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Relationship between pre- and post-metamorphic growth in the Pacific oyster Crassostrea gigas (Thunberg)

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Abstract:

Twenty male and 20 female parental oysters, originating from four sites located along the French Atlantic coast, were crossed together. The 400 crosses were performed separately and then pooled to give a batch of larvae with a large genetic base. Successive sieving after 17 days at 23°C enabled the separation of the largest larvae from the batch. These larvae (i.e., sieving groups) were left to metamorphose and fix onto flat PVC collectors changed daily. Four groups of larvae representing distinctly different growth rates were successively separated during the attachment and metamorphosis of the whole population. This lasted 12 days, from the 17th day to the 29th after fertilisation. A part of each sieving group was settled separately as replicates on cultch. The post-metamorphic height was recorded weekly on 100 oysters per sieving group generating 400 growth curves. The oysters were removed from the collectors and weighed. The effect of the date of settlement (i.e., developmental rate) and sieving group (i.e., larval growth rate) affected (P<0.0001) the spat growth rate significantly. The correlation between sieving groups (i.e., larval growth) and spat growth rate was positive. After 11 months of growth under intensive conditions, the sieving group still had a significant effect on the total weight of juveniles settled on cultch (P<0.0001). These results justify the size-grading of larvae in bivalve hatcheries and show the great importance of early growth on growth in later stages in *Crassostrea gigas*.

Keywords: Growth; *Crassostrea gigas*; Metamorphosis; Settlement

1. Introduction

In many marine invertebrates, metamorphosis involves the change from a free-living, planktonic life to a relatively sedentary, benthic one. An important physiological alteration occurs during metamorphosis (Baker and Mann, 1994), so larval growth may involve very different mechanisms compared to juvenile growth. In order to investigate the implications of metamorphosis on juvenile growth, experiments have been carried out on some invertebrate species in which the length of the larval period or the nutritional condition of the larvae was altered and the effects on subsequent juvenile growth studied (Balanus amphitrite, Pechenik et al., 1993; Crepidula plana and C. fornicata Pechenik and Eyster, 1989). These studies showed that a delayed metamorphosis affects juvenile growth in Balanus amphitrite but not in Crepidula fornicata. Other studies have been performed in order to focus on possible genetic correlation between larval and post-metamorphic growth but the results published to date are inconsistent. A positive relationship between larval and spat growth was found in Crassostrea virginica (Losee, 1979; Newkirk et al., 1977). Newkirk and Haley (1982) reported a lack of correlation between height of larval period (and larval size) and size of juvenile and adult European oysters, Ostrea edulis. Furthermore, Hilbish et al. (1993) found no significant genetic correlation between growth of 10-day-old larvae and 9-month-old juveniles in Mercenaria mercenaria. Heffernan et al. (1991) showed that selecting for faster growth in adult Mercenaria mercenaria leads to slower larval growth and no substantial relationship was found between larval and juvenile growth in Crepidula fornicata (Pechenik et al., 1996).

Larval and juvenile growth rates are very variable among individuals and appear to be heritable (Mytilus edulis: Mallet et al., 1986; Strömgren and Nielsen, 1989; Mercenaria mercenaria: Rawson and Hilbish, 1990; Hadley et al., 1991; Hilbish et al., 1993). In this context,

a correlation between larval and post-larval growth would be of great interest for selective breeding. Moreover, in bivalve hatcheries, the most common practice is the systematic culling of the smallest larvae in order to reduce the time of larval rearing and to reduce size variability (Bardach et al., 1972). However, the effect of this sieving operation on post-metamorphic growth is still unknown, since the relationship between larval and juvenile growth remains unclear.

In the present study, a batch of larvae of the Pacific oyster Crassostrea gigas was obtained under laboratory conditions. Successive sieving enabled the separation of the largest larvae from the batch. These larvae were left to settle on collectors which were changed daily. This maximised the temporal distribution of the settlement of the batch after sieving as a whole. This experiment aimed to establish a relationship between larval growth, as measured by the length of their larval life, and early post-settlement growth.

