

Effects of elevated levels of suspended particulate matter and burial on juvenile king scallops *Pecten maximus*

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ABSTRACT: The effects of exposure to elevated levels of suspended particulate matter (SPM) and burial on juvenile king scallops *Pecten maximus* L. were assessed in 2 separate experiments. Shell gape activity was monitored during exposure to no SPM and 'low' (50 to 100 mg l⁻¹) and 'high' (200 to 700 mg l⁻¹) levels of SPM for 18 d. The frequency of shell 'claps' (a complete shell closure) and shell movements (of ≥10°) differed significantly among treatments. Shell 'claps' and movements were significantly greater under high SPM than under low or control conditions. Scallops under low and high levels of SPM showed significantly lower growth rates compared to scallops under control conditions. The response to burial was assessed under varying burial duration (1 to 8 d), depth (0 to 5 cm) and size-fraction of sediment (fine: 0.1 to 0.3 mm, medium fine: 0.4 to 0.8 mm and coarse: 1.2 to 2.0 mm diameter). All 3 conditions had a significant influence on the ability of scallops to emerge from burial, as well as on mortality while buried. Emergence was higher at shallower depths and in coarse to medium grain sizes. Mortality rates while buried under coarse and medium grain sizes were low and appeared unrelated to depth, while within fine sediment, mortality increased with depth of burial. Survival decreased across all 3 sediment types with increasing burial duration. Comparison with earlier studies indicates that *P. maximus* appears more tolerant of burial and elevated levels of SPM than the queen scallop *Aequipecten opercularis*. Elevated SPM did not have any short-term effects on survival; however, the reduction in growth rate observed has implications for the management of scallop fishing grounds.

KEY WORDS: Sedimentation · Aggregate extraction · Dredging · Scallop fisheries · Growth rate

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INTRODUCTION

Near-shore marine environments are naturally subject to a large variation in suspended particulate matter (SPM) levels, driven by oceanographic and atmospheric cycles (Orpin et al. 2004), wave action, extreme weather events and increased river output following high rainfall. Major storms can deposit a layer of additional sediment of several centimetres at 20 m depth and several millimetres at 40 m; for example, 4 to 10 cm of sand deposition was recorded at 28 m after a storm in the Helgoland Bight, southern German Bight (Hall 1994). Scallops present in highly dynamic environments are expected to

demonstrate some tolerance to naturally elevated SPM levels; however, there may be a threshold above which negative impacts occur. In coastal areas, anthropogenic disturbance from towed bottom fishing gear (Black & Parry 1994) and aggregate extraction (the aggregate screening process returns large quantities of sediment to the seabed) can cause further increases in SPM and potential burial or smothering of organisms by sediment. SPM levels during aggregate extraction are similar to those of major storm events (Last et al. 2011).

The response of benthic fauna to elevated SPM and burial vary widely among species and taxonomic groups (Last et al. 2011). On the southeast coast of

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England, fishing for king scallops *Pecten maximus* often occurs in the vicinity of aggregate extraction sites, with the 2 activities occasionally overlapping (Foden et al. 2010, Vanstaen et al. 2010). Scallop landings almost doubled between 2006 and 2010, and the fishery is now the third most valuable in the UK (Almond & Thomas 2010). With sediment loading in some coastal areas likely to increase over the coming decade due to changing climatic conditions (Pryor et al. 2005, Gregow et al. 2011) and increased demands for marine aggregates (Limpenny et al. 2011), quantification of the impacts of increased SPM and burial on scallops is important for successful management of the fishery.

Large plumes of suspended particles can produce SPM of up to 71 mg l^{-1} within a few hundred metres of an aggregate extraction site (Last et al. 2011). During the dredging process, the natural cohesion between sediment particles is broken, leaving behind finer particles that are more likely to be re-suspended during subsequent disturbance (Black & Parry 1994). Fine sediments require lower energy to suspend, tend to travel furthest and can be deposited up to 2 to 3 km from an aggregate extraction site (Desprez 2000, Robinson et al. 2005). Sediment plumes created by fishing gears also cause elevated SPM; sediment concentrations a few metres behind a scallop dredge can be 2 to 3 orders of magnitude greater (up to $60\,000 \text{ mg l}^{-1}$) than natural levels and up to 200 mg l^{-1} at a distance of 200 m behind the dredge (Black & Parry 1994). The size, spatial and temporal extent of the plume generated by either activity is site specific, depending on particle size, the quantity suspended, local hydrodynamics and the frequency of dredging (Boyd & Rees 2003).

Resuspension of bottom sediments during aggregate dredging can smother organisms and interfere with growth, feeding and survival rates (Rogers 1990, Gilmour 1999, Meager & Batty 2007). Energetic costs to bivalves associated with increased levels of SPM are due to increased shell closures (to facilitate clearing of sediment from the mantle), particle clearance rates and pseudofaeces production (during filter feeding). Increased levels of SPM affect feeding efficiency in *Pecten maximus* (Gibson 1956) and elicit a significantly higher frequency of shell closures or 'coughs' (to clear sediment from the mantle) and 'claps' (an escape response) in the queen scallop *Aequipecten opercularis* (Last et al. 2011). Shell closures result in an accelerated heart rate, a decrease in blood oxygen concentrations and invocation of anaerobic metabolism in bivalves (de Zwaan 1977, Gudderley & Portner 2010). Scallops require a long

period of aerobic recuperation after such activity (Grieshaber & Gade 1977, Jenkins & Brand 2001), and physical responses take several hours to return to normal levels in exhausted scallops (Thompson et al. 1980, Marsh et al. 1992, Fleury et al. 2005), with implications for survival and fitness due to the metabolic costs involved.

