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Incorporating temporal variability of stressors into studies: An example using suspension-feeding bivalves and elevated suspended sediment concentrations

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Abstract

While spatial scale is increasingly incorporated into ecological experiments, the effect of temporal scale is explicitly investigated less frequently, despite the potential for temporal-scale dependent results. This study was designed to investigate the effect of variations in stress duration on responses, in a situation where stress duration is driven by natural storm events. Specifically, the utility of combining short-term laboratory and longer-term field transplant experiments in assessing the effect of increased suspended sediment concentrations on suspension-feeding bivalves (*Austrovenus stutchburyi* and *Paphies australis*) was tested. Short-term (2 days) feeding responses did not reflect feeding or biomass responses over slightly longer time-scales (8–14 days). Also, stronger biomass responses to suspended sediment concentrations were observed after three months in the field, than after 14 days in the laboratory. For unimodal responses, increased stress duration decreased the peak and shifted its location to lower suspended sediment levels. Using continuous measures of field suspended sediment concentrations, the study was able to determine the temporal scale of variability most related to the response. With such information, field surveys and transplants together make a useful tool, preventing co-occurring factors and changes in the duration and intensity of the factors of interest from obscuring results.

Keywords: Feeding rates; Integrating studies; Scaling functions; Suspension feeding; Temporal scale

1. Introduction

Complex processes are frequently difficult to isolate and manipulate. Frequently these processes are large-scale (e.g., changes in land use, fishing), but many small-scale processes can also prove difficult to investigate due to either interactions with processes operating over larger-scales or co-occurring factors affecting the process (Pacala and Deutschman, 1995; Tegner et al., 1997; Thrush et al., 1997). There is also a strong potential for artefacts and incorrect isolation of factors with experimental manipulations of such processes (Dayton and Oliver, 1980; Peters, 1991; Huston, 1997). Some combination of experimental manipulations of tractable portions (either in the laboratory or the field) and field surveys is often indicated as a solution (Eberhardt and Thomas, 1991; Bell et al., 1995), although the results are likely to be both spatially and temporally scale dependent (Allen and Hoekstra, 1991; Levin, 1992; Petersen et al., 1999). Increasingly, spatial scale is incorporated into experiments (Smith and

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Brumsickle, 1989; Whitlatch et al., 1997), however, with the exception of disturbance/recovery experiments, few experiments explicitly investigate the effect of temporal scale or incorporate it into predictions (but see Hobbie et al., 1995; Bell et al., 2003). Despite this, temporal scale is likely to be particularly important for responses that can be affected by changes in energy allocation to different physiological processes, or for responses to events naturally varying in intensity and duration, such as storms and ice scour.

Feeding is a small-scale process, which for many suspension feeders may be affected by a number of co-occurring environmental factors operating at a variety of spatial and temporal scales. For example, temperature (Cranford and Hill, 1999; Denis et al., 1999), flow (Lesser et al., 1994; Pilditch and Grant, 1999), and variations in seston quantity and/or quality (Kiorboe et al., 1980; Newell et al., 1989; Hawkins et al., 1999). In particular, variations in seston are likely to be temporally variable, with wave events increasing resuspension of marine sediments and high rainfall events increasing inputs of terrestrial sediment entering estuaries and nearshore waters. Laboratory experiments are commonly used to determine feeding responses to changes in environmental factors, although problems associated with differences in types of chamber/flume have been discussed (Riisgard, 2001). Another potential problem is that the effect of changes in feeding, both for individuals and for populations, is manifested at a variety of temporal scales due to differential growth, survival and reproduction. However, laboratory experiments are generally conducted for relatively short periods of time, often <10 days, (Riisgard, 1988; Iglesias et al., 1992; Urrutia et al., 2001).

