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Aspects of veliger larval growth and byssus drifting of the spat of *Pecten maximus* and *Aequipecten* (*Chlamys*) *opercularis*

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Veliger larvae of *Pecten maximus* were reared from the early "D" larva stage to metamorphosis at 9, 12, 15, and 18°C. Growth rates and Q_{10} values were calculated at the different temperatures. In conjunction with data from previous studies, the average length of planktonic life for *P. maximus* larvae was estimated to range from 78 days at 9°C to 24 days at 18°C.

To investigate the potential for post-larval dispersal, the sinking rates of wild collected post-larvae (spat) of *P. maximus* and *Aequipecten (Chlamys)* opercularis, and laboratory reared spat of *P. maximus*, were measured in a glass tube. Spat of both species were sometimes able to slow their descent dramatically and it is proposed that, as with other bivalves, this was achieved by the production of a long, fine byssus drifting thread. The behaviour of some spat suggested that they could detach from the drifting thread and then secrete a further thread during their descent in the tube.

The data are discussed in relation to the differing dispersal capabilities of these two scallop species, an important consideration for the management of their fisheries.

Key words: pectinids, veliger larvae, growth, temperature, spat, byssus drifting.

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Introduction

The effective management of scallop (Pectinidae) fisheries ultimately depends upon a full understanding of the life cycle, population genetics, and biology of the scallops in the fishery. Although much is now known about the biology, population genetics and larval development of scallops (Beaumont and Zouros, 1991; Cragg and Crisp, 1991; Shumway, 1991; Beaumont, 1991), there remain aspects of the early life cycle which are the subject of some speculation.

First, little is known about the effects of food availability or temperature on the duration of the planktonic veliger larval life. During this phase, larvae may be carried many miles from their origin, or, by virtue of cyclical currents, may travel only a short net distance before metamorphosis. Both the duration of planktonic life, and the hydrography of the area, will therefore affect dispersal and both components need to be supported by real data when attempting to model dispersal (Darby and Durance, 1989).

Second, it is not always clear how metamorphosed, and therefore apparently immobile, post-larvae (traditionally termed "spat") or juvenile scallops are recruited onto the adult beds. For example, in offshore beds off the southwest coast of the UK, small spat (< 2 mm) are occasionally recorded attached to hydroids within adult beds. Elsewhere, larger spat (5–15 mm) are found attached to algae, or free living on gravel in settlement areas which are remote from adult beds (Dare and Bannister, 1987). It is not known whether spat from such settlement areas perish or whether they are able to disperse to the adult beds. If they do disperse, this might be accomplished by floating or rafting (Highsmith, 1985) or by the swimming of juveniles. However, an alternative mechanism for secondary dispersal of spat, byssus drifting, has been demonstrated for other bivalves (Sigurdsson *et al.*, 1976; Lane *et al.*, 1985) and gastropod molluscs (Martel and Chia, 1991).

Sigurdsson *et al.* (1976) showed that spat of certain bivalves are able to secrete rapidly a single, long, fine thread from the byssus glands in their foot. This thread acts as a drogue enabling spat to be entrained into the water column at low current speeds. Although invisible to the naked eye, the threads can be visualized microscopically by Alcian blue staining (Sigurdsson *et al.*, 1976). In a detailed study of byssus drifting in *Mytilus edulis* spat, Lane *et al.* (1985) collected drifting threads on grids and viewed them under an electron microscope. Threads were

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typically 1–3 µm in diameter and could reach 7 cm in length for a 750 µm shell-length mussel spat. The deployment of such threads typically reduced sinking rates of small mussel spat from 8 mm s^{-1} to 1 mm s^{-1}.

It is now widely accepted that byssus drifting is an important behavioural mechanism for secondary dispersal in planktotrophic bivalves and also for primary dispersal in other mollusc species that lack a planktonic stage (Martel and Chia, 1991).