The present study aims to quantify the short-term impact of elevated levels of suspended sediment on juvenile *Pecten maximus* (~1 yr old). Two laboratory-based experiments were performed (1) to investigate the effect of different concentrations of SPM on scallop behaviour and growth and (2) to test the emergence and survival rate of juvenile scallops while buried under different sediment types, depths and duration of burial. The results of the present study provide empirical evidence that can inform sustainable resource management.

MATERIALS AND METHODS

Sample collection

Pecten maximus (1 yr old; mean shell height \pm SD: $29.5 \pm 2.256 \text{ mm}$) were obtained from Northwest Shellfish, Mulroy Bay, north-west Ireland. Sediment in the bay varies from coarse sand to soft mud in sheltered areas. The scallops were acclimatised in holding tanks in the aquarium at the School of Ocean Sciences, Menai Bridge (Wales, UK), for 2 wk prior to the commencement of the experiments. A continual supply of ambient seawater from the main aquarium intakes provided a food supply to the scallops, which was supplemented 3 times a week with a mixed solution of cultured microalgal species: *Pavlova lutheri*, *Tetraselmis chuui*, *T. iso* and *Rhinomonas reticulata*.

Suspending sediments in aquaria

Sediments were re-suspended in custom-built, cylindrical aquarium tanks based on designs published by Last et al. (2011) but using smaller tanks (tank diameter 46 cm, volume 60 l, paddle width 15 cm; Fig. 1) and a small pump to drive the uplift rather than an air supply. This type of system allows control of the current flow and sedimentation rate (Davies et al. 2009). The system had a continuous supply of seawater throughout the duration of the experiments (approximately 12 l h^{-1} per tank, ranging from 14.2 to 17°C during the course of the experiment).

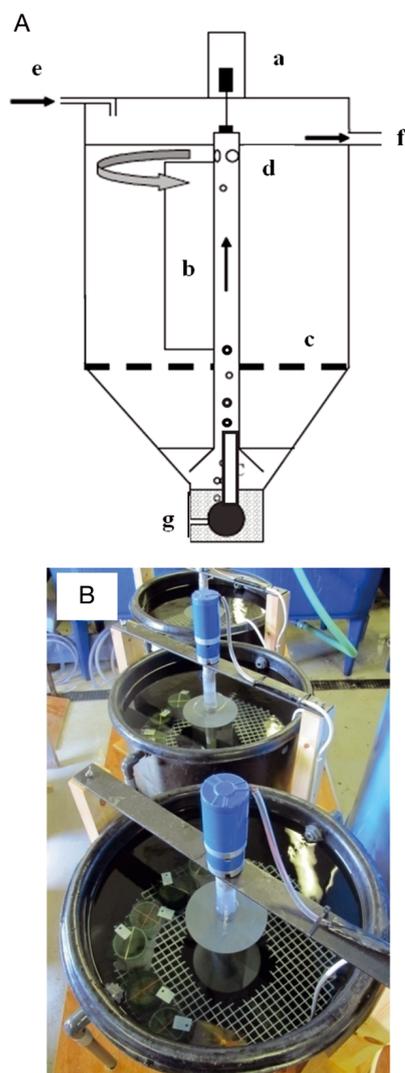


Fig. 1. (A) Paddle vortex resuspension tank (pVoRT). Components include (a) a motor to drive the paddle, (b) paddle, (c) horizontal plastic grid, (d) holes for water and sediment outflow, (e) seawater inflow, (f) water outflow and (g) pump. Source: Last et al. (2011). (B) Experimental set-up showing the 3 pVoRTs

Effect of SPM on behaviour

To measure the effects of increased SPM on scallop activity levels, shell gape activity was monitored using Hall-effect sensors (Wilson et al. 2005). The approach works by attaching a small magnet to one side of the bivalve shell and a Hall-effect sensor (that detects the presence of the magnet on a linear scale) to the other. The movement of the magnet in relation to the sensor was logged and calibrated to the distance between the magnet and sensor at the end of the experiment. Calibration was done by opening the scallop shells at the point furthest from the hinge

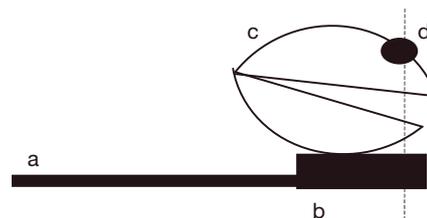


Fig. 2. Set-up for individual scallops *Pecten maximus* for the suspended particulate matter (SPM) experiment: (a) waterproof cable; (b) Hall sensor enclosed in epoxyresin; (c) scallop; (d) magnet. Dashed line indicates the position of the magnet, directly above the Hall sensor

using plastic callipers and taking sensor output values when the distance between the 2 shells was 1 cm, 0.5 cm and when the shell was fully closed. The following formula was used to calculate gape angle in degrees: $\theta = 2 \times \arcsin(0.5 W/L)$ after Wilson et al. (2005), where W is the distance between the 2 shells, and L is the distance between the hinge and the edge of the shell (shell height). The Hall sensor output values were regressed against the shell gape measurements to produce a calibration curve, and the values were used to transform the Hall sensor output values to the shell gape angle in degrees.

