

SEASONAL CHANGES IN OXYGEN CONSUMPTION OF THE GIANT SCALLOP, *PLACOPECTEN MAGELLANICUS* (GMELIN)

SANDRA E. SHUMWAY, JANEEN BARTER, AND
JAMES STAHLNECKER

State of Maine Department of Marine Resources
West Boothbay Harbor, Maine 04575

ABSTRACT Rates of oxygen consumption ($\dot{V}O_2$) by the giant scallop, *Placopecten magellanicus* were measured monthly over a period of fifteen months. In addition, scallops were acclimated to a series of temperatures (T_a) in the laboratory and the rates of oxygen consumption monitored. In acclimated animals, $\dot{V}O_2$ increased with experimental temperatures with a concomitant decrease in Q_{10} value. Although the $\dot{V}O_2$ of scallops from the field was consistently higher than values obtained from acclimated scallops at similar temperatures, the general trend was in keeping with rates which varied with the environmental temperature. It was shown that the seasonal changes in respiration rate are intimately related to changes in the gametogenic cycle with the highest rates exhibited during the summer months (ripening of the gonads) and the lowest rates during the winter months. While the observed changes in metabolic rate generally follow the changes in environmental temperature, it is suggested that seasonal changes in food availability and reproductive stage have a greater affect on $\dot{V}O_2$ than temperature *per se*.

KEY WORDS: Scallop, *Placopecten magellanicus* oxygen consumption

INTRODUCTION

The giant scallop, *Placopecten magellanicus*, represents one of the major fisheries in the Gulf of Maine. The species supports a large commercial fishery throughout its range and is currently considered as a prime species for aquaculture efforts. In spite of its economic importance, a recent review of the existing literature on this species (Shumway et al., in preparation) and the development of a preliminary model for the giant scallop ecosystem by Campbell (1985) revealed a number of aspects of the biology of this species that are still in need of investigation. These information gaps severely limited our ability to accurately model the system and included such basic data as seasonal changes in fecundity, growth rate, food availability, respiration rates and the effects of temperature on these parameters. A number of studies were undertaken to fill these gaps and the results have been reported elsewhere (Langton et al., 1987; Shumway et al., 1987; Schick et al., 1987; Barber et al., 1988; Schick et al., 1988a,b).

There are few data available on respiration rates of scallops in general, or *P. magellanicus* in particular. Vahl (1978), Shafee (1982), Shafee and Lucas (1982), Barber and Blake (1985), MacDonald and Thompson (1986a,b) and Bricelj et al. (1987) have all reported on seasonal changes in the metabolic rate in various scallop species and their results are summarized in the Discussion.

In a recent series of papers, MacDonald and his co-workers (1985a,b; 1986a,b; 1987) reported on the influences of temperature and food availability on the ecological energetics of *P. magellanicus* from Newfoundland. In his studies, water depth was used as a model for variable food supply and temperature. Water depth *per se* was not of particular interest, but rather the conditions at those depths. Although his station depths were only separated by approximately 20m, he was able to demonstrate marked differ-

ences in growth rates, gamete production, reproductive effort and other parameters as a result of differences in food and temperature. Our studies extend the depth factor (and associated environmental factors) considerably in that our stations range from approximately 20 to 180 m.

Since the peculiarities of any given environment affect the fishery locally, it is important to establish a comprehensive data base for individual areas if fishery management is to be efficient. Further, before any major aquaculture efforts can be undertaken, it is essential to have a firm understanding of the species' biology and the effects of variations in environmental factors on their performance. The majority of energy losses, or 'costs of living' (Sibley and Calow, 1986) can be measured as heat losses or respiration rates. In the present paper, we report on the seasonal changes in respiration rate for *P. magellanicus* in coastal Maine waters. The study is part of an ongoing research program designed to establish such a data base for *P. magellanicus* in Maine waters and the subsequent production of a model to describe growth and spawning in this species.

