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Physiological costs of reproduction in the Sydney rock oyster *Saccostrea glomerata*

How expensive is reproduction?

Abstract In this study, triploid Sydney rock oysters *Saccostrea glomerata*, which do not reproduce and have only limited gonadal development, were used to calculate the cost of producing and maintaining somatic tissues. The consumption of oxygen was measured and converted to units of energy expended. The consumption of oxygen of diploid oysters, in different stages of the reproductive cycle, was also measured. Knowing the costs of producing and maintaining somatic tissues (obtained from the triploid oysters), it was possible to calculate the energy demand of somatic and reproductive tissues of diploid oysters. The focus of this study was to test whether this method would work, to investigate if this method would give results in accordance with modern life-history theory and to test hypotheses about costs of reproduction in oysters. It was found that in diploid oysters, 27% of the consumed oxygen was needed for reproductive processes. It was also found that the costs of production and maintenance of reproductive tissues were on average 84% of those of somatic tissues. Costs for the production and maintenance of somatic tissues decreased over time. Costs for reproduction also decreased, but were dependent on the stage of gonadal development. If the relative mass of gametes in the gonads was large, the costs were relatively small; if the mass was relatively small, the costs were large. Differences between traits of males and females were never significant, suggesting that reproductive effort and costs were similar in males and females. It was estimated that if diploid oysters did not reproduce, they could gain 64% more somatic ash-free dry mass. Thus, in terms of growth, reproduction is an expensive activity.

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Introduction

Knowledge of energy budgets of individuals or species is essential to explain important factors of their life history (Reznick 1992) such as trade-off between reproduction and rate of growth and mortality (Madsen and Shine 2000), longevity (Djawdan et al. 1996; Simmons and Bradley 1997) and future reproductive success (Hirshfield 1980; Jönsson and Tuomi 1994; Sinervo and Svensson 1998; Abell 2000; Neuhaus 2000; Ruusila et al. 2000). Life-history decisions are made within what is physiologically possible. Therefore, physiological costs of reproduction help to define the limits within which natural selection can act. It is, however, very difficult to measure the allocation of energy to reproduction or the physiological costs of reproduction (Hunter and Leong 1981).

Energy allocated to reproduction can be expressed as the reproductive effort, which is defined as the proportion of resources available (ingested food) that is used for reproduction (Calow and Woollhead 1977) and has been measured in many studies, e.g. Tinkle and Hadley (1975), Wootton and Evans (1976), Wootton (1979), Hirshfield (1980), Hunter and Leong (1981), Adams et al. (1982), Diana (1983) and Thompson et al. (1996). Although considered to be a poor estimate (Hirshfield and Tinkle 1975; Tinkle and Hadley 1975; Hirshfield 1980; Thompson et al. 1996), reproductive effort is still used to measure allocation of energy to reproduction.

Rather than measured as an *effort*, the amount of energy allocated to reproduction can also be measured as a real *cost*. By doing this, energetic costs of making gonads and gametes were taken into account. To estimate the costs of reproduction, species that did not feed (Diana 1983) or were deprived of food during gametogenesis (Calow and Woollhead 1977) were used, i.e. gametogenesis occurred at the expense of somatic tissues. The

decline in energy content of the soma was a measure of the costs of reproduction.

Since the late 1960s (Jönsson and Tuomi 1994), costs of reproduction have been defined, in ecological terms, as trade-offs between components of an animal's life history (Reznick 1992; Jönsson and Tuomi 1994) and this, generally, does not imply measuring physiological costs.

Despite the shift from a physiological to an ecological perspective, there are two main reasons why knowledge about physiological costs are still important in life-history theory, (1) to explain constraints of variability (Stearns 1992), i.e. variation of traits is limited by what is physiologically possible, and (2) because physiological costs can influence life-history traits directly (Sinervo and Svensson 1998). However, so far, the physiological costs of reproduction have been measured in only a few studies (Djawdan et al. 1996; Simmons and Bradley 1997).

In this paper I describe a method that can be used to estimate the physiological costs of reproduction. The consumption of oxygen was used as a measure of metabolic costs in infertile triploid and normal reproducing diploid Sydney rock oysters (*Saccostrea glomerata*). This method is new and can possibly be used in all species where gametogenesis can be inhibited without changing or affecting other physiological processes.