Field measurements are always needed, either to validate model extrapolations, or to determine whether short-term laboratory responses reflect longer-term field responses. Field studies also have the advantage that they integrate over co-occurring factors, interactions with processes operating over larger-scales, and with changes in durations and intensities of the factors of interest. Surveys integrate over the largest time scale, but lack causality (Eberhardt and Thomas, 1991; Peters, 1991), and, for comparisons between animals, may be compromised by differences in size and natural differences in physiological cycles (Mohlenberg and Riisgard, 1979; Cranford and Hill, 1999). Surveys also may not be possible, as sufficient individuals may not be found over the natural range of interest. Field transplant experiments solve these problems and integrate over a medium time scale, but can be limited by the levels of the factor of interest that naturally occur over the duration of the transplant. Variation of other factors affecting the response may also cause difficulties.

To overcome the potential problems noted with the different methodologies and different time scales, a combination approach of short-term laboratory and longer-term field transplant experiments was used to investigate the effect of variations in seston quantity on suspension-feeding bivalves. The study was not designed to scale from effects on feeding to effects on growth or population dynamics, but to investigate the effect of event duration on stress responses. Seston quality and quantity are of interest as, in many areas of the world, such as US, South America, New Zealand, Malaysia and China, the potential for increased sediment concentrations in the marine environment as a result of anthropogenic influences is becoming recognised (GESAMP, 1990). Moreover, increased variability is likely associated with the increased frequency of extreme rainfall events predicted, by climate warming models, for some of these areas. Two species were used in order to extend the generality of the findings: *Austrovenus stutchburyi* and *Paphies australis*. Both species are intertidal, occur in the same estuaries, have short siphons and live near the sediment surface. However, they occur in different sediment types, and this may reflect a potential for different responses to increased seston quantity.

2. Methods

2.1. Species

A. stutchburyi, the New Zealand cockle, grows up to 60 mm (longest shell dimension) and is commonly found in the intertidal zone in both mud and sandflats. It has short siphons, lives within 5 mm of the sediment surface and feeding rates are strongly periodic. *P. australis*, grows much larger, up to 100 mm (longest shell dimension). Adults are commonly found in silty-coarse sand, near the mean low water spring, where tidal currents are strong. Juveniles are generally found higher up the shore in both mud and sandflats. *Paphies* also have short siphons, but frequently live deeper in the sediment than *Austrovenus* and are strong burrowers. Feeding rates in adults appear to be less strongly linked to tidal state, possibly as they are covered by water most of the time (pers. obs.).

At our field collection sites (Whitford Embayment, Hauraki Gulf, New Zealand), *Austrovenus* and *Paphies* reproduced during August–November and May–October respectively. Laboratory experiments were run in February, 2001 and the transplant experiment was started in March, about 2 weeks after the laboratory experiments were concluded. Donor sites for the laboratory and transplant experiments were the same, although they differed for the two species.

2.2. Laboratory experiments

Shellfish for the laboratory experiments were acclimated for 24 hours in 5 μm Pall C10P-CB5 carbon block filtered seawater in a temperature controlled room, at the approximate temperature observed at the collection sites (20 °C) and a 16:8 hour light:dark cycle. After 24 hours, shellfish were placed in eighteen 20 l aquaria filled with 5 μm filtered seawater. Each aquarium was randomly allocated to a sediment treatment. A single additional aquarium containing no animals was used as a control for non-animal related sedimentation for each treatment. Experiments were run separately on *Austrovenus* and *Paphies*. Six *Austrovenus* (35–40 mm) and 3 *Paphies* (60–65 mm) were used in each treatment replicate.

A range of six suspended marine sediment concentrations, between 15 and 680 mg l^{-1} was used. Most New Zealand estuaries normally have suspended sediment concentrations between 20 and 100 mg l^{-1}, although, in periods of high sediment runoff this may increase to as much as 1000 mg l^{-1} (Fahey and Coker, 1992). Sediment was added every 4 hours to preserve the approximate concentration and kept in suspension using aerators. Algae (*Isochrysis galbana*) were added to the aquaria approximately every 3 hours during the light cycle, and then again before the dark cycle began. The total amount of food added per day was based on natural levels of chlorophyll *a* (Safi, 2003).