2. Material and methods

Crosses

In order to build a population with a large genetic base, 40 parental oysters originating from 4 sites located along the French Atlantic coast were crossed in the IFREMER hatchery in La Tremblade (Charente maritime, France). In order to ensure an equal gametic contribution of each parent, 400 factorial crosses were performed separately with 40 parents: 20 males crossed with 20 females (5 males and 5 females per population). Spermatozoids were collected first, by stripping the male gonad. The sperm was diluted with 1 µm filtered sea water, its concentration was estimated using Thoma slides coupled to an image processing system (Alcatel), and stored at 4°C. Oocytes of the female were then collected using the same procedure and counted using

Malassez slides. For each female, 3,000,000 oocytes were distributed in each fertilisation beaker and fertilised separately by each male at a ratio of 100 spermatozoa per oocyte. Four hundred in vitro fertilisations were performed separately by this method and all the fertilised oocytes were pooled together 3 hours after fertilisation. The mean percentage of embryos developed was 87.6%. Larvae were reared in 4 GRP (Glass Reinforced Polyester) 300 litres tanks filled with 1 µm filtered sea water (temperature 23°C and salinity 28‰) and were fed Isochrysis galbana and Extubocellulus criberiger. The total amount of algae provided was 60 cells.µl^{-1}. This concentration was in excess (Nascimento, 1980) to avoid competition for food between larvae and to maximise phenotypic variability. Larval concentration at day 1 was 13 larvae.ml^{-1} and was progressively reduced down to 1 larva.ml^{-1} at day 17, by discarding a part of the population without any selective sieving.

Sieving groups

Every 48 hours, all the larvae were collected by sieving and a sample was counted (Cell counter) and measured (Profile projector, Nikon). When the first pediveliger larvae appeared, the largest larvae (height greater than 280 µm) were retained after sieving on a 200 µm-mesh and left to settle. The remaining larval population was kept in the larval rearing tanks. Successive sieving operations were performed in the same way. Each time, the largest individuals were transferred to the settlement raceways and the smaller individuals were returned to the larval rearing tanks. Thus, sieving group (SG) 1 corresponds to the fastest-growing larvae and sieving group 4 to the slowest-growing larvae.

Settlement procedure

PVC boards, covered with a layer of wax and a second layer of polyester resin were used as collectors. The wax layer allows easy removal of the oysters from the collector at a very early stage without damaging them, while the resin layer is a good substrate for attachments and metamorphosis of the animals. At each sieving operation, the larvae were split between the PVC sheet collector raceway and a cultch tank in order to have a large reserve of animals of the 4 sieving groups. The PVC collector system consisted of four 37.5 x 50 cm boards per raceway with 10 µm-filtered sea water at 26°C, automatically aerated for 15 min every 2 hours. A sample of larvae was taken from the first settlement raceway every day and examined and numbered. The collectors were then replaced for a new day of settlement. For each sieving group except the first there was a variable number of days of settlement. After attachment and metamorphosis, the collectors were maintained vertically in 800 litre tanks with Skeletonema costatum enriched sea water.

Growth recording

A large proportion of the animals were removed from the boards at random to reduce competition for space. For each pair of overlapping individuals, the biggest and the smallest was alternatively discarded. Therefore, no competition for space occurred among the remaining oysters. Out of these animals, 100 were chosen at random from each sieving group and individually identified by writing the number directly on the board, near the hinge of the oyster. The height from the hinge to the edge of the upper valve was recorded 4 times, weekly, with a digital calliper to an accuracy of 0.01 mm. The last measurement was made 58 days after fertilisation when all the animals were removed from the boards, labelled and then weighed with a precision of 0.1 g. Weighing was repeated after 7 days. The overall spat growth rate (GR, $g.d^{-1}$) was calculated by dividing this weight by the time of spat growth (number of days after

settlement). The date of attachment and metamorphosis is referred to as DSET.

The sieving groups obtained by the cultch rearing method were transferred to the IFREMER nursery in Bouin (Vendée, France) and reared under the same food and density conditions. 100 animals per sieving group were weighed 11 months after fertilisation.

Data analysis

The overall spat growth rate (GR) was analysed using the following model:

$$GR = \alpha.SG + \beta.DSET + \varepsilon$$

The effect of SG and DSET on GR were tested by analysis of variance using SAS software (SAS Institute, 1988), with SG and DSET respectively as a fixed effect factor and a random effect factor nested within SG. The effect of sieving date (SG) on the spat growth rate and the live weight at 11 months were also analysed by analyse of the variance. The initial difference between larvae at metamorphosis and attachment is supposedly negligible. Multiple comparisons were performed using the Student-Newman-Keuls' test.