In triploid oysters, gametogenesis is severely retarded. Although there is some gonadal development and production of gametes (Allan and Downing 1986; Allan and Downing 1990; Cox et al. 1996; Kiyomoto et al. 1996; Ruiz-Verdugo et al. 2000) or the production of viable offspring (Akashige 1990; Guo and Allan 1994a; Ruiz-Verdugo et al. 2000), the allocation of energy to reproduction is thought to be only minor compared to that of diploid oysters (Guo and Allan 1994a). Therefore, it was assumed that the oxygen consumed by triploid oysters only reflected the costs of growth and maintenance of somatic tissues. The information obtained from triploid oysters was then used to calculate the consumption of oxygen of the somatic tissues of normal diploid oysters. The difference between the measured consumption of oxygen of diploid oysters and the calculated consumption of oxygen of the somatic tissues was the oxygen consumed to fuel reproduction. In this study the consumption of oxygen was measured over a period of 17 months and started when the oysters were 13 months old. Based on information obtained from the literature it was possible to test a number of hypotheses (see following paragraphs) concerning the costs of reproduction.

Gametes contain large amounts of energy-rich compounds and are costly to produce resulting in faster metabolic rates during gametogenesis (Vahl 1978; Bayne et al. 1983; Vahl and Sundet 1985; Bricelj et al. 1987; Stoeckmann and Garton 1997). Therefore, I predicted that, per unit of mass, the metabolic costs are larger for gonadal than for somatic tissue.

Until now, metabolic differences between male and female molluscs have to my knowledge only been addressed once. Males of the bivalve *Chlamys islandica* consumed significantly more oxygen and had slower rates of growth than females (Vahl and Sundet 1985). The authors stated that 'the energetic costs of producing a unit weight of sperm may therefore be larger than producing a unit weight of egg'. In the present study, the consumption of oxygen of males and females was compared to test the prediction that production and maintenance of sperm would be more costly than that of eggs.

Triploid oysters only allocate a small part of their total consumption of energy to reproduction, so more energy is available for somatic growth (Ruiz-Verdugo et al. 2000, 2001) resulting in faster rates of growth of triploid oysters compared to diploid oysters (e.g. Allan and Downing 1986; Nell et al. 1994; Wang et al. 2002). Therefore, I predicted that triploid oysters would gradually become heavier than diploid oysters.

Materials and methods

Juvenile Sydney rock oysters (*Saccostrea glomerata*) were obtained from cultures kept at Port Stephens Fisheries Research Centre, Taylors Beach, NSW, Australia. Eggs and sperm were obtained by means of natural spawning of normal diploid oysters in August 1999. Eggs from 11 females were divided into two groups and fertilised with sperm from 5 males. Triploidy in one group of fertilised eggs was induced with cytochalasin B, as described in Nell et al. (1996). Larvae were cultured as described in Nell et al. (1994).

By the end of March 2000 diploid and triploid oysters with a shell-length between 14 and 18 mm were selected. For each ploidy, three groups of 300 individuals were transferred to sectionalised commercial oyster trays with a mesh size of 8 mm. Each tray (180×90×6 cm (l x w x h)) was divided into 12 equal sections. Each section contained 25 oysters from the same group. The trays were covered with another tray to prevent loss of oysters and held on intertidal racks in Cromarty Bay, Port Stephens.

Samples to determine total mass, ash-free dry mass (AFDM) of gonads and soma and oxygen consumption were taken at 5 June 2000 (weights only), 12 September 2000, 5 December 2000, 1 February 2001, 18 June 2001, 5 October 2001 and 21 January 2002. At each sampling time, 16 individuals per tray were chosen; one randomly from each of the 12 sections of the tray and four others randomly from each of four other sections. Remaining oysters were cleaned of fouling organisms and redistributed in the tray. Collected oysters were air-dried for 30 min. and their total weight measured using a Mettler Toledo PB 303 precision balance. After weighing, oysters were labelled with shellfish tags attached to the upper valve with super-glue, transferred to the laboratory and placed in a tank with 750 l of aerated and running seawater. They were left undisturbed for 2 days in order to empty their digestive tract (depuration).