MATERIALS AND METHODS

Specimens of the sea scallop, *Placopecten magellanicus* Gmelin, were collected by divers at a depth of approximately 20m, from the lower Damariscotta River on a monthly basis between October 1984 and January 1986. Immediately after capture, the animals were transported to the laboratory, scrubbed free of epiphytes and maintained in running seawater from Boothbay Harbor prior to use in experiments. Vahl (1978) found that oxygen consumption in *Chlamys islandica* decreased during the first 20 days in the laboratory. Preliminary experiments indicated that no differences in rates of oxygen consumption ($\dot{V}O_2$) were apparent between the day of capture and up to 4 weeks after capture, as long as the temperature remained constant.

Since it was our intention to monitor, as closely as possible, the changes in $\dot{V}O_2$ under ambient conditions, measurements were made within 1–2 days of capture. Seawater temperatures at the collection site were within 2°C of the seawater in the laboratory and all experiments were run at ambient temperatures. Each month, $\dot{V}O_2$ was determined on scallops of a wide size range (0.01–18g dry tissue weight; approximately 10–130 mm shell height). The number of individuals measured varied (see Table 1). Dry tissue weights were obtained by oven drying to constant weight at 60°C for 24–48h.

Rates of oxygen consumption were determined for individual scallops using a Radiometer oxygen electrode in a closed system (Taylor and Brand, 1975; Shumway, 1983). Preliminary experiments indicated that $\dot{V}O_2$ was independent of oxygen tension (PO_2) only to approximately 70% saturation. Similar results have been shown for other species of scallops (van Dam, 1954; Vahl, 1978; MacKay and Shumway, 1980). Therefore, ambient PO_2 was not allowed to drop below approximately 80% saturation. Sexes were not separated. Since the animals were freshly collected and $\dot{V}O_2$ measurements taken immediately, the rates reported for the seasonal study are assumed to represent a 'routine' rate of oxygen consumption (see Bayne, 1976; Bayne and Newell, 1983).

Results are expressed as least squares regression according to the formula:

$$Y = aW^b$$

where Y is the predicted rate of oxygen consumption in ml oxygen hour⁻¹, W is the dry tissue weight in g, a is the intercept and b is a constant. All regression and statistical

TABLE 1.

Parameters of the regression equations relating oxygen consumption ($\dot{V}O_2$; ml $O_2 \cdot h^{-1}$) to tissue dry weight (W; g) for *Placopecten magellanicus*. Data were fitted to the equation: $\dot{V}O_2 = aW^b$. Values preceded by an * are significantly different ($P < 0.05$) from the previous value. Values of b are given \pm s.e.

DATE	b	a	r ²	n	T (°C)
20 Oct 1984	0.838 \pm 0.029	0.363	0.992	19	10
27 Nov 1984	0.740 \pm 0.039	*0.304	0.969	12	9
28 Dec 1984	0.714 \pm 0.052	*0.220	0.949	12	6
29 Jan 1985	0.761 \pm 0.049	*0.069	0.964	11	1
26 Feb 1985	0.755 \pm 0.057	*0.196	0.951	11	4
29 Mar 1985	0.752 \pm 0.037	*0.283	0.976	12	5
25 Apr 1985	0.848 \pm 0.026	*0.259	0.990	13	8
25 May 1985	0.862 \pm 0.062	*0.344	0.960	10	11
3 Jul 1985	0.837 \pm 0.053	*0.386	0.968	10	17
31 Jul 1985	0.837 \pm 0.037	0.399	0.985	10	19
5 Sep 1985	0.820 \pm 0.030	0.428	0.984	14	16
1 Oct 1985	0.831 \pm 0.104	*0.361	0.875	11	15
31 Oct 1985	0.814 \pm 0.039	*0.382	0.973	14	11
15 Nov 1985	0.736 \pm 0.039	*0.281	0.962	16	9
10 Jan 1986	0.740 \pm 0.081	*0.162	0.903	9	3

analyses were carried out on an IBM 370 computer using SAS programs (SAS, 1985).