For this experiment, 48 scallops of similar size were selected, measured (shell height in mm) and wet-weighed immediately prior to the start of the experiment. A total of 24 Hall-effect sensors (Honeywell) were potted in epoxy resin, and an individual scallop was glued (curved shell down) to each sensor using superglue. A 6 mm diameter \times 3 mm high neodymium magnet was then glued to the top scallop shell, directly in-line with the sensor underneath (Fig. 2). During the experiment, the magnets detached from 4 of the scallops, and during the calibration and data analysis a further 8 scallops were eliminated due to issues with the data collected by the sensors (for example, insufficient resolution due to too large a distance between magnet and sensor). This meant that for the analysis, data from 3 scallops in the control, 4 in the 'low' SPM and 5 in the 'high' SPM treatment (see below for treatment details) were used.

The Hall-effect sensors were linked to a custom built data-logger by 3-strand PVC coated waterproof cable, sampling at 1 Hz. The sensor and scallop were then attached to a plastic grid base in the tanks using cable ties. Eight scallops were attached inside each of 3 separate cylindrical tanks in this way, with their shell opening facing into the direction of the current (their naturally preferred orientation to water flow; Eckman et al. 1989, Bricelj & Shumway 1991). Eight control scallops were also placed in each of the

3 tanks, inside a large-meshed plastic pot to minimise interference of water flow but prevent escape of the scallops. All individuals were left for 16 h to acclimatise in the aquaria before any sediment was added. Fine sediments of 0.1 to 0.3 mm were used for sediment loading, as these take the longest time to settle after disturbance and therefore are expected to have the most prolonged effects on filter feeding organisms. A different SPM treatment was maintained in each of the 3 tanks: no SPM (control), low (50 to 100 mg l⁻¹, mean 66.1 mg l⁻¹) and high (200 to 700 mg l⁻¹, mean 432.8 mg l⁻¹) SPM. The low SPM loading is similar to that which may be found during above-average wind conditions or within a few hundred metres of an aggregate extraction site (Last et al. 2011), and the high SPM loading is similar to that which may be experienced in close proximity (within ~50 m) of a passing scallop dredge (Black & Parry 1994). SPM levels were monitored daily and varied throughout the experiment due to sediment being entrained within the tanks and not available for uplift or lost through the outflow of the system. SPM levels in the 3 treatments were clearly different over the duration of the experiment (Fig. 3). Suspended sediment was measured by removing 500 ml of water from each treatment to be suction-filtered, dried in an oven at 90°C for a minimum of 6 h and weighed. During the SPM experiment, each tank was supplemented with 3 l of cultured algae daily (see 'Sample collection' for species). The ratio and species of algae used each day varied due to the availability of stock cultures; however, identical amounts of each species were added to each tank during each feeding event. The scallops remained in the tanks for 18 d, after which they were removed and the control scallops were re-measured and wet-weighed. The frequency of full shell closures, or 'claps', was analysed using the raw data (a sensor output reading for each second) over a 14 h period (16:00 to 06:00 h) each day for 7 d. This time period was selected for analysis as there were no periods of disturbance on any of the days during these times, and there was no observed change in shell activity between day and night hours.

The analysis was conducted on data from Days 11 to 17 of the experiment because during the first 5 d, satisfactory SPM levels had not been achieved in the aquaria, and there was an issue with the data logger on Days 9 and 10 causing data loss. Two periods with disturbance, when maintenance on the pumps was required (11:30 to 12:30 h on Day 12 and 11:30 to 13:30 h on Day 13), were omitted from the data set.

A clap was defined as an occurrence of shell gape angle of <10% of the total gape, immediately pre-

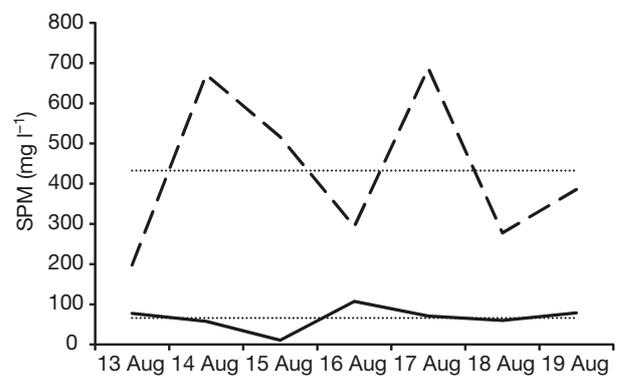


Fig. 3. Suspended particulate matter (SPM) levels in the low SPM (solid line) and high SPM (dashed line) treatments. Thin dotted lines represent mean values for the 2 treatments

ceded by an angle of >10% of total gape. Full shell closures were infrequent; therefore, the frequency of shell closures to an angle of <20° was also calculated. The frequency of shell movements was calculated as the frequency of events when shell gape angle changed (either increased or decreased) by ≥10°.

Mean Hall-effect sensor output values per minute were calculated for each individual, and the aggregated data were used to calculate the modal gape angle for each treatment over 7 d, expressed as a percentage of the maximum gape angle for each individual. A shell closure was considered to be an angle of <10% of the maximum recorded shell gape, and a maximum shell gape was defined as 90 to 100% of the maximum individual gape recorded throughout the duration of the experiment. This 10% window was used to allow for noise in the sensor output signal.

Growth rate was calculated from the pre- and post-experimental weights of the control scallops and expressed as the increase (or decrease) in weight over the 18 d experiment (g d⁻¹).