After depuration, the rate of consumption of oxygen ($\mu mol \cdot h^{-1}$) of each individual was measured, using Strathkelvin type 1302 Oxygen electrodes connected to a Strathkelvin 928 Oxygen System, in sealed respirometers of 750 ml. Oxygen runs lasted for about 1.5 h. Animals that remained closed, and from which the consumption of oxygen would be severely underestimated, were excluded from further analysis. After consumption of oxygen had been measured, the gonads (including gametes) from each individual were separated from the soma under a dissection microscope. From each individual, gonads and soma were transferred to porcelain crucibles. A very small sub-sample of the gonads was taken in order to determine the sex of each oyster (male, female, or unknown sex) and notes about the gonadal development were made. Triploid oyster showing gonadal development similar to that of diploid oysters were considered to be diploids (about 10–15% of all triploid individuals could be expected to be diploids (Cox et al. 1996; Guo et al. 1996; Nell et

al. 1996) and omitted from further analysis. Tissues were dried for 48 h at 80°C in a ventilated oven, cooled to room temperature in a desiccator and weighed to the nearest 0.01 mg. After weighing, tissues were ashed at 560°C for 4 h. The crucibles containing ash were cooled to room temperature in a desiccator and weighed again. The AFDM (loss of mass during combustion) of gonads and soma was then calculated.

In order to compare the consumption of oxygen by triploid (V_{tripl}) and diploid (V_{dipl}) oysters per unit mass, the consumption of oxygen of triploid oysters had to be calculated for an oyster with the same mass as the mass of the soma of a diploid oyster. An allometric relationship has been established between (ash-free) dry mass and physiological rates. For more details, see Bayne and Newell (983):

$$V = aW^{\beta}$$

where V is the physiological rate, W is the (ash-free) dry mass, and a and β are intercept and slope of the regression fitted through Ln-transformed data of mass and rate, respectively. Because it was not possible to obtain triploid oysters spanning a suitable size-range, I could not establish this relationship and, therefore, a value well within the range of published values, $\beta=0.65$ was used (Bayne and Newell 1983; Bricelj et al. 1987; Bricelj and Shumway 1991). To calculate the oxygen consumption for a standard body mass (W_{st}) the following (rewritten for our purposes) formula was used (Bayne et al. 1999):

$$V_{st} = V_{tripl} \cdot \left(\frac{W_{st}}{W_{tripl}}\right)^{\beta}$$

where V_{tripl} and W_{tripl} are the measured physiological rate and the measured AFDW of the individual triploid oyster, respectively, W_{st} is the average weight of the soma of each group of diploid oysters and V_{st} is the physiological rate of a diploid oysters with weight = W_{st}. Thus, the consumption of oxygen by somatic tissues of each replicate group of diploid oysters was calculated using the oxygen consumption of all tissues of all individuals (n individuals) of the three replicate groups of triploid oysters as a reference. The resulting $3\times n$ calculated 'observations' were analysed to see whether there were significant differences among the three replicate groups. If the oxygen consumption among the three groups of oysters was not significantly different ($P>0.05$), the overall mean of the standardised consumption of oxygen ($\bar{V}_{st}$) and its variance (using all individual measurements as replicates) was calculated. If the consumption of oxygen among the groups was significantly different, the same average ($\bar{V}_{st}$) was used but with the (larger) among-treatments variance. The average value ($\bar{V}_{st}$) and its associated standard error were taken to represent the consumption of oxygen of one replicate group of diploid females, males or oysters of unknown sex. The average consumption of oxygen of the gonads of each group of diploid oysters ($\bar{V}_{gon}$) was the difference between the average measured consumption of oxygen of that particular group of diploid oyster ($\bar{V}_{dipl}$) and the consumption of oxygen of the soma calculated for that group ($\bar{V}_{st}$): $\bar{V}_{gon} = \bar{V}_{dipl} - \bar{V}_{st}$. To calculate the standard error of the consumption of oxygen of the gonads, the standard errors of ($\bar{V}_{dipl}$) and the consumption of oxygen of the soma calculated for that group ($\bar{V}_{st}$) and ($\bar{V}_{st}$) were summed. In order to compare the consumption of oxygen of gonads and soma over time, it was calculated per 100 mg of tissue. These rates were expressed in units of energy per unit time using a conversion factor of 0.456 J per μmol of consumed oxygen (Gnaiger 1983).