For experiments to determine the effects of acclimation temperature on the scallops, animals were collected as above and maintained in ambient seawater and constant temperatures for 3 weeks prior to use in experiments. No food other than that which was available in the seawater supply was provided. For temperature acclimation which involved large changes in temperature, a step-wise series of acclimations was carried out whereby animals were maintained at an intermediate temperature for at least a week prior to being subjected to the final temperature of acclimation. This procedure eliminated mortalities due to temperature shock. Metabolic rates (routine) were measured as described above.

RESULTS

Figure 1 shows the weight-specific rates of oxygen consumption for scallops acclimated to a series of experimental temperatures. There was a steady increase in the rate of oxygen consumption with increasing temperature coupled with a decrease in the calculated Q_{10} value. These data have been used to calculate the 'expected' $\dot{V}O_2$ at the various environmental temperatures (shown in Figure 2). With the exception of January, the observed rates of oxygen consumption were higher than the predicted values; however, the general trend was in keeping with rates that varied with the environmental temperature. Similar Q_{10} values for routine metabolic rate were reported for *C. varia* by Shafee (1982).

The monthly rates of oxygen consumption by *P. magellanicus* are summarized in Table 1. While the slopes of the lines are not significantly different as a group or individually, significant differences ($p < 0.01$) between levels of $\dot{V}O_2$ were found. The seasonal changes in $\dot{V}O_2$ are summarized in Figure 2 where it can be seen that the oxygen consumption rates generally followed the changes in environmental temperature. There were two major exceptions to this trend: 1) during the late winter and early spring where oxygen consumption rates increased at a much more rapid rate than would be predicted from the temperature changes alone and 2) during the late spring and early summer when rates of oxygen consumption remained fairly constant despite a fairly steep rise in environmental temperature. In addition, two significant decreases in $\dot{V}O_2$ occurred between March and April (when the temperature actually increased by 3°C) and between August and September (when the temperature only decreased by 1°C). Both of these decreases are significant ($p < 0.05$) and are indicated in Figures 2 and 3 by arrows.

DISCUSSION

Metabolic rate in scallops has been studied by few workers. Vahl (1978) monitored the changes in metabolic rate of the Iceland scallop, *Chlamys islandica* (O. F.