Data on the duration of larval life, and the potential for secondary dispersal by byssus drifting, are both important components in any management models for scallop fisheries. This paper reports on the effect of temperature on the duration of the planktonic life of the veliger larvae of *Pecten maximus* (L.) and also presents data which demonstrate that the spat of both *P. maximus* and the queen scallop, *Aequipecten opercularis* (L.), are capable of retarding their sinking rate in the water column, presumably by secreting a byssus thread.

Materials and methods

Veliger larval culture

P. maximus veliger larvae were produced in September 1990 at the IFREMER hatchery at Argenton in Brittany, France. Two ripe Rade de Brest scallops were used in the spawning and there was little or no self-fertilization. Three days after fertilization, veliger larvae were produced which were then cultured for a few days at 18°C with 8 ppm of the antibiotic chloramphenicol added. Eight days after the spawning, larvae were transported, in a thermos flask, by sea and road to Menai Bridge, where they were cultured, without antibiotics, following the procedure given by Gruffydd and Beaumont (1972). Duplicate 2-l plastic beakers were used to culture the larvae at four temperatures, 18, 15, 12, and 9°C. Cultures were set up at a density of approximately 5 larvae ml^{-1}, were given a change of filtered sea water (0.2 µm pore size; UV sterilized) every 2 or 3 days and were fed a mixture of *Pavlova lutheri* (Droop) Green and *Rhinomonas* (*Rhodomonas*) *reticulata* (Lucas) Novarino at a ratio of 40 to 10 cells μl^{-1}, respectively.

Samples of larvae were photomicrographed at various times during the trial and shell lengths of 100 individual larvae from each sample were measured directly from enlarged negatives (Beaumont and Budd, 1982). A larva was regarded as having metamorphosed when the gill buds and post-larval shell were visible.

Spat sinking rates

Spat for the sinking rate trials were obtained from two sources. *A. opercularis* spat and larger *P. maximus* spat were taken from a collector bag deployed in the Kyle of Lochalsh, Scotland, and brought by road to Menai Bridge. Spat were held alive in running sea water at ambient temperature until required. Smaller *P. maximus* spat were obtained from the cultures of larvae reared at 18°C and 15°C in the larval rearing trial.

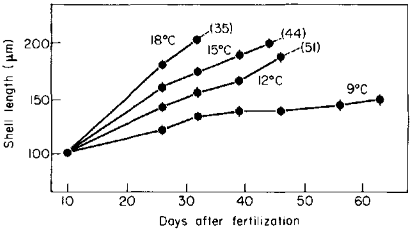

Figure 1. Growth of *P. maximus* veliger larvae at different temperatures. Points on graph represent means from two replicate cultures: vertical lines are standard errors. Numbers in parentheses indicate number of days after spawning when 25% of larvae in a culture had metamorphosed. Cultures reared at 9°C failed after 65 days and produced very few metamorphosed individuals.

A 2.3-m high x 7-cm diameter glass tube similar to that used by Lane *et al.* (1985) was filled with filtered sea water at 32‰ salinity. The water was allowed to equilibrate to ambient laboratory temperature (16 ± 1°C) before experiments were carried out in order to avoid thermally induced currents within the tube. The sinking rates of spat introduced into the column were recorded using a hand-held switch linked to a BBC microcomputer which recorded the time taken for an indivdual spat to fall successive distances of 5 cm down the column.

Individual spat were photomicrographed before being introduced into the column and shell lengths were measured later from the negatives. A tap was fitted to the bottom of the column to enable spat to be retrieved after each trial. Some of these spat were then killed, using formalin, and, after a brief period, were reintroduced into the column as controls.

Results

Larval growth at different temperatures

Results of larval growth at different temperatures are given in Figure 1. A few metamorphosed post-larvae were eventually observed in cultures reared at 9°C after 65 days, but most larvae had died or were moribund by this time and these low temperature cultures were therefore discontinued. All other cultures produced spat and the times taken for 25% of the larvae to reach metamorphosis at the different temperatures are given in Figure 1. The warmest culture condition (18°C) produced 25% metamorphosis within 35 days from fertilization, while the

Table 1. Growth rates and Q_{10} values for *P. maximus* veliger larvae reared to metamorphosis at different temperatures. Data from Gruffydd and Beaumont (1972) are given in parentheses.