Results

Patterns of reproduction and growth

The sex of diploid oysters could be successfully determined during spring and early summer (September–February). During winter (June) only a small percentage
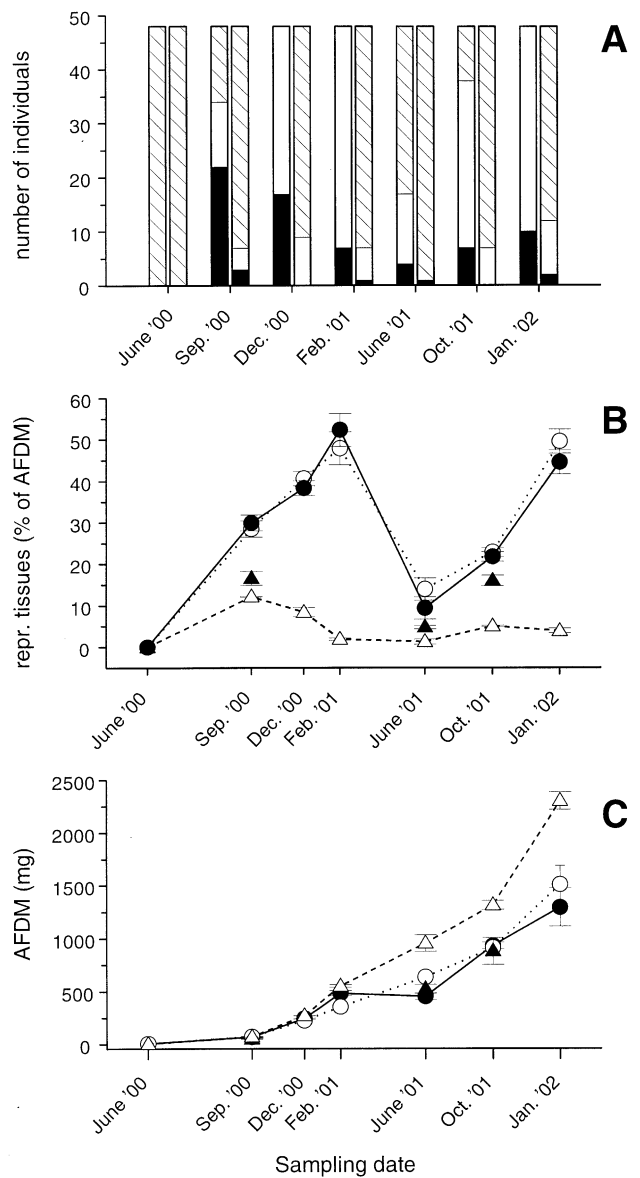

Fig. 1 A Sex of diploid and triploid oysters (*left-hand* and *right-hand column* of each set of *bars*, respectively). The *solid black* part of the *columns* represents the numbers of males, the *white part* the numbers of females and the *dashed part* the numbers of those of unknown sex. **B** The percentage of reproductive tissues and **C** the total ash-free dry body-mass of diploid males (●), females (○) and those of unknown sex (▲) and triploid oysters (°)

of all individuals could be sexed. In all cases but one, more than half of the sexed individuals were female; only in September 2000 were more diploid males than females observed. For triploid oysters, never more than 12 out of 48 individuals could be sexed (Fig. 1A).

Generally, at each sampling date, gametes of diploid female oysters had a similar shape and mobile sperm was observed in almost all males, particularly in December 2000, February 2001 and January 2002. Eggs of triploid oysters were generally deformed, very small or very large and mostly present in small numbers. Normal eggs