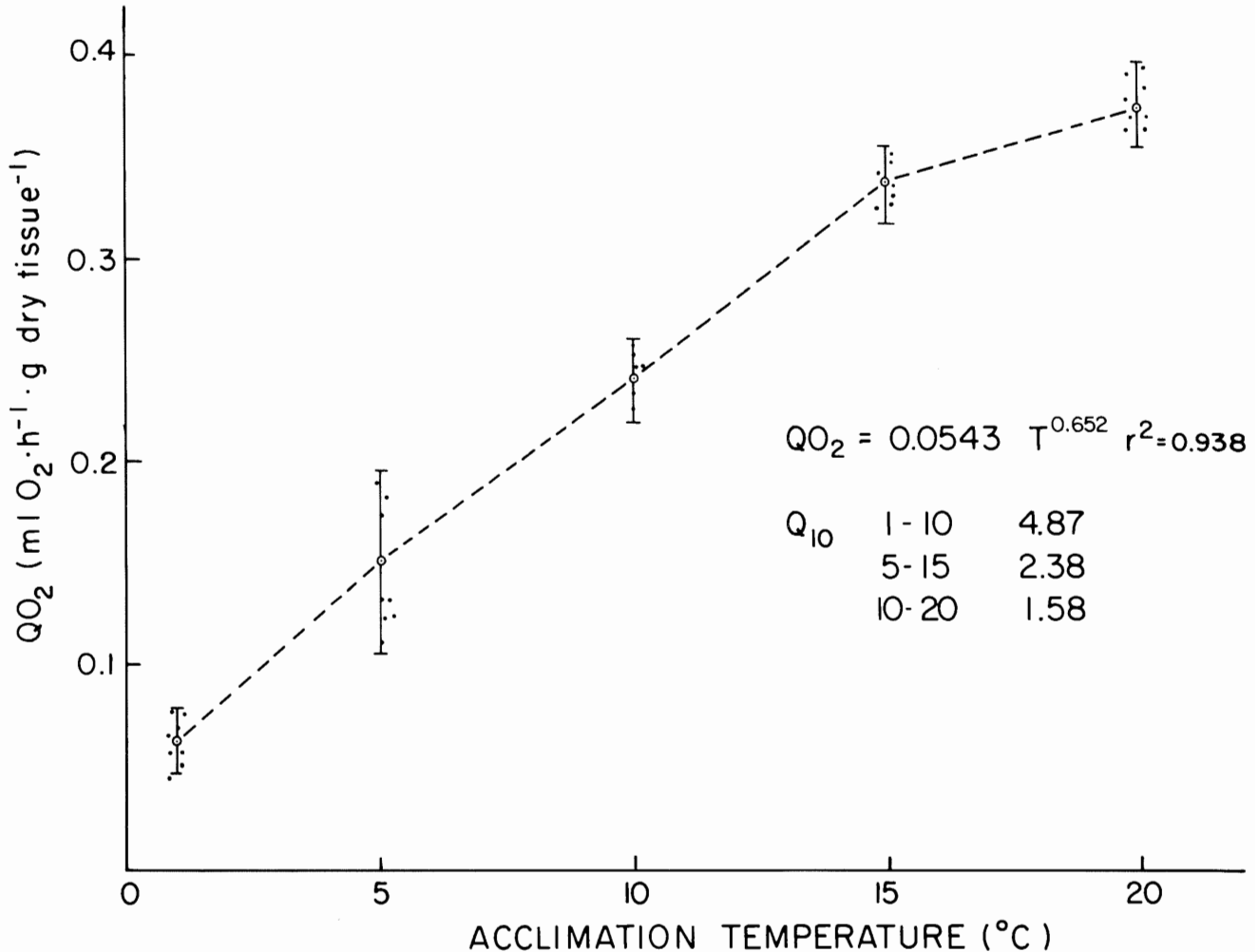


Figure 1. $\dot{V}O_2/T_a$ curve for *Placopecten magellanicus* over the range of normally experienced temperatures. Data are plotted for a standard scallop of 1 g dry tissue weight.

Muller) throughout the year. In addition, he determined seasonal changes in the relationship between body size and respiration rate. His results showed that the rate of oxygen uptake increased rapidly in the beginning of April, reached maximum levels in late April and May and thereafter decreased. This corresponds to the later part of the growth period of both shell and gonad in this species. He concluded that the seasonal variations in oxygen consumption exhibited by *C. islandica* were not explained by the seasonal variations in temperature but more likely were due to seasonal variability of the food supply. In addition, he showed significant seasonal variation in the dependence of oxygen consumption upon body weight. The exponent of the allometric equation relating $\dot{V}O_2$ to body weight for the period May-February was 0.78 while the exponent for the period March-April was approximately 0.90.

Shafee (1982) reported a common slope of 0.72 for all seasons in the Black scallop, *Chlamys varia*. He demonstrated a marked seasonal fluctuation in respiration rate with highest values in August/September and lowest values

during February/March corresponding to periods of high temperature/peak gonad development and low temperature and little or no gonad activity respectively. Similarly, Bricej *et al.* (1987) found that the oxygen consumption of the bay scallop, *Argopecten irradians irradians* (Lamarck) closely paralleled seasonal changes in water temperature. They showed that temperature explained 93% of the seasonal variation in metabolic rate with minimum values recorded in January/February and maximum values during June/July.