3. Results

Larval rearing

The total number of larvae obtained at day 1 was 16,240,000. After progressive adjustment of concentration, this number was reduced to 1,134,000 at day 17. The average larval growth curve followed an exponential pattern (Figure 1). The mean larval height before sieving at day 17 was 271.7 ± 51.0 µm giving a coefficient of variation of 18.8 %. The coefficient of variation increased from 3 % at day 1 to 9 % at day 6 and finally stabilised around 20 % from day 9 to day 17. The first pediveliger larvae and individuals larger than 280 µm

(minimum size for larvae retained on a 200µm-mesh sieve) appeared at day 17. The sieving operations were performed 17, 20, 23 and 26 days after fertilisation and led to the separation of the sieving groups (SG) numbered 1, 2, 3 and 4 respectively. Mean larval height measured after sieving and mean larval growth rates is higher for the 1st sieving group and lower for the 4th sieving as shown in Table 1. The larvae were allowed to settle for periods lasting 1, 4, 2 and 4 days, respectively, for the sieving groups 1, 2, 3 and 4 to have enough animals fixed. No larvae remained in the settlement tank at the end of the settlement period in any of the sieving groups.

Spat growth

The coefficient of variation of spat height ranged from 18.8 % to 43.8 % for the whole population between days 37 and day 58 after fertilisation. No spat died between the first day and the last day of measurement. The raceways had no significantly effect on the post-metamorphic growth rates (data not shown).

Growth curves of the 4 sieving groups are given in terms of number of days after fertilisation (Figure 1) and number of days after settlement by using the 1st day of settlement of each sieving groups (Figure 2). The growth curves for all the combination of the 4 sieving groups and settling dates are shown in terms of days after settlement (Figure 3).

The overall spat growth increments were 49.89 ± 2.38, 22.03 ± 1.36, 18.58 ± 0.81 and 11.63 ± 0.84 $g.d^{-1}$ respectively for the sieving groups SG1, SG2, SG3 and SG4. The model was significantly improved when SG and DSET were included over the simple factor models. The effect of SG (i.e. larval growth rate) on the spat growth rate is highly significant (Table 2). DSET also appears to have a significant effect. The correlation between the larval growth rate (rank of the sieving group) and the spat growth rate is significant ($F = 39.2$ $P = 0.0001$, $n = 381$,

Figure 4).

The relationship between the total weight after removal of the oysters from the PVC collectors and the spat height on collectors gave mean R squared statistics equal to 0.52, 0.79, 0.78 and 0.83 respectively for sieving groups 1, 2, 3 and 4. The rank of the sieving group still affects the total weight very strongly, both on removal from the collectors ($P < 0.0001$) and 7 days afterwards ($P < 0.0001$).

Juvenile growth

After 11 months of growth, the sieving groups obtained with the cultch method had a mean total weight of 21.6 ± 1.4 g, 18.7 ± 1.2 g, 18.3 ± 1.3 g and 12.1 ± 1.1 g for sieving groups 1, 2, 3 and 4 respectively. The rank of the sieving group significantly affects the final live weight at 11 months ($P < 0.0001$, Figure 5).

4. Discussion

The early spat growth rate is dependent on the date of settlement

In the present experiment, an effect of the date of metamorphosis (i.e. rate of development) and the date of sieving (i.e. rate of larval growth) on overall early spat growth rate was found in Crassostrea gigas when environmental conditions (temperature, salinity, amount and quality of food) were maintained as constant as possible during all the larval and post-larval stages. However, because of the experimental design, date of attachment and metamorphosis is nested within sieving date which leads to difficulties in analysing these factors separately.

Larval growth rate and spat growth rate were found to be strongly correlated in

Crassostrea virginica (Newkirk et al., 1977) and a weaker correlation was found in Crepidula fornicata (Pechenik et al., 1996). In the same way, the length of larval period (after release of the larvae by the brooding females) appears to be negatively correlated with the height at 5 months in Ostrea edulis (Newkirk and Haley, 1982), but in this analysis, the height itself was used as the growth parameter and was not corrected for the date of settlement. In the light of the present results, the effect of the larval period on the post-settlement growth rate could be due to a difference in the growing time. The present work shows the importance of considering the date of settlement rather than the date of fertilisation for analysing growth kinetics, the best approach being to compute growth rates for at least the early spat stage. Losee (1979), showed a difference in the growth rate 29 weeks after attachment between spat of Crassostrea virginica settled at different dates. However, the short delay between sieving groups was not taken into account and all the cohorts were weighed the same day. Three days in settlement separates settlement of Losee's groups of larvae and the difference in growth detected 29 weeks later is consistent with 3 days of early growth. A delay of 2 or 3 days in growth due to different date of attachment still has consequences several months after, because the speed of growth is very high at an early stage and decreases at later stages (Quayle, 1969), as shown in the present study. Newkirk et al. (1977) obtained 4 settlement groups in Crassostrea virginica by changing the collectors every 2 days. The mean size of settlement groups was negatively correlated with the rank of the settlement group. Again, two days of post-metamorphic growth can easily explain the differences in size between settlement groups or at least the correlation observed between growth before and after settlement. Settlement groups of Ostrea edulis were obtained similarly by Newkirk and Haley (1982) and a correlation was found between the duration of the larval period and the size of 5-month-old spat. As shown by the growth kinetics in terms of time after fertilisation (Figure 1), this correlation can be explained by the growth delay existing between

settlement groups.