Fig. 2 Consumption of oxygen (µmol·h⁻¹) of all tissues (*dashed bars*), somatic tissues (*open bars*) and reproductive tissues (*solid bars*) of **A** females, **C** males and **E** those diploid oysters of unknown sex at the different sampling dates. The consumption of oxygen of the soma and reproductive tissues are converted to units of energy per standard mass of 100 mg per hour (kJ·100 mg·h⁻¹) for **B** females, **D** males and F those of unknown sex. The *open bars* represent somatic tissues and the *solid bars* the reproductive tissues. ∗ indicates that data were available for only two out of three replicates
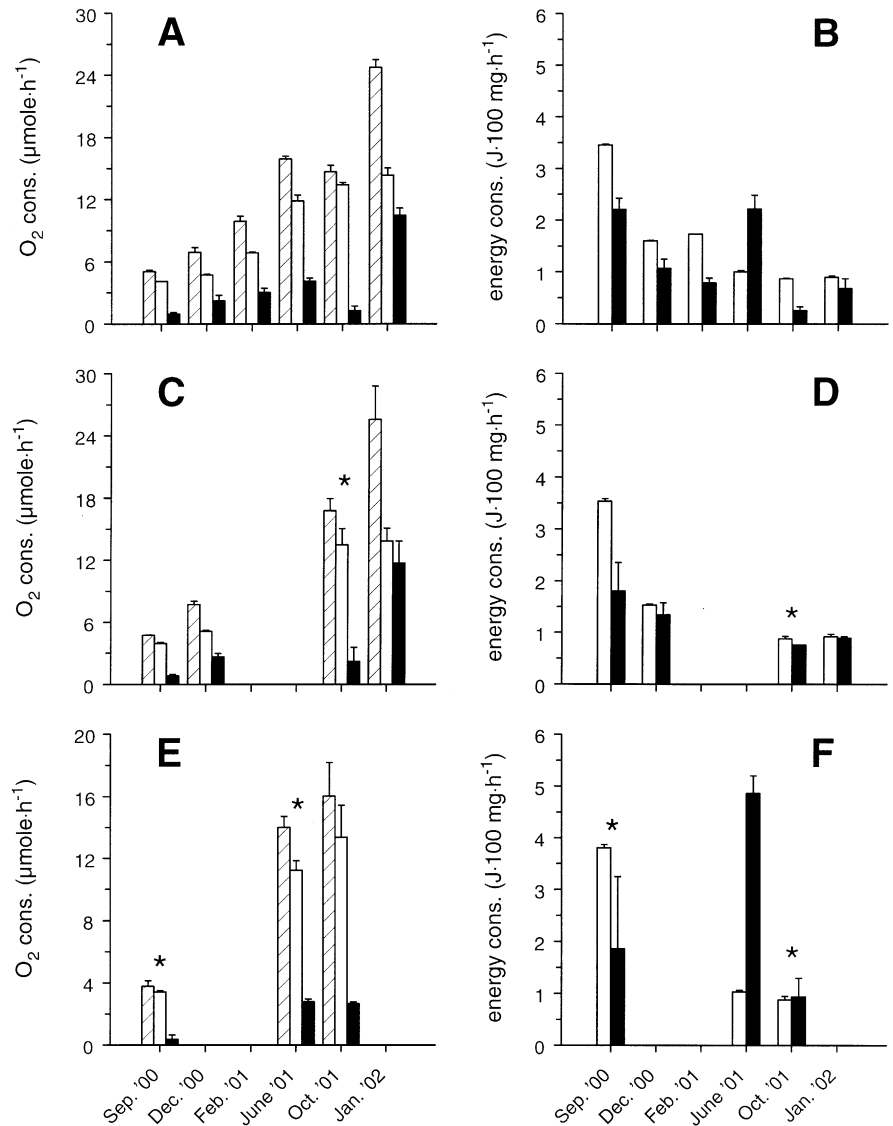
(indistinguishable from eggs of diploid females) were occasionally observed, sometimes in very large numbers. If sperm was observed, they appeared normal, but were always immobile. Only once, in June 2000, was a male that was indistinguishable from a diploid male observed. Triploid oysters from the same spawning event but used in a different experiment had a triploidy level of 91.7% (Hand, personal communication).