Temperature in °C	Growth rate in µm day^{-1}	Q_{10}
9	0.97	
12	1.88 (2.63)	2.00 (2.9)
15	2.44 (4.14)	
18	3.13 (5.91)	1.90 (2.4)

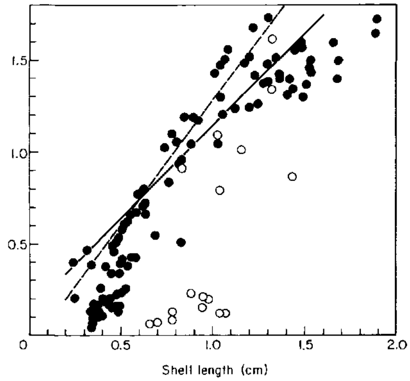

Figure 2. Sinking rates in cm s^{-1} of *P. maximus* (closed circles) and *A. opercularis* (open circles) in relation to size. Each point represents the slowest sinking rate recorded over a 5-cm distance during the descent of a single spat. The average sinking rates of killed spat from each species were regressed against size, and are shown by the continuous regression line for *P. maximus* and the broken line for *A. opercularis*.

coolest successful cultures (12°C) required 51 days to reach this stage.

Growth rates and Q_{10} values at the various temperatures are given in Table 1, and are both low in comparison with data given by Gruffydd and Beaumont (1972).

Spat sinking rates and byssus drifting

Sinking rates were recorded for more than 100 living *P. maximus* spat, of which 66 were recovered, killed, and reintroduced into the column as controls. Figure 2 shows the minimum sinking rates of scallop spat in relation to their size, and regression lines, based on the average sinking speeds of killed spat, are included for comparison. A very large proportion of *P. maximus* spat smaller than 500 µm shell length had considerably lower sinking rates than killed controls. We have called such spat "byssus drifters" (Sigurdsson *et al.*, 1976).

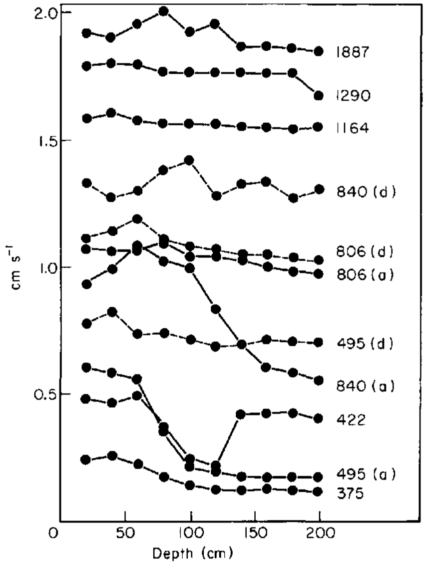

Figure 3. Sinking rates of live *P. maximus* spat introduced into a 2.3-m sea-water column. Points represent average sinking rates over 20-cm intervals. Individual spat are labelled according to their shell length (in µm) on the right hand side of the figure. Some individuals were introduced into the column twice, the first time alive (a), and the second time after having been retrieved and killed (d).

Byssus drifting threads of bivalve spat are typically between 1 and 3 µm in diameter and it is not possible to detect them with the naked eye (Lane *et al.*, 1985). Nevertheless, we are certain that some of the scallop spat in our experiments were secreting byssus drifting threads because occasional spat were observed which had become adhered to the pipette before they were introduced into the water column. Such individuals remained connected to the pipette, or to the water surface, but often descended several centimetres down the column without breaking the connection. By passing a seeker between the spat and the surface it was easy to see that the two were connected and thus demonstrate the presence of an invisible thread.

Examples are given in Figure 3 of an individual *P. maximus* spat [806(a),(d)] which sank down the column at the same rate whether alive or dead, and other individuals (byssus drifters) which were able to retard their sinking rate significantly when alive [840(a),(d); 495(a),(d)]. Certain byssus drifters (e.g. 422) were clearly able to vary their sinking rate in some way during their descent of the column.