In the only published account on *P. magellanicus*, MacDonald and Thompson (1986) measured seasonal changes in metabolic rate and found no significant differences in weight exponents (common slope = 0.89), but significant differences in metabolic rates between seasons. Measured rates were lowest during January-May and much higher during summer, June-September. Further, they found differences with depth in that rates for scallops from shallow water were highly correlated with water temperature whereas those from deeper water (31 m) were not.

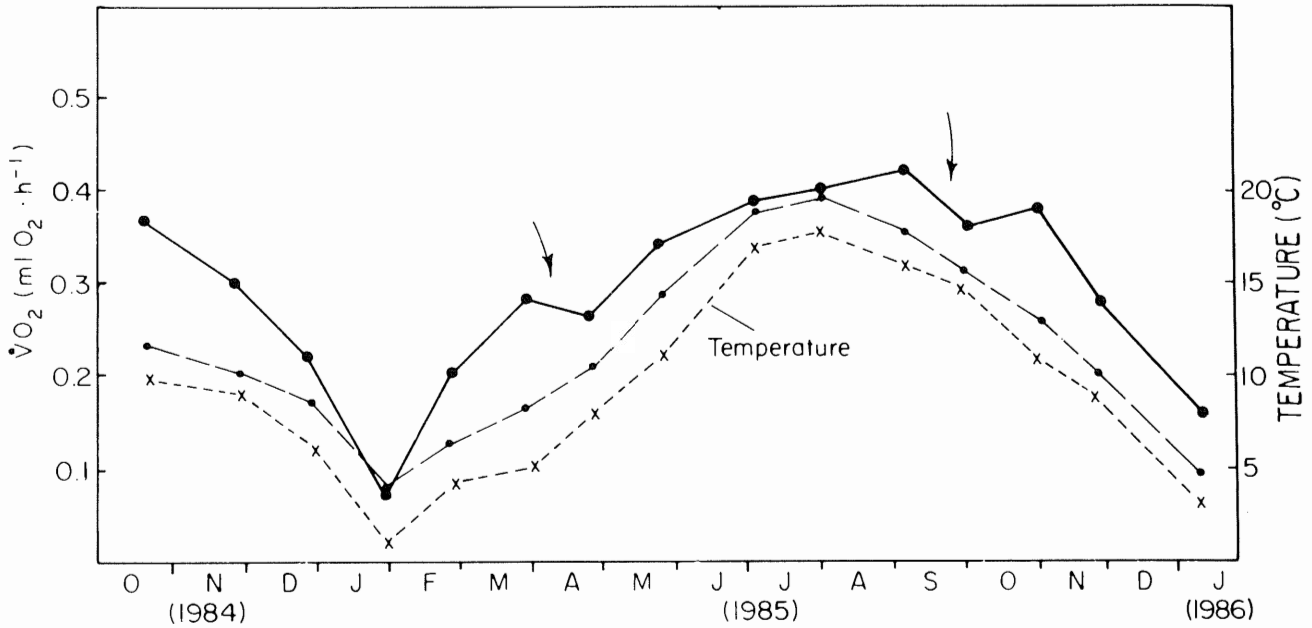


Figure 2. Seasonal changes in oxygen consumption of *Placopecten magellanicus*. (●—●) represents measured $\dot{V}O_2$, (●—●) expected rates of $\dot{V}O_2$ based on acclimation data (see Figure 1) and the environmental temperatures (x—x). Data presented are for a standard animal of 1g dry tissue weight.

Seasonal changes in metabolic rate reflect the various interactions between food availability, temperature, growth and reproductive activities. *P. magellanicus*, like other scallops (Mason, 1958; Ansell, 1974; Comely, 1974; Barber and Blake, 1981, 1983), exhibits a distinct annual reproductive cycle and as shown in Figure 3, the gametogenic cycle and energy utilization are intimately related. This in turn affects metabolic rate (see Barber and Blake, 1985).