Feeding was measured as clearance and filtration rate per g of animal dry weight, four times during each experiment (days 2, 5, 8 and 14), calculated from biodeposits (Hawkins et al., 1996).

$$\text{Filtration rate}(\text{mg min}^{-1}) = \text{IBD}/(\%\text{ISSC}_{T1} \times T \times \text{NDW})$$

$$\text{Clearance rate}(\text{ml min}^{-1}) = \text{Filtration rate}/\text{SSC}_{T1}$$

where IBD = inorganic fraction of biodeposits, ISSC = inorganic suspended sediment concentration, SSC = total suspended sediment concentration, T = time in minutes between T1 and T2, and NDW = dry weight of animal flesh. These rates were adjusted for natural settlement of sediments out of suspension by the subtraction of settlement rates measured from the control aquaria.

At the end of the each experiment, measurements of biomass were made on each individual animal (see below for the method).

2.3. Transplant experiment

Shellfish were transplanted to eight sites that were predicted to experience different suspended sediment concentrations based on mud content of the sediment and distance to tidal creeks. All animals of a particular species were collected from a single donor site, which was also included as a transplant site, so that we could evaluate the effect of transplanting.

Due to the mobility of the species, cages (made of 4 mm plastic mesh, sized 30 × 30 × 10 cm) were required to contain the animals after transplanting. Cages were embedded into the substrate and half to two thirds filled with sieved sediment. Cages containing *Paphies* were located in drainage channels at each site, thus positioning the Paphies near the low tide mark, whereas cages containing *Austrovenus* were placed on the tidal flats at mid-tide. Ten pre-measured animals, of a similar size to those used in the laboratory experiments, were added to the cages.

Sites were visited every 2 weeks over a three-month period, so that cages could be checked for biofouling and cleaned if necessary. In reality, very little cleaning was necessary, some barnacles were removed with care taken that these did not enter the cage, and on one occasion a cage had a small amount of weed wrapped around it. In June, after 11 weeks, the experiment was terminated. Sediment samples were taken from within each cage, and from 3 random locations around the cage, for analysis of sediment particle size and organic content. All animals were brought back to the laboratory and biomass measurements made as for the laboratory experiments. Extra animals were collected from the ambient sediment of donor sites to test the effect of the caging.

2.4. Sediment and bivalve measurements

Suspended sediment concentrations were determined by filtering water through ashed and pre-weighed GF/F 25 mm filters, which were then dried to constant weight at 60 °C before reweighing. The filters were then ashed at 450 °C for 5.5 h and the weight loss used to determine the amount of organic particulate matter. Dry weight and organic content of biodeposits and individual animal flesh were similarly calculated. For the bivalve biomass, the organic weight was used as a measure of biomass unaffected by any sediment held internally. The biomass was then divided by the shell dry weight. All future references to biomass relate to this standardised measurement.

A number of methods were used to determine suspended sediment levels in the field. Optical backscatter sensors (OBS) were deployed at all sites. Not all sensors collected consistently, but OBS data from all sites was available for the last month of the study. The electrical voltages logged by the OBS were converted into concentrations of suspended sediment by calibration curves set up for each instrument before deployment. Once per month, small sediment traps, 2 cm diam. and 20 cm deep, were set up to collect over one tidal cycle. Sediment from all traps was analysed for organic content.

Salinity and temperature were also measured for each site. Variations in both of these were low, with higher variation over days and weeks than between sites or at a site over a tidal cycle, suggesting that variation was driven by storm events. Depth-averaged tidal current velocities, for ebb and flood tides, were available for each site from the hydrodynamic model 3DD (Black, 1995). Average and maximum significant wave height, and wave orbital speed at the bed, were calculated using a cell size of 20 × 20 m.