Pechenik et al. (1996) sorted Crepidula plana larvae into 3 groups of slow-growing, medium-growing and fast-growing individuals and measured them 3, 6 and 9 days after metamorphosis finding no significant differences in juvenile growth rates between the 3 groups. Furthermore, Hilbish et al., 1993, found no significant genetic correlation between growth of 10-day-old larvae and 9-month-old juveniles in Mercenaria mercenaria.

These inconsistencies in the results in the literature may be partly explained by the use of different growth variables by the authors (absolute parameters and growth rates).

The final live weight at 11 months is different between sieving groups in the present experiment. This could be because the individuals did not have exactly the same amount of time to grow as spat. The delay in growth between sieving groups 1 and 4, corresponds roughly to 10 days of spat growth, 0.54 g at 66 days after fertilisation. If we consider this delay constant over time, it would give a difference at 11 months of 2.7 g between the 2 groups. However, the measured difference is 9.5 g, much higher than expected for the shortened growing time. This can be interpreted by the effect of the sieving group (i.e. rate of larval growth) discussed above, or to the delay in growth that get higher with time.

Does time of metamorphosis depend on the age or on the size of the larvae ?

For the 4 sieving groups, only larvae which had reached a height greater than 280 µm at a given date were left to attach and metamorphose. The coefficient of variation for larval height around 100 µm ranged between 8.5 % and 18.7 % from day 6 to 9, which is very high compared to the mean of 4.0 % obtained by Nascimento (1983) for larvae of a similar height. This is a consequence of the absence of selective conditions which was maintained throughout the larval

rearing (low larval densities and non limiting amount of food). Therefore, in this experiment, sieving group is a good indicator of the larval growth rate. Comparing the larval and spat growth rates using sieving groups based on the date of settlement (Newkirk et al., 1982) requires that the date of metamorphosis is dependent on size rather than age of the larvae. However, Pechenik and Heyman (1987) showed that the larvae do not become competent at a particular size in Crepidula. Pechenik et al. (1996) showed that larvae could become competent even when larval growth was halted by starvation. Pechenik et al. (1996) showed that the onset of metamorphic competence in Crepidula fornicata could be uncoupled from the process of growth, in that starved larvae did not grow at all but did slowly became competent to metamorphose. Coon et al. (1990) showed that competence of Crassostrea gigas larvae to settle occurred earlier than competence to metamorphose. Factors determining when metamorphosis occurs have been discussed many times. In the present work, the larvae were left to settle in non-selective rearing conditions, without any settlement inducers. At each sieving operation the smallest individuals were returned to the GRP larval tank where no settlement occurred in spite of the fact that GRP is a highly attractive substrate for settlement of C. gigas larvae (Holliday, 1996; personal observations). The larvae retained by the sieve (> 280 µm) settled quickly when placed onto the settlement board. These observations are consistent with a settlement dependent on size under these experimental conditions. In the present study, the date of sieving affects the growth rate only at a early stage (44 days after fertilisation).

New settlement methods for growth experiments

The advantage of attachment on flat collectors for the purpose of this experiment was that all the variability in size was kept and no competition for space or food occurred between individuals. Very high attachment and survival rates were obtained with a system using glass plates (Ostrea edulis, Rodriguez et al., 1992) and PVC slats (Crassostrea gigas and

Crassostrea virginica, Hidu et al., 1981). PVC slats have also been used previously as a growing method after settlement (Smith et al., 1995). The growth appeared to be more efficient on this type of rearing system compared to cultch. This could be explained by the absence of spatial competition. On such a collecting surface, the growth is very homogeneous and is closely related to the total weight as observed on oysters settled on scallop shell (Haley and Newkirk, 1978). The high variability in size between the individuals just settled (a factor of between 3 and 4) shows that all the variability in size of spat is conserved and that both slow-growing and fast-growing spat have the same chance of reaching later stages.

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Tables

Table 1: Growth parameters for the larvae in Crassostrea gigas. SG = sieving group. Sieving date and attachment dates are given in days after fertilisation. H = mean height after sieving on a 200 µm-mesh sieve to retain larvae larger than 280 µm (mean ± s.e.), LGR = mean overall larval growth rate (mean ± s.e.).