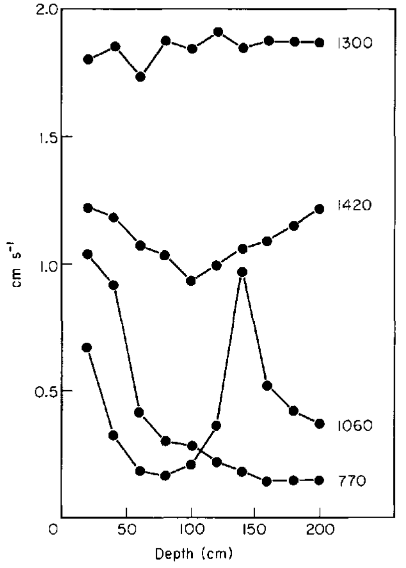

Figure 4. Sinking rates of live *A. opercularis* spat introduced into a 2.3-m column of sea water. Points represent average sinking rates over 20-cm intervals. Individual spat are labelled according to their shell length (in µm) on the right hand side of the figure.

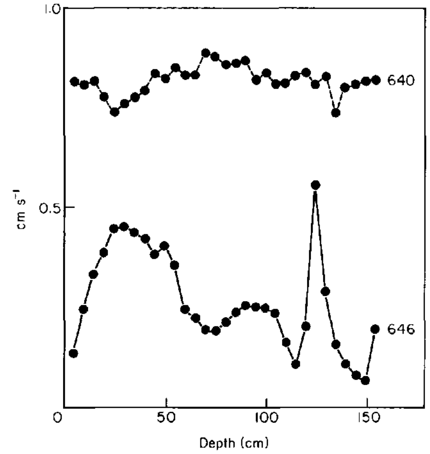

Figure 5. Sinking rates of one dead (broken line) and one living (solid line) spat of *A. opercularis* introduced into a 2.3-m column of sea water. Points represent sinking rates over 5-cm intervals. Shell length of specimens is given (in µm) on the right hand side of the figure.

Sinking rates were recorded for 17 living and 16 killed *A. opercularis* spat (Fig. 2), and it is clear that byssus drifting behaviour was much more widespread, and occurred in larger spat of this species compared with *P. maximus*. Records of the descent of living individuals (Fig. 4) showed that a spat of 1420 µm was able to reduce its sinking rate considerably before increasing again, a 770 µm spat slowed down from about 1.1 cm s^{-1} to 0.15 cm s^{-1} over a distance of 1.5 m, and an individual of 1060 µm demonstrated the ability to alter its sinking rate dramatically over the range of 0.2 to 1.0 cm s^{-1}. A more detailed analysis of this behaviour is given in Figure 5 where a byssus drifter of 646 µm is compared with a killed control of a similar size. The expanded vertical axis and the use of 5-cm depth intervals enable the minor fluctuations in sinking rate (0.8 ± 0.05 cm s^{-1}) of the killed control to be seen. These are probably the result of random changes in orientation during the descent. In contrast, not only does the live spat descend at a much slower rate overall (0.25 cm s^{-1}), but its speed of descent changes over 5 or 10 cm intervals.

It was noticeable that live *P. maximus* spat usually descended more slowly than dead spat within the first 20 cm of the column whether or not they went on to exhibit byssus drifting. Data for 22 individual spat (recorded both alive and dead) are given in Figure 6(a) as percentages of the sinking rate of dead versus live individuals over the first 20 cm. The trend is clear: on average, live spat which did not show any evidence of byssus drifting in the column, somehow, actively slowed their fall over the first 20 cm. It may be that the foot was extended and provided a small amount of drag, but we were not able to make observations to confirm this possibility.

In contrast, so many *A. opercularis* spat exhibited apparent byssus drifting that it was not possible to demonstrate any initial decline in the sinking rate of those that did not (Fig. 6b).