The percentage of gonadal material was relatively small, about 10% of total AFDM in winter (June) increasing to 50% in summer (January and February, Fig. 1B). Differences between gonadal mass of males and females were, whenever sufficient replicates were available, never significant (*P*>0.05). The percentage of the gonadal mass of triploid oysters was generally significantly smaller than that of diploid oysters (all comparisons *P*<0.01) with a maximum value of about 10% in September 2001. Only in June 2001 were differences not significantly different. The relative amount of gonads of

diploid oysters of unknown sex was similar to that of triploid oysters in September 2001 and similar to that of diploid oysters in June and October 2001 (Fig. 1B).

AFDM of triploid oysters was always larger than that of diploid oysters, though only significantly so in June and October 2001 and January 2002 (*P*<0.01). Although a drop in the percentage of the gonads was observed between February and June 2001 (Fig. 1B) this was not reflected in a drop in total AFDM of females or males (Fig. 1C). Differences between males, females and those of unknown sex were, whenever it could be tested, never significant.

Consumption of oxygen by gonads and soma

The total consumption of oxygen of diploid females, males and of those of unknown sex showed a continuous increase over time. Although the series for males and for
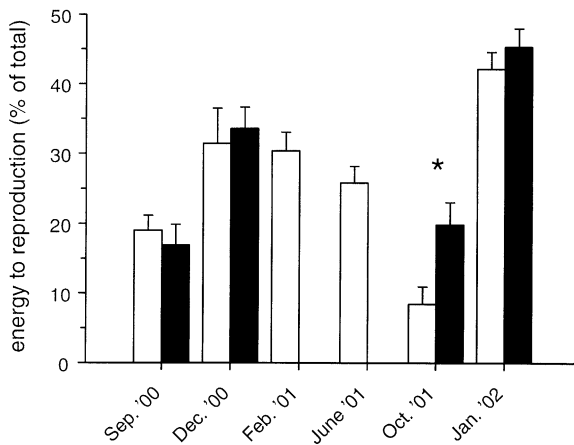
Fig. 3 Energy allocated to reproduction (% of total oxygen consumption respired in reproductive tissues) of female (*open bars*) and male (*solid bars*) diploid oysters. ∗ indicates that data were available for only two out of three replicates

those of unknown sex were incomplete (no groups or only two replicate groups) this trend appeared to be general (dashed bars in Fig. 2A, C, E for females, males and those of unknown sex, respectively).

Data of the consumption of oxygen of triploid oysters (V_{tripl}) were used to calculate the consumption of oxygen by somatic tissues of each replicate group of diploid females, males and of unknown sex. The consumption of oxygen by the soma of females increased over time (Fig. 2A). The incomplete data for males (Fig. 2C) and for those of unknown sex (Fig. 2E) showed a similar pattern.

At each time $(\bar{V}_{gon})$, i.e. $(\bar{V}_{dipl} - \bar{V}_{st})$ was calculated for each sex (solid bars in Fig. 2A, C, E). In females the general pattern showed a continuous increase (Fig. 2A). The incomplete data on males and those of unknown sex (Fig. 2C, E, respectively) supported the pattern observed for females.

The costs of maintaining and making somatic and gonadal tissues were calculated per 100 mg tissue at each sampling date. For the soma decreasing costs were observed. Costs were largest in September 2000 (3.46±0.01 J·h^{-1}) and smallest in October 2001 and January 2002 (0.89±0.02 J·h^{-1}; Fig. 2B). A similar general pattern was observed for the costs of making and maintaining gonads, but relatively large costs for gonadal development were observed in June 2001. At almost all sampling dates, the costs per 100 mg gonads were significantly smaller, on average 84% of those of soma ($F_{(6,24)}$=22.32, $P<0.0001$). In June 2001, however, the costs were significantly larger and in January 2002 the costs were similar. The patterns observed for males (Fig. 2D) and for oysters of unknown sex (Fig. 2F) were similar to the pattern observed for females.

Differences between males and females could only be tested for the data obtained in September 2000, December 2000 and January 2002. There were no significant differences ($P>0.05$) between costs of maintenance and growth of the soma and gonads of males and females

[$F_{(1,8)}$=0.29, 0.43 and 1.27 in September 2001, December 2001 and January 2002, respectively] nor were there any significant differences between the amount of oxygen used by reproductive processes of males and females [Fig. 3, $F_{(1,4)}$=0.34, 0.13 and 0.78 in September 2001, December 2001 and January 2002, respectively]. These processes used 10–45% (average 27%) of all consumed oxygen (Fig. 3).