Effect of burial on behaviour and survival

Three independent cylindrical aquarium tanks (see 'Suspending sediments in aquaria') were used for this experiment to provide 3 replicates of each treatment. Two hours prior to the start of a burial procedure, the scallops in the holding tanks were provided with a mixed solution of cultured microalgal species (see 'Sample collection') to allow feeding to take place. One litre of algal culture was added to each ~17.5 l holding tank. The density of the cultures varied between 64 and 2304 cells μl⁻¹ over the duration

of the experiment due to extremes of warm weather. Scallops were randomly selected from the tanks for use in the experiments, and any epifauna attached to the shells was gently removed.

Three experimental burial depths were chosen: 1, 3 and 5 cm based on the deposition of sand expected after a major storm or aggregate dredging event. The deepest (5 cm) was based on the MarLIN burial tolerance assessment criteria, and these depths are the same as those used to assess the tolerance of *Aequipecten opercularis* (Last et al. 2011).

Individual burial chambers were constructed of sections of plastic tubing 6.5 cm in diameter and 2.5, 5.5 and 7.5 cm in height secured to a plastic base using elastic, and a plastic mesh was secured over the top of the chamber to prevent escape. Kiln-dried marine sediment was obtained from Specialist Aggregates Ltd. in 3 size compositions: fine (0.1 to 0.3 mm diameter), medium fine (0.4 to 0.8 mm diameter) and coarse (1.2 to 2.0 mm diameter). Each scallop was placed on a minimum of 1 cm layer of sediment in the bottom of a burial chamber and then buried under a selected amount of sediment (scallops were randomly assigned to treatments) with a 0.5 cm gap between the top of the chamber and the plastic mesh. Controls were placed on top of a 1 cm layer of sand in the burial chamber with no further sediment added. Burials were conducted for each sediment type at each depth and left for either 1, 2, 4 or 8 d depending on the assigned treatment. Burial durations were based on results for *Aequipecten opercularis* where >80% of individuals died following 2 or 4 d burial (Last et al. 2011). There were 3 replicates of each burial depth for each duration and sediment type. A procedural control for each treatment was also used, consisting of a scallop secured in a mesh bag and weighted down to prevent escape or being caught up in the motor or paddles. The current flow in the aquaria was maintained between 2 and 3 cm s⁻¹ to facilitate oxygen exchange in the burial pots and mimic natural tidal stream conditions. At the end of each treatment, the scallops were removed from the burial pots and visually assessed for survival. Scallops that had died during the treatment gave no resistance from the adductor muscle, and the sand around the scallop had turned black from oxidisation.

Statistical analysis

Mean maximum shell gape angle, frequency of claps, shell gape angles <20°, shell gape movements of ≥10° and mean growth rates (g d⁻¹) were compared

among treatments using 1-way analysis of variance (ANOVA). For pairwise comparisons, respective contrasts were examined.

For the burial experiment, generalised linear models (GLMs) with a binomial error distribution were formulated for the response variables—the emergence from sediment and mortality while buried—for the 3 experimental factors of depth, duration and sediment type. GLMs were performed in R utilizing the MASS package. Model simplification from the full model, i.e. all main experimental factors and interactions ($\gamma \approx \text{depth} \times \text{duration} \times \text{sediment type}$), was conducted using the stepAIC function. This was followed by investigating the significance of each factor and interaction term. Non-significant interactions were subsequently removed if the removal did not significantly affect the performance of the model, favouring the simpler model over a slightly improved Akaike's information criterion (AIC) (Zuur et al. 2009). Significance testing of main effects and interactions was conducted by fitting individual terms sequentially to form the optimal model in a hierarchical approach. The contribution of each effect to the explained deviance was tested by the χ^2 -test (p-values).

RESULTS

SPM tolerance

One of the control scallops in the control treatment died during the experiment, but all remaining control and treatment scallops across all treatments survived the full duration. There was no significant difference in the mean maximum shell gape angle of scallops among treatments (ANOVA: $F_{2,9} = 0.331$, $p = 0.727$), with mean maximum gape angle ranging from 36.60° (± 1.35) in the high SPM treatment to 39.02° (± 2.85) in the control (no SPM) treatment. Both the lowest and highest individual maximum gape angles were in the control, with 32.45° and 42.50°, respectively. Across all treatments, the mean gape angle per minute was ≥50% for >99% of the time. The frequency of shell clapping behaviour (defined as closure to <10% of maximum recorded shell gape angle) was low across all treatments (between 0 and 10 occurrences per 14 h sample period from each day). However, there was a significant difference among treatments (ANOVA: $F_{2,9} = 6.072$, $p = 0.010$, Fig. 4A), with post-hoc testing indicating that the frequency of shell claps were significantly higher in the high SPM treatment than in the control ($p = 0.015$).