Previous authors have studied the pattern of gonad development in *P. magellanicus* from various areas with contrasting results. Thompson (1977) showed that reproductive development in Newfoundland begins in spring and the gonads mature in the summer. He further showed that energy reserves from the previous year played no part in gonadal development. In contrast, Robinson et al. (1981) found that gametogenesis began in December/January in animals from Boothbay Harbor, Maine and that gonad de-

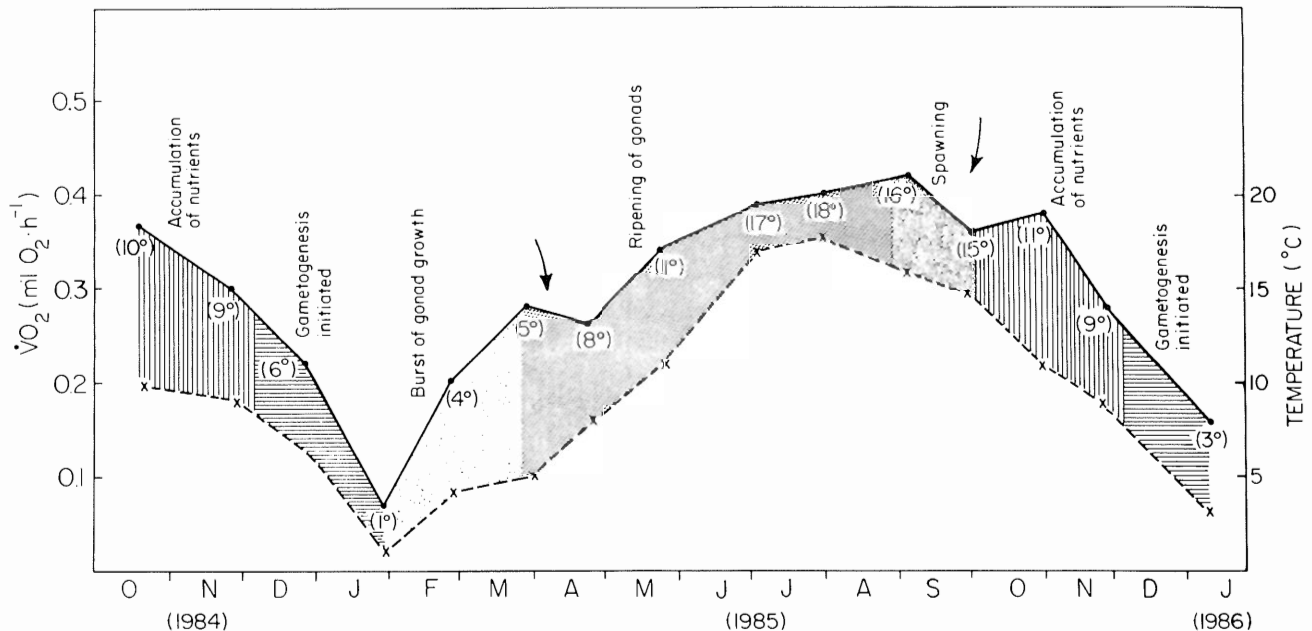


Figure 3. Seasonal changes in oxygen consumption of *Placopecten magellanicus* (from Figure 2) and approximate periods of the gametogenic cycle in the Gulf of Maine.

velopment takes place during January-March concurrently with somatic tissue growth. The energy reserves in the somatic tissues were lost in late spring-summer after the maturation of the gametes, i.e. energy for gametogenesis comes from both the stored reserves and from the ingested ration unlike the more northern populations in Newfoundland where energy reserves from the previous year play no part in gonadal development.