SG	Sieving	Settlement	H (µm)	LGR (µm.d^{-1})
1	17	17	314.7 ± 3.4	18.7 ± 3.0
2	20	20, 21, 22, 23	328.2 ± 3.1	16.5 ± 2.6
3	23	23, 24	331.6 ± 3.5	14.5 ± 2.3
4	26	26, 27, 28, 29	340.6 ± 3.8	13.1 ± 2.1

Table 2: A. Results of MIXED model testing the effect of sieving group (SG) and the date of attachment and metamorphosis (DSET, nested within SG) on the growth rate in Crassostrea gigas. DSET and SG are treated as a random and a fixed effect factors respectively; B. Student-Newman-Keuls grouping distinguishes groups different with a 0.05 probability. For all data n = 363.

A.

Factor	F	p
SG	67.0	0.0001
SG(DSET)	8.5	0.0001

B.

SG	DSET(SG)	Mean ± s.e.	n	SNK Groups	
1	17	0.48 ± 0.02	99	-	A
2	20	0.52 ± 0.06	29	A	-
	21	0.45 ± 0.07	29	B	-
	22	0.40 ± 0.04	29	BC	-
	23	0.42 ± 0.08	9	C	-
2	All	0.45 ± 0.03	96	-	B
3	23	0.35 ± 0.03	50	A	-
	24	0.37 ± 0.03	49	B	-
3	All	0.36 ± 0.02	99	-	B
4	26	0.30 ± 0.03	31	A	-
	27	0.27 ± 0.03	25	B	-
	28	0.25 ± 0.04	23	C	-
	29	0.25 ± 0.04	8	BC	-
4	All	0.28 ± 0.02	87	-	C
All	All	0.40 ± 0.01	381	-	-

Figure legends

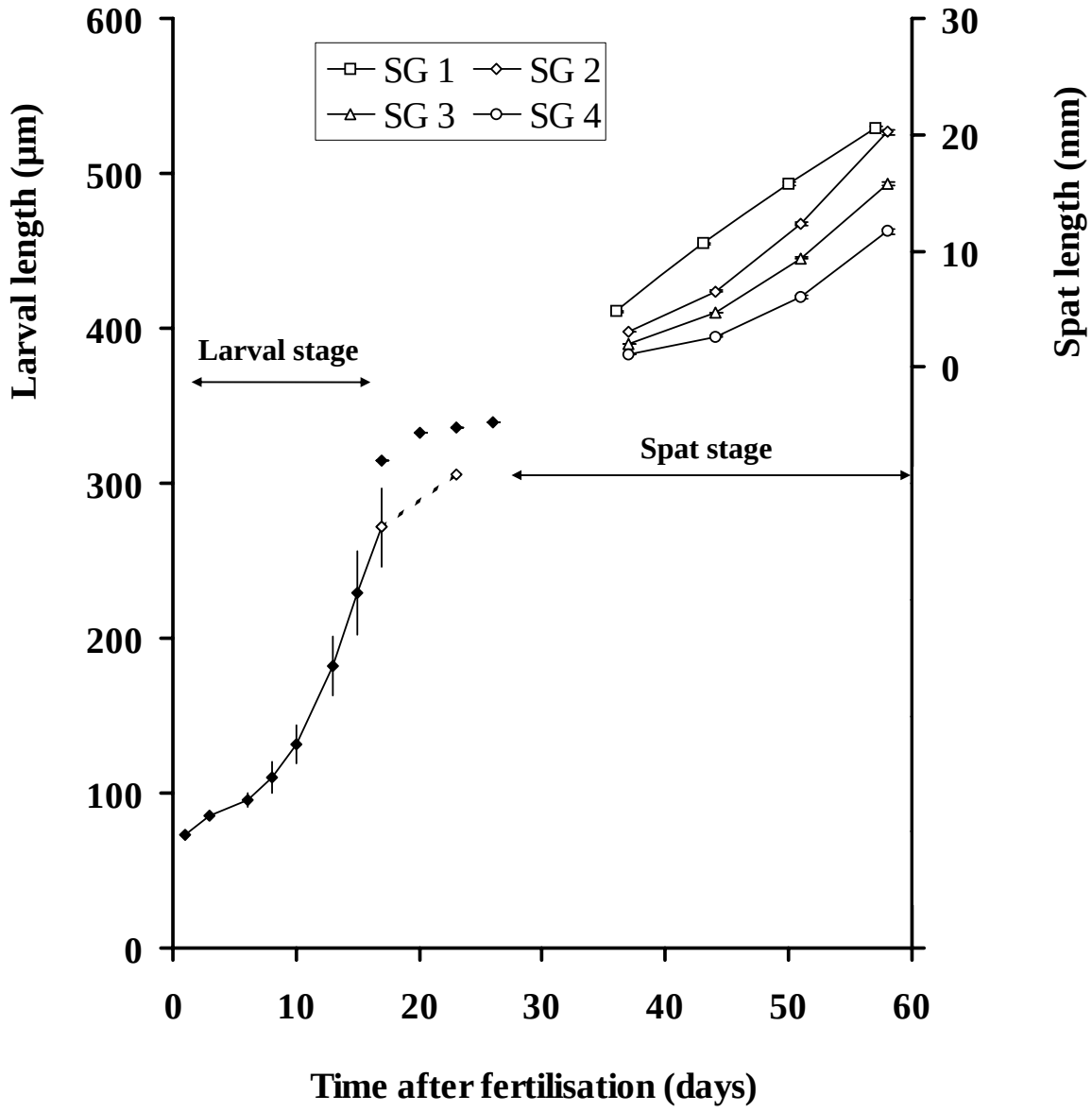
Figure 1: Growth and kinetics at larval and spat stages in Crassostrea gigas. Larvae were all reared together (0 to 17 days post fertilisation). Four sieving operations and attachment onto boards led to 4 sieving groups (SG) which attached and metamorphosed from 17 to 29 days after fertilisation and were then recorded for growth 4 times. SG1 represents the fastest growing larvae, SG4 represents the slowest growing larvae. Data are mean ± s.e.