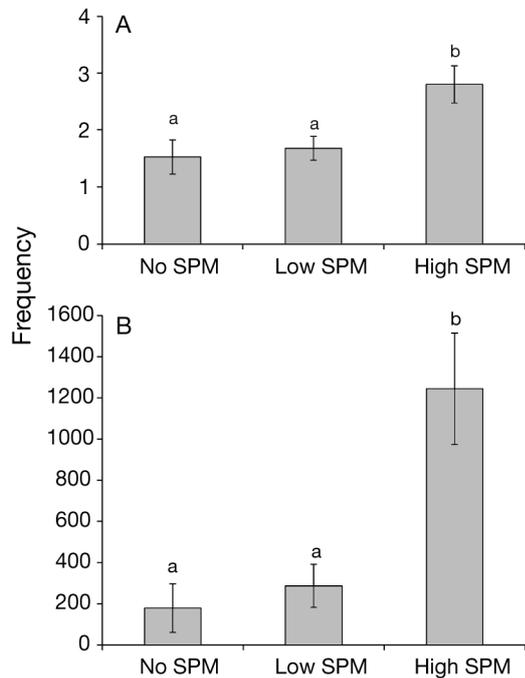


Fig. 4. *Pecten maximus*. (A) Mean frequency of 'claps' (shell closure to <10% of the maximum recorded shell gape angle) per 14 h period, over 7 d. (B) Mean frequency of occurrences of shell gape angle of <20° per 14 h period, over 7 d. For both panels, error bars indicate ± 1 SE. Different letters indicate significant differences between treatments. SPM: suspended particulate matter

and low SPM ($p = 0.034$). The difference in frequency of shell claps between the control and low SPM was not significant ($p = 0.972$).

The magnitude of shell movements was greater under elevated SPM levels, and the frequency of partial shell closures (defined as the occurrence of a shell gape angle of <20°) occurred much more frequently during the experiment; for example, 1 individual in the high SPM treatment exhibited over 5000 movements in a single 14 h period. A significant difference was found between treatments for the time spent at shell gape angles of >20° (ANOVA: $F = 5.97$, $df = 2$, $p = 0.0224$), with the frequency increasing with increasing SPM levels. It was significantly higher in high SPM than in low SPM (ANOVA: $p = 0.0343$) and in the control ($p = 0.0108$); however, the difference between the control and low SPM was not significant ($p = 0.41$, Fig. 4B). Partial shell closures were frequent, as indicated by plots of shell movements per second for individual scallops, which show differences in shell gape activity among SPM treatments (Fig. 5). In the no SPM treatment, the gape angle of both scallops shown in Fig. 5 did not fall below 55% during a 1 h time period, but there were

frequent movements of ~10% of full shell gape. In the low SPM experiment, larger shell movements, of at least 20% of full gape, were frequent. Movements of at least 20% of full gape were more frequent under high SPM than under low SPM, demonstrating a greater magnitude of shell movements under elevated SPM levels. Shell gape remained consistently lower in the high SPM treatment than in the other 2 treatments, at ~25 to 30% of full gape, compared to ~70 to 90% under low SPM and ~65 to 70% under no SPM. The maximum individual gapes for the scallops in Fig. 5 are 40.17° and 30.50° for no SPM, 32.06° and 27.58° for low SPM and 29.98° and 29.25° for high SPM.

There was also a significant difference among treatments in the frequency of shell movements (an increase or decrease in shell gape angle) of $\geq 10^\circ$ (ANOVA: $F_{2,9} = 45.267$, $p < 0.001$). Generally, there was an increase in the mean frequency of $\geq 10^\circ$ shell movements with increasing SPM levels; however, the lowest frequency recorded for an individual was 3.3 (± 0.5) per 14 h period in the low SPM treatment. The highest frequency recorded was 116 (± 14.9) per 14 h period in the high SPM treatment. Contrasts indicated that the frequency of $\geq 10^\circ$ shell movements was significantly higher in high SPM than in low SPM ($p < 0.001$) and the control ($p < 0.001$). The difference between the control and low SPM was not significant ($p = 0.855$).

The mean growth rate of the control scallops was highest in the no SPM treatment ($0.004375 \text{ g d}^{-1}$) and was lowest in the treatment with high SPM ($0.000844 \text{ g d}^{-1}$). The difference among the 3 treatments was significant (ANOVA: $F_{2,11} = 5.243$, $p = 0.015$; Fig. 6), with post-hoc testing indicating significant differences between the no SPM and high SPM treatments ($p = 0.023$) and the control and low SPM ($p = 0.049$). The difference in growth rate between the low and high SPM treatments was not significant ($p = 0.993$).

Burial tolerance

In total, there were 108 treatment individuals, 108 potted control scallops and 36 unpotted control scallops. All of the procedural and treatment control scallops survived the experiments and were thus removed from further analysis, and only 19 treatment scallops died during burial (18%). The majority of these were buried under fine sediment. There was no significant relationship between wet-weight at the start of the experiment and survival of the scallops