The gametogenic cycle for *P. magellanicus* from Maine can be summarized as follows: During January, gametogenesis has already reached the early developmental stage; energy reserves are at their lowest level (Robinson et al., 1981), and energy must be mobilized from the accumulated reserves. During the spring, gametogenesis is underway, gonad size increases, feeding begins with coincidental spring phytoplankton blooms and energy reserves begin to accumulate. During the summer (June-August), food is plentiful, gametes are ripening and energy is derived from spring storage and from food intake (Robinson et al., 1981). Spawning takes place in September/October and the animals enter a reproductively quiescent or 'rest' period. Barber et al. (1988) found that primary oogenesis was initiated in February, secondary oogenesis in March and vitellogenesis after June in *P. magellanicus* from Boothbay Harbor, Maine. Spawning and resorption of mature ova was evident in September and to a greater extent in October after which the animals were in a period of recovery (December/January).

In the present study, we have shown that respiration rates of *P. magellanicus* exhibited pronounced seasonal fluctuations which generally followed the changes in environmental temperature. While seasonal changes in metabolic activity are probably more closely related to food supply or reproductive activity than to temperature *per se*, in *P. magellanicus* there is a strong relationship between environmental temperature and seasonal changes in metabolic rate. These results are in general agreement with those of MacDonald and Thompson (1986a,b). Highest rates are exhibited during the summer months (ripening of the gonads) and lowest rates are exhibited during the winter months when gametogenesis is initiated.

It is demonstrated here that seasonal variations in metabolic rate are intimately linked with the gametogenetic cycle as has been demonstrated for several other species of molluscs (see Bayne and Newell 1983 for review). This cycle is not strictly related to temperature. During the spring and summer months, glycogen is stored and during the autumn and winter months this energy store is utilized for metabolism (including gametogenesis, see Gabbott, 1975). In scallops, glycogen stored in the adductor muscle is the major energy substrate (Ansell, 1974; Barber and Blake, 1981; Robinson et al., 1981).

The greatest discrepancy between the observed rates of respiration and those expected based on Q_{10} values occurred during February and March when there was a

sudden increase in $\dot{V}O_2$ coupled with only a slight increase in environmental temperature. This increase is most likely associated with the increased energy requirements of the scallop to fuel the sudden increase in gonad growth. This further supports the suggestion of Vahl and Sundet (1985) that the attainment of sexual maturity has an energetic cost. The observed $\dot{V}O_2$ from the end of January and the end of March is greater than would be expected based on Q_{10} values. Gonad development is an energy demanding process usually requiring mobilization of nutrients from ingested food or the storage and subsequent utilization of reserves from the body tissues. This period of time may correspond to the period of proliferation of the gonad/differentiation of gametes which is then followed, between April and August, by the less (?) energetically demanding process of gamete ripening.

The two 'unexpected' decreases in $\dot{V}O_2$ observed during March/April and August/September are of particular interest (see Figures 2,3). Similar decreases have been seen previously for this and other species. Ehinger (1978) concluded that reproductive stage had no effect on the rate of respiration. Closer examination of her data, however, reveals that the trends in her study were similar to those reported here and in fact, the same decrease after spawning is reported in her thesis. Bricelj et al. (1987) noted a similar decrease in $\dot{V}O_2$ after spawning in *A. irradians*. Barber and Blake (1985) reported a similar decrease in $\dot{V}O_2$ between mid- and late June (temperatures virtually the same) at about the time cytoplasmic growth of oocytes was initiated in *A. irradians* from Florida. He also noted a concomitant increase in RQ and O/N ratio both indicative of a shift toward greater carbohydrate utilization. March/April is the period of secondary oogenesis in *P. magellanicus* (Barber et al., 1988). It is possible that the initial decrease in $\dot{V}O_2$ observed in early spring by Barber and seen in this study is the result of the invocation of this metabolic machinery. The second decrease, corresponding to spawning, is accompanied in bay scallops by a shift from carbohydrate catabolism to protein catabolism (Barber and Blake 1985) and similar mechanisms are probably in effect in *P. magellanicus*.

It is difficult to separate the effect(s) of food, temperature and reproductive stage on metabolic rate because they all vary simultaneously. Only when we have a clear knowledge of the seasonal changes in food availability and feeding strategies in this species can the allocation of energy between somatic and gametogenic growth be clearly understood.

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