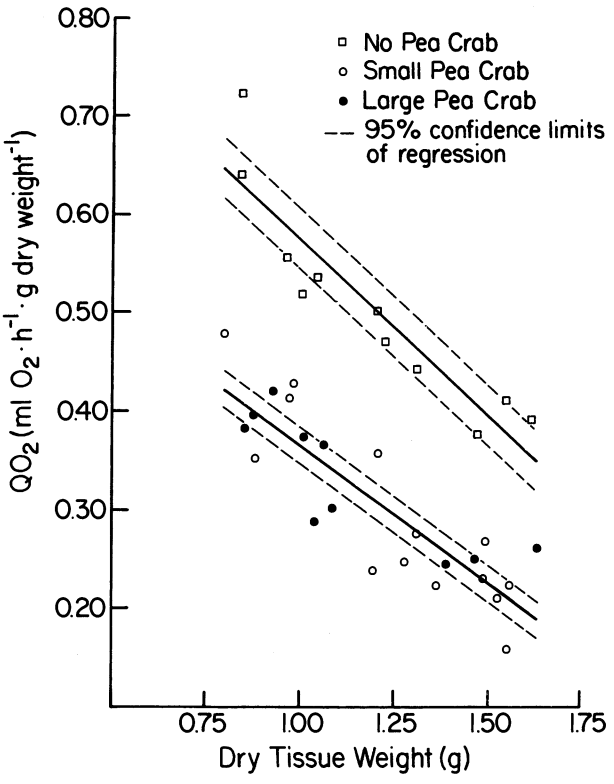

Fig. 3. The relationship between oxygen consumption and body weight in mussels with and without pea crabs.

cation and containing a large pea crab have significantly decreased growth rates (over a 3-month period) when compared to mussels without pea crabs (Bierbaum 1985). There is no detectable difference in shell increments for mussels with and without pea crabs under high nutrient conditions over the same short growth period. Other deleterious effects associated with the presence of a large pea crab such as smaller follicle size in male mussels, egg size in females and total gonad glycogen also become more apparent (Bierbaum 1985). Mussels with reduced oxygen consumption associated with the presence of a symbiont are presumably in a depleted physiological condition to withstand other environmental perturbations; therefore, the consequences for hosts harboring a pea crab depend both on the length of residence and favorability of the environment. The effects range from immediate and reversible (slower metabolic rate) to cumulative but reversible (decreased gametogenesis) to cumulative and irreversible (altered shell shape) (see Bierbaum 1985). Over the short-term, mussels respond to pea crab infestation and the resulting food deprivation by decreasing metabolic rate. Over the course of a season, effects become cumulative and are manifested in decreased energy reserves and reduction of gonadal

material. Over several years, the cumulative effects of a reduced metabolism and energy reserves become irreversible. Our results suggest that even under favorable conditions, the infested mussels are at an energetic disadvantage relative to mussels without pea crabs.

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