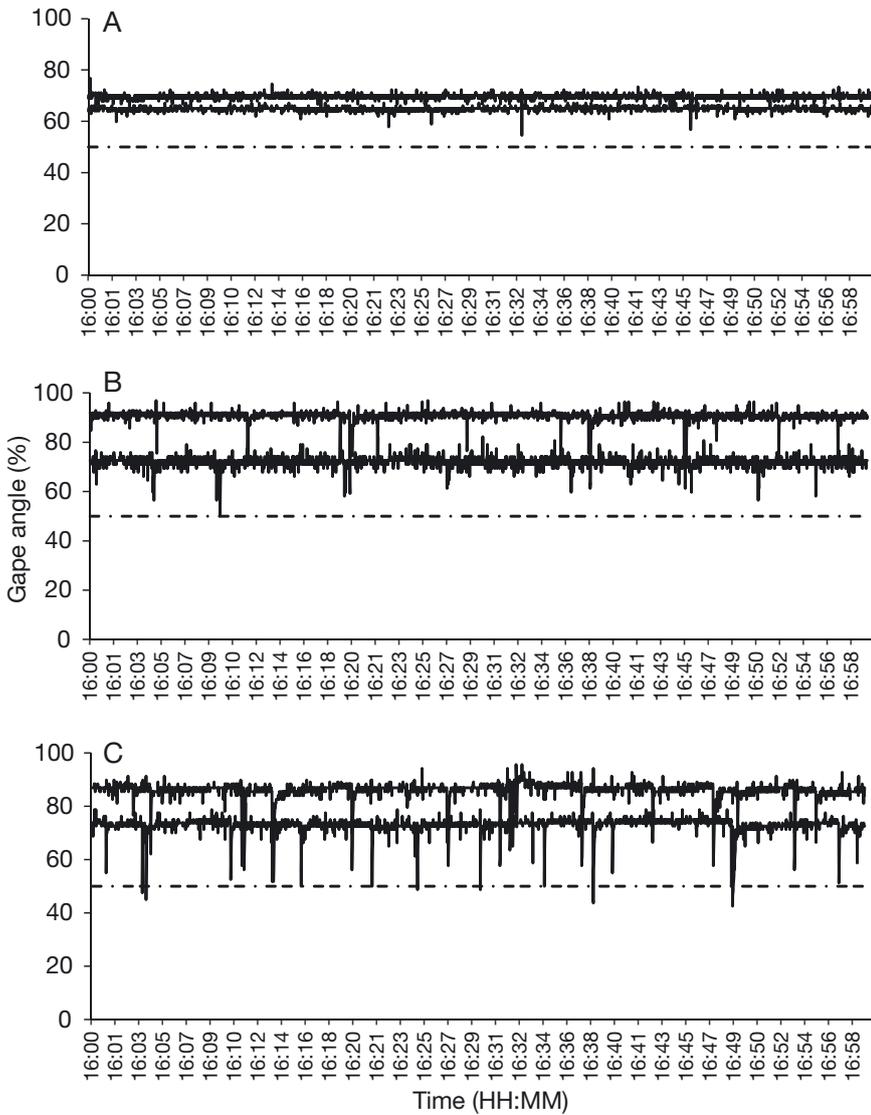


Fig. 5. *Pecten maximus*. Activity plots showing the shell opening and closing behaviour of 2 scallops from each experimental treatment over a 60 min period: (A) no SPM; (B) low SPM; (C) high SPM. ‘Gape angle’ represents the size of the gape angle as a percentage of the maximum gape angle recorded for the individual over the whole experiment. Dashed line indicates 50% gape angle

used in the burial experiment (Pearson’s $\chi^2 = 0.678$, $df = 1$, $p = 0.381$) ($n = 216$); therefore, weight was eliminated as a covariate in the subsequent analysis.

The results of the GLMs demonstrated that depth, sediment type and duration were all significant factors in determining the likelihood of scallops emerging from burial or dying while buried (Table 1). The deviances explained by the models were above 51%, demonstrating good model fits (Table 1). The model indicated that emergence from burial was significantly influenced by the interaction of depth and sediment type (Table 1, Fig. 7A) and the interaction between depth and duration (Table 1, Fig. 7B). The ability of scallops to emerge after burial decreased with decreasing sediment size fraction and increasing depth of burial (Fig. 7A,B). Scallops emerged more frequently from coarse sediment than medium or fine sediment. Overall, emergence was least frequent from burial under fine sediment, with no scallops emerging from 3 or 5 cm of fine sediment (Fig. 7A). It was observed that scallops emerged within 1 d of burial and at shallow depths almost immediately.

The interaction between sediment type and depth was significant in determining mortality while buried (Table 1, Fig. 7A). Overall mortality was low under coarse and medium sediment types, where only 4 of the 27 scallops that remained buried

Table 1. Generalised linear models (binomial) showing the responses of buried scallops. Factors and interactions included for each response variable represent the optimal model. Values for degrees of freedom (df), explained deviance by factor and interaction, and p-values (χ^2 -test) (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$) are shown as well as the AIC of the optimal model versus the full model in brackets: $y \approx \text{Depth} \times \text{Duration} \times \text{Sediment}$

Response variable	Null deviance	df	Residual deviance	df	Deviance						
					Depth	Duration	Sediment type	Depth × Duration	Depth × Sediment type	Total deviance explained	AIC optimal (AIC full)
Emerged	149.68	107	41.26	100	63.53***	0.53	22.63***	5.47*	16.23***	72 %	57.26 (60.86)
Died buried	100.47	107	48.53	101	4.82*	10.15**	27.32***		9.6**	51 %	62.54 (63.81)

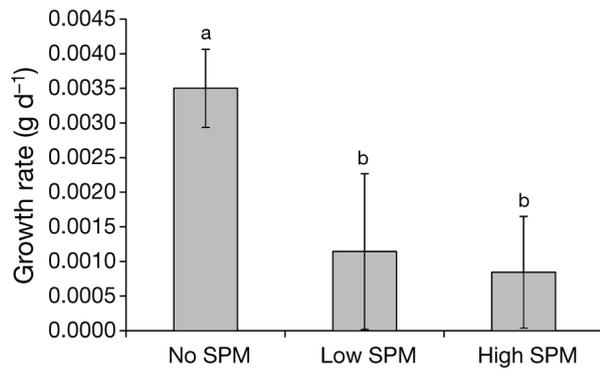


Fig. 6. *Pecten maximus*. Mean growth rate of control scallops in the 3 SPM treatments; error bars indicate 1 SE. Different letters indicate significant differences between treatments

died, whereas mortality under fine sediment was higher: 15 out of 24 scallops that remained buried died. The duration of the experiment had a significant effect on the mortality of scallops while buried (Table 1). With increased duration, mortality increased across all depths and sediment types (Fig. 7B,C). The effect of burial duration was greatest under fine sediment, with 100% mortality after 4 and 8 d burial (Fig. 7C).