Discussion

Larval growth

As expected, the temperature at which *P. maximus* larvae were reared had a significant effect on their growth rate, which ranged from 0.97 µm day^{-1} at 9°C to 3.13 µm day^{-1} at 18°C. However, data from Gruffydd and Beaumont (1972), presented for comparison in Table 1, indicate that much higher growth rates have previously been achieved in the larval culture of this species. Furthermore, Beaumont *et al.* (1982) reported average larval growth rates of between 3 and 4 µm day^{-1} at 15°C, regardless of season, over an 8-year period, and Cochard and Gerard (1987)

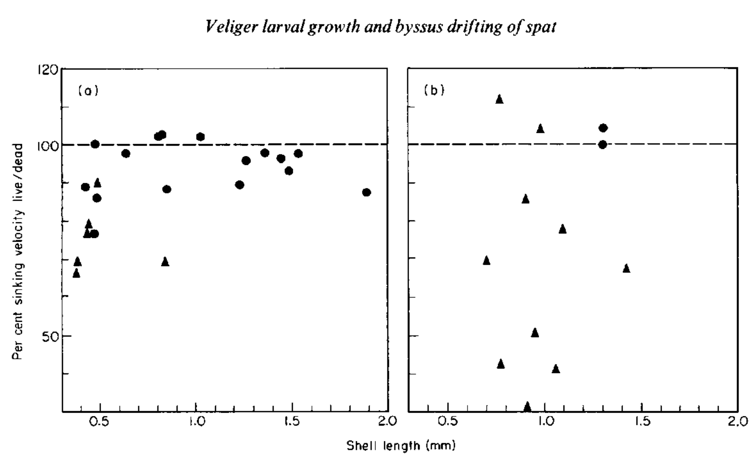

Figure 6. Rate of sinking of killed scallop spat down the first 20 cm depth of a column, given as a percentage of the sinking rate of the same individuals when alive. Spat which are assumed to have byssally drifted while descending the column alive are indicated by solid triangles; spat which did not drift are shown as solid circles. (a) *P. maximus*. (b) *A. opercularis*.

Table 2. Average growth rate and length of planktonic life for the larvae of *P. maximus* for the temperature range 9–18°C. Based on data as indicated in the text. * = data are derived from experimental trials; other figures are interpolated.

Average sea surface temperature °C	Average growth rate (μm day^{-1})	Average length of planktonic life (days)
9*	1.61	78
10	2.11	59
11	2.61	48
12*	3.13	40
13	3.44	36
14	3.75	33
15*	4.07	31
16	4.45	28
17	4.83	26
18*	5.21	24

and Paulet *et al.* (1988) give growth rates ranging from 3–8 μm day^{-1} at 18°C, depending on season. It is clear, therefore, that the growth rates achieved in the trial described here were lower than average for cultured larvae.

The Q_{10} values over the range of 12 to 18°C do differ somewhat between this study and that of Gruffydd and Beaumont (1972). However, our Q_{10} values are close to those given for *Mytilus edulis* veligers by Sprung (1984a; Q_{10} over 12–18°C = 1.9). Confirmation that our estimates for length of larval life at different temperatures (Table 2) are realistic comes from inspection of the relationship between temperature and time to metamorphosis for different pectinids given in Cragg and Crisp (1991). For example, larvae of cold-water species (6–8°C) take up to 70 days to reach metamorphosis (*Chlamys islandica*; Gruffydd, 1976), while only 10 days are required for warm-water species (20–28°C; *Argopecten irradians*; Castagna and Duggan, 1971).

There have been no systematic studies published that relate growth rates of scallop larvae in hatchery culture to their growth rates in the wild. This is not surprising in view of the practical difficulties associated with such a task. Differences in growth would be expected to result principally from differences in nutrition. Both algal and larval concentrations are likely to be very much lower in the wild than under hatchery conditions (Sprung, 1984b). On the other hand, availability of both particulate and dissolved organic matter is considerably reduced in the hatchery and these sources are now recognized as important components of the bivalve larval diet (Manahan, 1983). Sprung (1984a,b) cultured mussel, *M. edulis*, larvae at a range of algal densities, some of which were environmentally realistic, and concluded that larval behaviour depended on algal concentration. Although, as a result of studies like those of Sprung (1984a,b) we have a reasonable knowledge of bivalve larval feeding in laboratory conditions, we still do not know with any certainty how this relates to the situation in the wild.