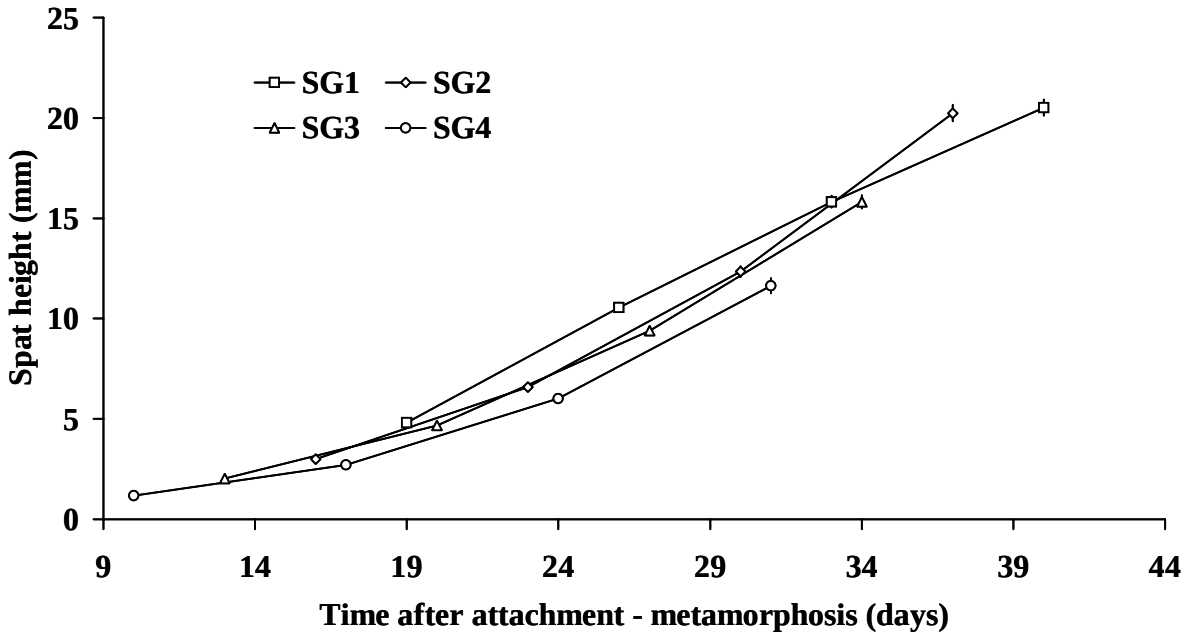
Figure 2: Spat growth curves of the 4 sieving groups in terms of date after metamorphosis in Crassostrea gigas. Time after attachment indicates days after the first day of attachment and metamorphosis. Data are mean ± s.e., n = 363.