DISCUSSION

Although the direct effects of aggregate extraction and scallop dredging on benthic communities are widely documented (Newell et al. 1998, Collie et al. 2000, Kaiser et al. 2006, Cooper et al. 2007, Hinz et al. 2011), the residual impacts of increased suspended sediment and burial on scallops are less well studied.

The present study demonstrates that both the behaviour and growth of *Pecten maximus* are affected by increased levels of SPM. The most frequent gape angle of >50% observed reflects the normal resting gape of *P. maximus* (Wilkens 1991). The number of shell claps exhibited by *P. maximus* was significantly higher under high SPM (200 to 700 mg l⁻¹), but there was no significant difference between the control and low SPM (50 to 100 mg l⁻¹) conditions. Generally, shell claps occurred infrequently (<1 h⁻¹) within the control and low SPM treatments. Less than 1% of the time was spent with the shell closed, reflecting the rapid shell adductions associated with mantle clearing (Wilkens 1991). Full shell closures (or 'claps') are the main mechanism used by *Aequipecten opercularis* to clear excess sediment from the mantle, and *A. opercularis* exhibited 4-fold more 'claps' under 'high'

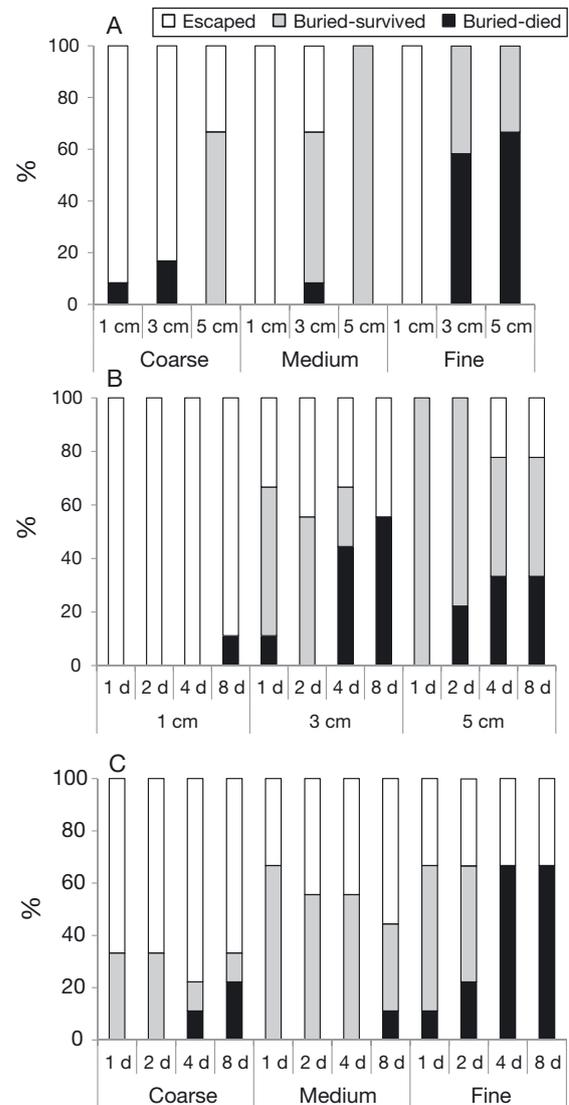


Fig. 7. *Pecten maximus*. (A) Response of scallops (% of total buried under different sediment fractions (coarse, medium or fine) by depth of burial (1, 3 or 5 cm) (n = 108). (B) Response of scallops buried under different depths of sediment (1, 3 or 5 cm) by duration of burial (1, 2, 4 or 8 d) (n = 108). (C) Response of scallops buried under different sediment types (coarse, medium or fine) by duration of burial (1, 2, 4 or 8 d) (n = 108). White: scallops emerged from burial; grey: scallops remained buried but survived; black: scallops remained buried and died

SPM (~71 mg l⁻¹) than under control conditions (Last et al. 2011). The 'high' SPM treatment used by Last et al. (2011) is comparable to the low SPM treatment in the present study, indicating that *P. maximus* have a higher threshold for increased levels of SPM, particularly in mantle clearance activity. However, *P. maximus* exhibited a significantly higher frequency of partial shell closures (<20° gape angle) under high SPM compared to other treatments, and these oc-

curred much more frequently than full shell closures. These results seem to indicate that *P. maximus* are able to keep the mantle clear of excess sediment with many shallow shell movements, without requiring complete shell closure, whereas *A. opercularis* exhibit a significantly higher frequency of complete shell closures under elevated SPM (Last et al. 2011). The differences in behavioural response to elevated SPM between the 2 scallop species may be due in part to their differing shell morphology and aerobic capacity or could be an adaptation by *P. maximus* to reduce the amount of energy required to clear the mantle by not fully closing the shell. *A. opercularis* frequently swim short distances (by repeated 'clapping' of the shells) to escape predators, while *P. maximus* exhibit this behaviour much less frequently and require a longer aerobic recovery time (Brand 2006).