Discussion

Patterns of reproduction and growth

Triploid oysters occasionally produced normal-looking eggs or sperm (however, always immobile) which is in contrast to the information supplied by Cox et al. (1996) who never observed mature gametes. Although a detailed histological study was not done, it seemed that the oysters in my study showed more advanced gonadal development than those used in the study of Cox et al. (1996). In triploid oysters never more than 10% of AFDM was allocated to reproduction (Fig. 1B). Thus, not only was gametogenesis retarded, but the amount of reproductive tissue was also much less in triploid than in diploid oysters (Allan and Downing 1990; Ruiz-Verdugo et al. 2000, 2001).

In June, during the southern winter, diploid oysters (males and females) appeared reproductively inactive and no mature gametes were observed. At the end of the year, gonadal development started and was completed shortly before spawning in January–March. In December and January all diploid individuals could be sexed, but from January until June, more and more animals had spawned and relict gametes resorbed resulting in fewer animals that could be sexed. These observations were closely related to those described by Cox et al. (1996). Triploid oysters were hard to sex; the maximum number was 12 (out of 48) in January 2000. Because the percentage triploidy is generally between 75% and 90% (Cox et al. 1996, Nell personal communication) and in our study possibly 92% (Hand, personal communication), it is likely that most (but not all) of the triploid individuals which could be sexed were normal diploids. These individuals were, therefore, omitted from further calculations.

Total mass (including the shell, data not presented) and AFDM of triploid oysters was, as expected (Hawkins et al. 1994; Nell et al. 1994), after 3 years of cultivation, 40% and 64% (Fig. 1C) greater than those of diploid oysters.

Evaluation of method

Because in my study animals were starved prior to measurements, it was assumed that oxygen used to collect, process and digest food was negligible and that consumed oxygen only reflected the costs of maintenance and growth. Absolute growth over the short time-span of

each measurement of oxygen consumption was immeasurably small but the energy allocated to growth probably was not. Up to 30% of the total consumption of oxygen during that period could have been allocated to growth (Parry 1983); the rest was used for other processes such as maintenance. Therefore, costs of maintenance and growth could not be separated.

To estimate the allometric relationship between mass of tissue and rate of consumption of oxygen, a β-value well within the range published in the literature ($\beta=0.65$) was used. Because many factors could affect β (Bricelj et al. 1987; Bricelj and Shumway 1991) it would have been better to estimate β for triploid oysters at all sampling dates, but no animals suitable for this measurement were available. The consequence of an underestimated β-value (i.e. actual $\beta>0.65$) would be that the rate of consumption of oxygen by somatic tissues $(\bar{V}_{st})$ would be slower than calculated and costs overestimated and that of gonadal tissues $(\bar{V}_{gon})$ faster and costs underestimated. Consequently, the conclusion that maintaining and producing reproductive tissue was cheaper than that of somatic tissues (see next section) would be weakened. The consequence of an overestimated β-value would be the opposite.

An assumption still to be tested is that the costs of producing and maintaining triploid tissues are similar to those of diploid somatic tissues. Contrasting results on this topic have been published. Triploids had smaller (Guo and Allan 1994b; Guo et al. 1996), similar (Laing and Utting 1994; Kesarcodi-Watson et al. 2001) or larger (Mason et al. 1988) metabolic costs. These observations thus did not provide any useful information about differences in metabolic costs. If, however, triploid Sydney rock oysters indeed have larger costs, then the costs of maintenance and production of somatic tissue of the diploid oysters are overestimated and the costs of reproduction underestimated. This will have similar consequences for the conclusions as described in the previous paragraph.

Another potential difficulty is the production of reproductive tissues by triploid oysters. It is very likely that costs per unit of mass of reproductive tissue are larger than those of somatic tissues, especially during the late (post-spawning) and early (onset of gametogenesis) stages of gametogenesis. If the costs are twice as large (June 2001 data in Fig. 2B) and if no more than 10% of the total AFDM is reproductive tissue in triploid oysters (Fig. 1B), then the overestimation of the costs of maintenance and production of somatic tissues will never be larger than 5%. Thus, it can be expected that the costs of maintaining and producing diploid somatic tissues may be slightly overestimated and costs of reproduction slightly underestimated, having similar consequences as described in the previous paragraphs.