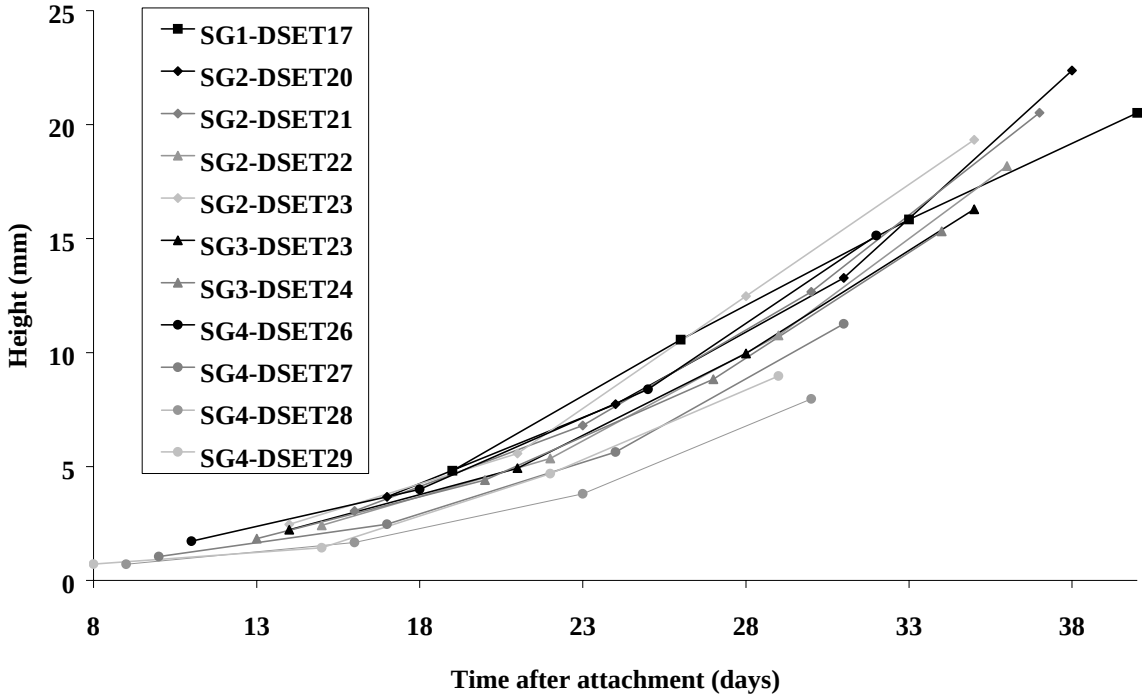
Figure 3: Spat growth curves for all combinations of SG and DSET in terms of date after metamorphosis in Crassostrea gigas. Data are mean ± s.e., n = 363.

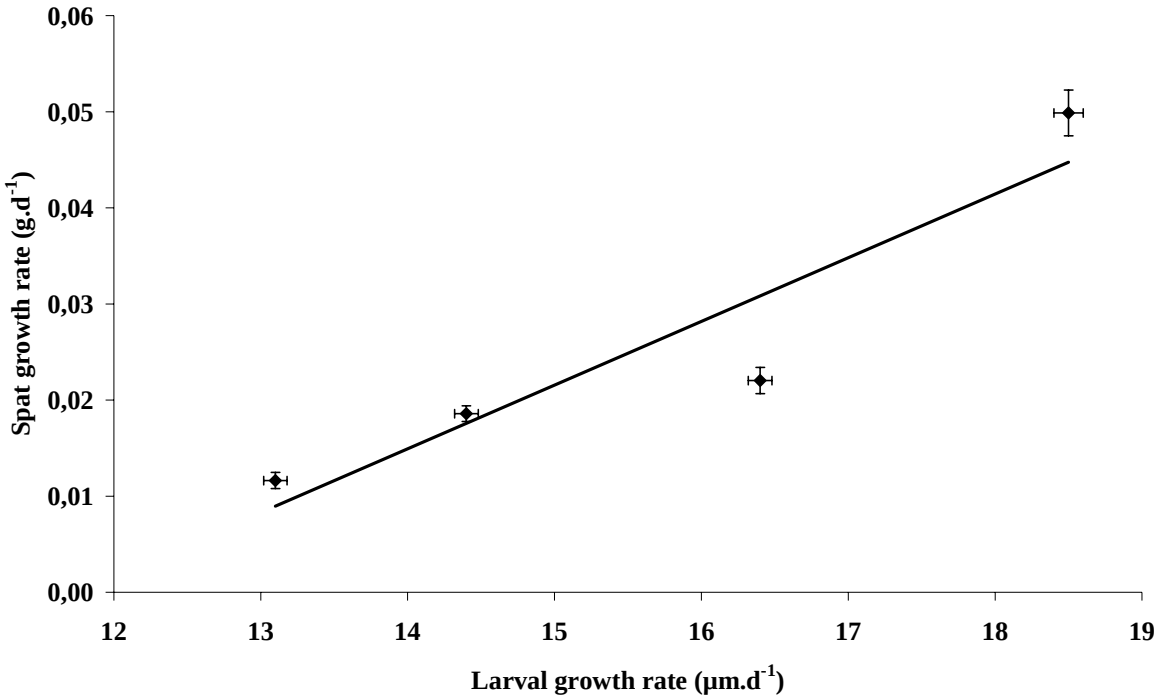
Figure 4: Relationship between larval growth rate and spat growth rate in Crassostrea gigas. Data are mean ± s.e.