If we can make the assumption that, for a given temperature, there is little difference between average growth rates of scallop larvae in the wild and in the hatchery, then the mean length of planktonic life in relation to sea surface temperature is likely to follow the pattern indicated in Table 2. These values have been estimated from the results of the larval rearing trial by assuming that the growth rates we achieved represent approximately 60% of the average hatchery growth rate. The figure of 60% has been arrived at by comparison with the French data (Cochard and Gerard, 1987) and the data of Gruffydd and Beaumont (1972) and Beaumont *et al.* (1982). It is further assumed that growth is linear, and that the initial shell length of the veliger larva is 100 µm and reaches 225 µm at metamorphosis.

Byssus drifting behaviour

The results from sinking-rate experiments clearly demonstrate that the spat of both scallop species are capable of retarding their free-fall down a water column. Comparison with the behaviour of the spat of other bivalves (Sigurdsson *et al.*, 1976; Lane *et al.*, 1985) indicates that this retardation is most probably caused by the secretion of a byssus drifting thread. This conclusion is supported by the occasional direct confirmation of the existence of some kind of connection, invisible to the naked eye, between individual spat and the surface of the water or the pipette used to introduce them into the water column.

An unexpected aspect of the results is the apparent difference in the byssus drifting capabilities of the two species. Large *A. opercularis* spat, up to 1.4 mm, exhibited byssus drifting behaviour, while very few *P. maximus* spat larger than 500 µm did so (Fig. 2).

An interesting observation, also seen in the post-larvae of other bivalves (Sigurdsson *et al.*, 1976; Lane *et al.*, 1985), is the ability of pectinid spat to change their sinking rate dramatically during their descent of the column. Sigurdsson *et al.* (1976) and Lane *et al.* (1985) have suggested that this may be a result of spat detaching from the drifting thread, falling freely for a while, and then secreting a new thread. Alternatively, Lane *et al.* (1985) propose that an additional length of drifting thread might be suddenly discharged with the result that the spat free-falls briefly before the slack is taken up and its descent is checked. This type of behaviour is well illustrated for *A. opercularis* (Fig. 4), where the live spat presumably detaches from its drifting thread at 115 cm depth and falls freely for 10 cm before rapidly secreting a new thread. In contrast, the much more gradual increase in sinking rate that takes place between 5 and 25 cm depth cannot be due to the spat detaching from its thread but, we suggest, might be due to the spat actively climbing back up the thread and so reducing thread length. It should also be noted that the recorded sinking rate over the first 5 cm of descent for the live spat in Figure 4 was 0.15 cm s^{-1}. This extremely slow rate of descent for the first 5 cm was almost certainly caused by the presence of a byssus drifting thread already secreted by the spat before it was introduced into the column.

One implication of our observations is that fishery models of potential post-larval dispersal need to be constructed using different parameters for the two scallop species. The potential for secondary dispersal by byssus drifting would appear to be much greater in *A. opercularis* than in *P. maximus*. Published data on post-metamorphosis growth rates of scallops are scanty, but Beaumont *et al.* (1982) indicate that 8–10 weeks of growth after settlement might be needed for *P. maximus* spat to reach a size of 1 mm, thus giving a possible byssus drifting period of up to 4 to 5 weeks. Nevertheless, much more information is needed about byssus drifting behaviour since we do not know when, how frequently, or under what circumstances this behaviour may be initiated.

A second implication is related to the fact that most *P. maximus* spat observed on algae, hydroids, or bryozoans are larger than 500 µm (Dare and Bannister, 1987). If, as our results suggest, larger *P. maximus* spat seldom secret byssus drifting threads, then further dispersal by byssus drifting from these early settlement substrata seems less likely. Thus, spat settling remote from adult beds are unlikely to be recruited into those adult beds by the process of byssus drifting. On the other hand, much larger *A. opercularis* spat are able to drift byssally and this mode of transfer from a remote settlement area to an adult bed would still appear to remain a strong possibility.

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