2.5. Statistical analyses

For biomass in the laboratory experiments, plots were used to identify the form of the response curve for each species. Then a regression model was run to develop a relationship between suspended sediment concentrations and biomass. A one-way ANOVA between the biomass of individuals on the day of collection and those in the control treatments was used to determine whether the laboratory conditions were affecting the animals.

For the transplant experiments, a one-way ANOVA between the biomass of transplanted-caged and ambient individuals, sampled from the donor sites at the end of the experiment, was conducted for each species. Two-way ANOVAs with site and cages as fixed factors were run for the measured sediment characteristics. Site was used as a fixed factor as it represented a gradient in current and wave exposure that we thought might affect sedimentation within the cages.

Multiple regressions, with backwards elimination using an exit value of $p = 0.15$, were used to determine the best predictors of differences in biomass between transplant sites. Variables included in the multiple regressions as predictors were the site descriptors of suspended sediment concentrations derived from the OBS meters, the average amount and organic content of sediment from the sediment traps, hydrodynamic variables (tidal current velocities, average and maximum wave height and average energy expended on the bed), salinity and temperature. Models were checked for dependence on the order of variable removal. Colinearity diagnostics were examined (see Belsley et al., 1980), but no problems were observed with the variables finally retained in the model.

2.6. Comparisons across time scales

Two comparisons of responses to suspended sediment concentrations were made for each species. (1) differences between the response of feeding rates over the duration of the laboratory experiment (2–14 days). (2) differences between the response of biomass at the end of the laboratory (14 days) and field transplant experiments (three months). For clearance and filtration rates, the clear change from a unimodal response to a more linear response precluded analysis of covariance, and responses were compared visually only. Similarly, differences in the functional form of the biomass responses limited this analysis to a visual comparison.

To standardise the comparisons, they were conducted on means. For filtration and clearance rates, means were calculated across treatment replicates. For the laboratory biomass measurements, the treatment mean was calculated from the mean biomass in each aquarium. For the transplant biomass measurements, a mean biomass was calculated for each site.

3. Results

3.1. Laboratory responses

For both species, there was no significant difference between the biomass of individuals immediately after collection from the field and individuals from the laboratory control treatments after 14 days ($p = 0.27$ and $p = 0.55$ for *Austrovenus* and *Paphies* respectively). This suggests that the algae used for feeding was not affecting biomass, nor was the additional time under water conferring an extra benefit in terms of additional feeding. Percent organic content of the water in the treatments was not well correlated with suspended sediment concentrations (Spearman's $\rho < 0.20$) and averaged 9%.

At the start of the laboratory experiment on *Austrovenus*, clearance rates were highest at suspended sediment concentrations <100 mg l^{-1} (Fig. 1a). This general pattern was continued over the duration of the experiment, although there was a general decrease over time in the clearance rate of *Austrovenus* for suspended sediment concentrations 100–500 mg l^{-1}. Filtration rates were higher for all suspended sediment concentrations >150 mg l^{-1}, for days 2–5, with maximum rates occurring between 150 and 500 mg l^{-1} (Fig. 1b).