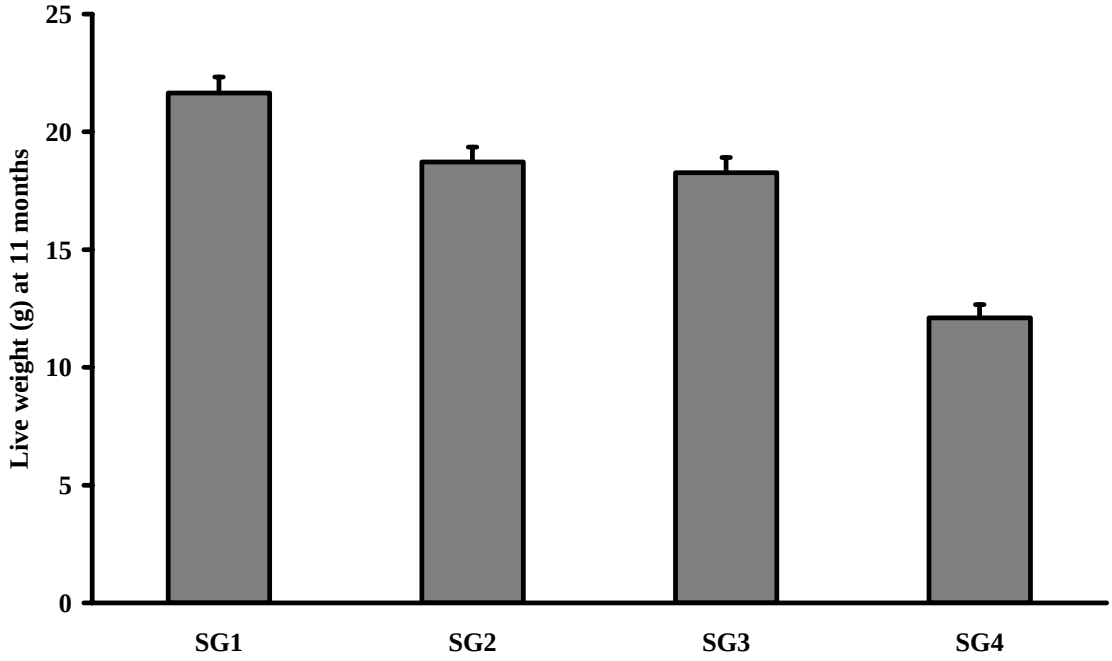
Figure 5: Total juvenile weight (g) at 11 months for the 4 sieving groups (SG) in Crassostrea gigas. SG1 represents the fastest growing larvae, SG4 represents the slowest growing larvae Data are mean ± s.e., n = 100 per SG.


SG 1
SG 2
SG 3
SG 4
Larval length (µm)
Spat length (mm)
Larval stage
Spat stage
Time after fertilisation (days)
600
500
400
300
200
100
0
30
20
10
0
0
10
20
30
40
50
60


SG1
SG2
SG3
SG4
Spat height (mm)
0
5
10
15
20
25
9
14
19
24
29
34
39
44
Time after attachment - metamorphosis (days)


SG1-DSET17
SG2-DSET20
SG2-DSET21
SG2-DSET22
SG2-DSET23
SG3-DSET23
SG3-DSET24
SG4-DSET26
SG4-DSET27
SG4-DSET28
SG4-DSET29
Height (mm)
0
5
10
15
20
25
8
13
18
23
28
33
38
Time after attachment (days)


0,06
0,05
0,04
0,03
0,02
0,01
0,00
Spat growth rate (g.d-1)
12
13
14
15
16
17
18
19
Larval growth rate (µm.d-1)


25
20
15
10
5
0
Live weight (g) at 11 months
SG1
SG2
SG3
SG4