Patterns of allocation of energy

An increasing total and somatic consumption of oxygen by diploid oysters was observed (Fig. 2A, C, E). Oxygen consumed by gonads of females increased almost continuously, but less obviously so in males and those of unknown sex (Fig. 2A, C, E). On average, 27% (range 10–40%) of consumed oxygen was used by reproductive processes, values well within the range of other published values (Bayne et al. 1983; Thompson 1984). In females, males and those of unknown sex, the metabolic costs of 100 mg of reproductive tissue were generally (but not in June 2001) smaller than those of the soma and decreased over time (Fig. 2B, D, F).

How can these patterns be explained? Early in life, when organs grow fast, the costs of growth and development are relatively large. Later, much of the body consists of structural mass (i.e. the minimal mass necessary to stay alive) and energy stores and consume relatively little energy (Kooijman 1993). The energetic costs per unit mass are, therefore, smaller for larger than for smaller individuals. Eggs of bivalves consist mainly of storage material and costs of maintenance are considered to be small or zero (Horstmann 1958; Kooijman 1993 p. 78 and Fig. 3.14) and thus the costs per unit of mass were found to be smaller for gonads than for soma (Fig. 2B). The costs of reproduction declined over time because the relative number of eggs increased as gametogenesis progressed. In June 2001 only a few residual eggs were present in the gonads and only 14% of total AFDM of females were gonads (Fig. 1B). Because this tissue was mainly active gonadal tissue recovering from spawning and preparing for a new gametogenetic cycle (Cox et al. 1996), the costs were relatively large (Fig. 2B, and last paragraph of previous section). The hypothesis that producing and maintaining reproductive tissues was more expensive than those somatic tissues was only confirmed by the data collected in June 2001. Therefore, for future research a more detailed hypothesis, including predictions about seasonal differences in costs, needs to be formulated and tested. For example, it can now be predicted that costs of producing and maintaining reproductive tissues will be larger that those for somatic tissues during the early stages of gametogenesis and will gradually become smaller until the smallest costs are reached shortly before spawning.

Differences between males and females were, whenever tested, always non-significant. Males and females produced the same amount of gonadal material (Fig. 1B, C) and used a similar percentage of oxygen for reproductive processes (Fig. 3). This resulted in similar costs for production and maintenance of soma and gonads (Fig. 2B, D) contrary to the only information found in the literature for a bivalve where males used more oxygen than females during gametogenesis, indicating larger costs for producing sperm (Vahl and Sundet 1985).

What does reproduction cost in terms of reduced somatic mass? The average costs of producing and maintaining reproductive tissue were 84% of those of

somatic tissue and on average 27% of metabolic energy was expended by reproductive processes. If oysters had not reproduced, this 27% could be expended by somatic processes producing 27%×0.84=22% somatic tissue. The total mass of females just prior to spawning consisted of 52% gonads and gametes. If all constituents of the gonads could have been used for production of soma, this could have led to 52%×0.84=44% extra somatic tissue. Therefore, a non-reproducing oyster could have been approximately 66% heavier than a reproducing one. The only data to verify this estimate were published by Nell et al. (1994); the dry weight of triploid oysters was 75±12% (mean±SD, their Fig. 3) heavier than that of diploid oysters. Our estimate, although smaller and without variance, fitted within this range and validated the suggestion that triploids can be used to calculate the physiological costs of reproduction.

To conclude, triploid oysters grew, as predicted, faster than diploid oysters. Diploid oysters used, on average, 27% of consumed oxygen to produce and maintain reproductive tissues and appeared to be cheaper to produce than a similar amount of somatic tissue. Therefore, the hypothesis that the costs for somatic tissues are smaller than for reproductive tissues was rejected. About 50% of the AFDM of diploid oysters consisted of reproductive material. It was estimated that if diploid oysters did not reproduce they could have been 64% heavier. In terms of growth, reproduction is thus expensive. Although some assumptions still need to be tested, using triploids to calculate costs of somatic growth and reproduction looks promising and can be a helpful tool in studying life histories of bivalves.

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