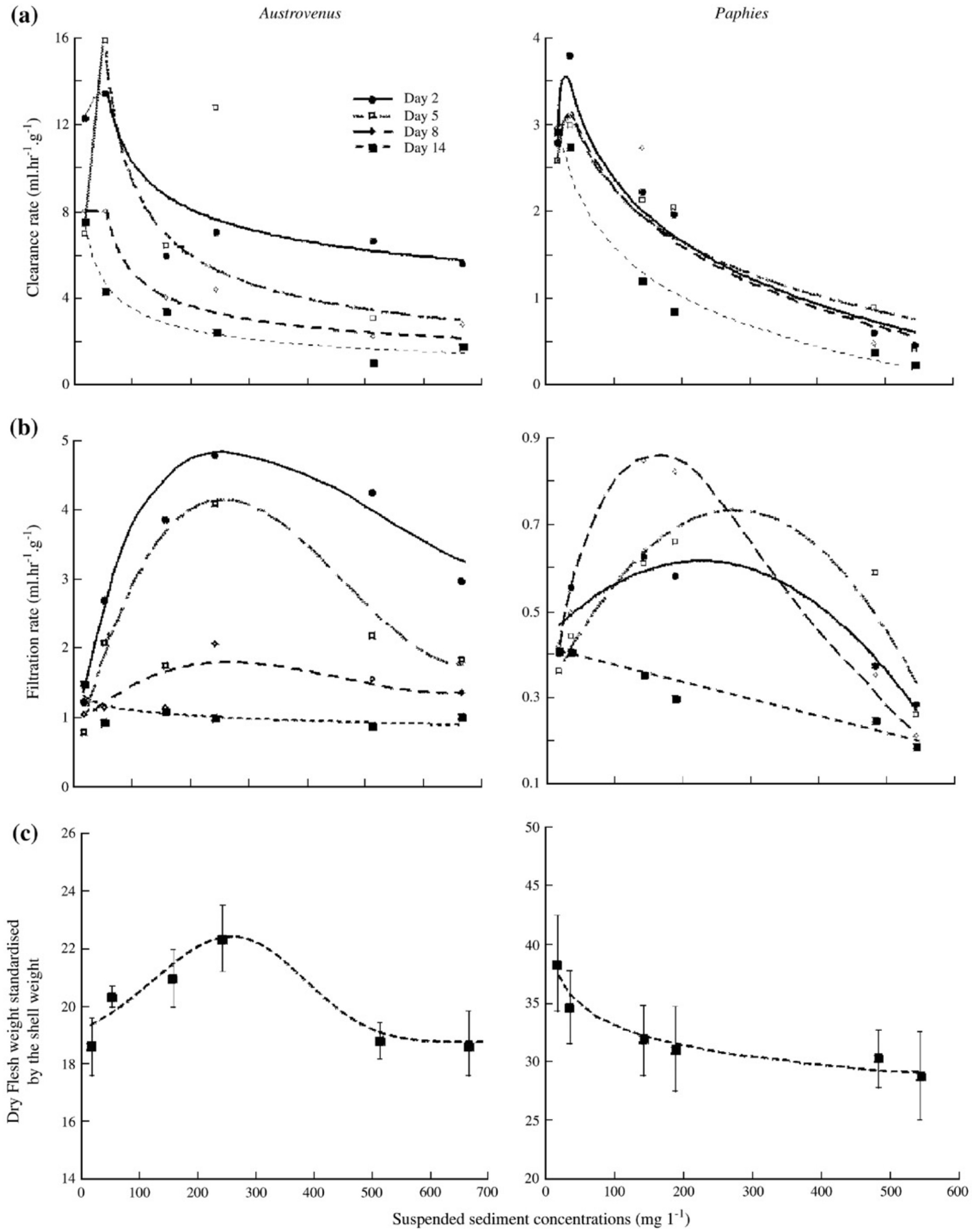

Fig. 1. Changes in (a) clearance rates, (b) filtration rates, and (c) standardised biomass of *Austrovenus* and *Paphies* over the 14 days of the laboratory experiment.

However, a strong decrease in filtration rates over time was observed in all treatments other than the controls. Thus, by day 5, the unimodal response was breaking down and by day 14, little variation in filtration rate with suspended sediment concentration was observed.

Experimental results from the *Paphies* in the laboratory were generally similar to those for *Austrovenus* (Fig. 1), although *Paphies* seemed more sensitive to increased suspended sediment. There was a decrease over time in the clearance rate of *Paphies* in suspended sediment concentrations > 500 mg l^{-1}, and the percentage change in clearance rates with increased suspended sediment was higher than for *Austrovenus* (Fig. 1a). Also, while a unimodal response of filtration rates was again observed, by day 14, filtration rate clearly decreased with increased suspended sediment concentrations (Fig. 1b).