A higher level of activity confers an energetic cost, due to the trade off between energy use for metabolic processes and somatic growth, and therefore has implications for fitness (for example, growth and reproductive investment). Increased levels of SPM affect feeding efficiency in *Pecten maximus* (Gibson 1956); additional energy is required for higher particle clearance rates and pseudofaeces production under exposure to elevated SPM. This was confirmed by the significantly lower growth rates observed in both treatments with elevated SPM levels and the significant increase in frequency of shell movements (changes in gape angle of $\geq 10^\circ$) under high levels of SPM.

Although the long-term survival of juvenile *Pecten maximus* subjected to elevated SPM was not assessed, all scallops were still alive 20 d after the experiment. Therefore, it is concluded that the short-term survival of *P. maximus* is not affected by increased SPM levels, although long-term effects require further investigation. Due to the proximity of scallop beds to aggregate extraction sites and the current increasing effort in the scallop fishery, potential repetitive exposure to increased SPM levels may have implications for growth rate and other costs associated with increased energetic output, such as reduced fecundity. Conversely, *Aequipecten opercularis* show high mortality after being subjected to elevated SPM for 6 d, and 100% mortality within 1 mo of exposure (Last et al. 2011).

The second experiment of the present study investigated the survival of juvenile *Pecten maximus* at different burial depths and sediment types. Survival while buried was significantly related to the duration of burial as well as to the interaction between sediment type and depth. Scallops ventilate during shell

closure through small gaps where the 2 shells meet; therefore, aerobic metabolism is possible during burial (Bricelj & Shumway 1991). Anoxic conditions in the wild can occur in < 1 cm depth of sediment, depending on local hydrodynamic conditions and oxygen flux (Fontanier et al. 2003). As oxygen exchange takes place at the surface of the sediment and oxygen levels decrease with depth, this could explain the reduced survival time of the scallops with increasing burial depth. Sediment size fraction also influenced survival, with the highest mortality in the fine sediment treatment. Increased oxygen availability (due to larger interstitial gaps between larger grains of sediment) and the higher frequency of emergence from coarse sediments could explain these findings.

Pecten maximus are able to tolerate longer periods of burial than *Aequipecten opercularis*, with $> 80\%$ survival across all treatments after 2 d burial and 46% survival after 4 d burial compared to $< 20\%$ survival in *A. opercularis* after 2 and 4 d burial (Last et al. 2011). The maximum burial duration of 8 d did not produce high levels of mortality in coarse and medium sediments, indicating that longer burial is required to determine the absolute tolerance of *P. maximus*. Different species of scallop have varying contributions of anaerobic and aerobic metabolism during muscle contractions (de Zwaan et al. 1980). *A. opercularis* have a relatively high metabolism for a mollusc (Guderley & Pörtner 2010), and this may explain their reduced survival under burial compared to *P. maximus*, although empirical testing is required to confirm this.

The influence of sediment fraction on emergence varies considerably among benthic species, probably due to the very different morphologies of organisms (Last et al. 2011). In the present study, *Pecten maximus* demonstrated the ability to emerge from a burial depth (5 cm) in coarse and medium sediment which was twice as deep as that from which *Aequipecten opercularis* is able to emerge. *A. opercularis* achieved $< 10\%$ emergence at shallow (2 cm) depth of sediment (Last et al. 2011). This could be attributed to morphological and habitat differences between the 2 species. *A. opercularis* do not recess into the seabed and display more frequent and effective swimming behaviour and therefore have a greater natural ability to avoid burial. *P. maximus* is normally found recessed in the sediment and has the ability to dig itself into and out of surface layers. Size may also influence emergence ability as juvenile *P. maximus* swim more actively and with a higher rate of shell adduction than larger scallops (Minchin 1992). Both *P. maximus* and *A. opercularis* show their

greatest emergence ability from coarse sediment. This could be due to the lower compaction of coarse sediment particles allowing the scallop to dislodge the sand grains more easily to aid emergence. However, commercial dredging produces finer sediment particles, which remain in suspension for longer than coarser particles. Indeed, the impact of sand deposition following dredging on organisms inhabiting the seabed can be more significant than the dredging itself (Desprez 2000). Sediments disturbed by commercial dredging can be re-suspended on subsequent tides, depending on the hydrodynamics and tidal regime of an area (Robinson et al. 2005). This makes prediction of the long-term effects of dredging difficult, especially when considering the fate of such particles and their effects on marine organisms (Eastwood et al. 2007). Scallops prefer coarse or fine gravel and sandy gravel (Mason 1982), so repeated dredging that alters the sediment composition of an area may also reduce the likelihood of future larval settlement.

The duration (Anthony & Fabricius 2000) and frequency (Anthony & Hoegh-Guldberg 2003) of exposure to high levels of turbidity plays a significant role in determining ecological stress levels. Often, dredging events are localised and occur over short time scales. However, repeated and intense dredging activity or that which occurs in tandem with other disturbances (such as fishing or storms) may produce cumulative effects that could negatively affect scallop populations.

The present study provides insight into the effects of suspended sediment and burial on juvenile *Pecten maximus* as well as highlighting species-specific differences in response. Although juvenile (~1 yr) king scallops appear to be well adapted to escape burial, prolonged exposure to SPM can affect feeding and growth rate. Due to the high commercial value of *P. maximus*, the increasing effort in the fishing and aggregate extraction industries and the proximity of scallop beds to licensed aggregate extraction areas, it would be prudent to restrict dredging activities near important fishing grounds or to temporally restrict activities. Comprehensive management based on empirical data will help to mitigate the effects of the aggregate and fishing industries and secure a sustainable future for both.

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