These changes over time resulted in clear changes to standardised biomass. *Austrovenus* biomass showed a unimodal response after 14 days in the laboratory (Fig. 1c), such that biomass increased with increasing suspended sediment concentrations, up to ~ 350 mg l^{-1}, and then decreased. Biomass of *Austrovenus* at >400 mg l^{-1} was similar to or less than the biomass at <100 mg l^{-1}. Unlike the *Austrovenus*, *Paphies* showed a logarithmic decrease in biomass with increased suspended sediment concentrations above that of the control (Fig. 1c).

3.2. Field transplant results

A number of measurements were made to determine whether the cages were affecting results. For both species, animals were transplanted into cages at donor sites. Comparison at the donor sites of average biomass of animals in the cages and untransplanted animals outside the cages showed no significant differences for either species by the end of the experiment (Table 1). Sediment characteristics were also compared at the end of the experiment, between sediment in the cages and ambient sediment for each site. There were no significant differences in particle size or organic content between inside and outside the cages, across the 8 sites, and no indications of site interactions (Table 1). This suggests that the cages were not increasing sedimentation of fine particles.

Table 1
Comparisons between inside and outside transplant cages, by 2-way ANOVA on arctransformed sediment data across all sites and t-tests on standardized biomass of the animals from donor sites

Variable	Factor	SS	*df*	*F*	*p*-value
Organic content	Cage	0.002	1	0.00	0.9759
	Site	6.738	7	0.54	0.7993
	Cage * site	9.168	7	0.73	0.6466
	Model	57.281	32		
	Residual	15.908	15		
% Particles sized > mud	Cage	72.675	1	0.39	0.5375
	Site	968.799	7	0.74	0.6400
	Cage * site	924.019	7	0.71	0.6671
	Model	5984.55	32		
	Residual	1965.49	15		
% Clay sized particles	Cage	0.218	1	0.33	0.5693
	Site	4.390	7	0.95	0.4824
	Cage * site	3.696	7	0.80	0.5926
	Model	21.100	32		
	Residual	8.304	15		
% Silt sized particles	Cage	32.680	1	1.57	0.2196
	Site	45.977	7	0.32	0.9417
	Cage * site	142.697	7	0.98	0.4641
	Model	667.130	32		
	Residual	221.355	15		
Austrovenus biomass	Cage	0.717	1	0.05	0.8301
	Residual	242.281	18		
Paphies biomass	Cage	324.841	1	2.72	0.1176
	Residual	2031.76	18		

SS (Sum of squares) are not given for the biomass analyses as these were done by t-tests.

Table 2
Average daily rain (mm) and wind speed (m s^{-1}) for the first two months of the study and the last month when continuous OBS data was collected at the 8 sites

	Rainfall		Windspeed	
	First two months	Last month	First two months	Last month
Minimum	0	0	1.5	0.7
Lower quartile	0	0.2	2.5	2.0
Median	0.76	2.6	4.8	4.0
Average	4.3	5.7	4.2	4.2
Upper quartile	6.6	6.4	6.7	6.3
Maximum	57	49.8	9.6	8.7

Average rain and wind conditions were similar, although variable, for the three months of the study (Table 2), with wind predominantly from the east and south direction with an average daily wind speed of 4.2 m s^{-1}. The last month of the experiment had slightly more consistent rain than the previous two months, although the maximum daily average was less (49.8 mm vs 57 mm, Table 2). The similarity in conditions over time suggest that the suspended sediment concentrations derived from the OBS data over the last month are likely to be representative of the whole duration of the experiment.

Suspended sediment concentrations were characterised for each site by calculating the maximum, 95th percentile, upper quartile (75 percentile), median (50 percentile), lower quartile (25 percentile), 5th percentile and minimum. Differences in suspended sediment concentrations at the sites, over the month prior to the experiment ending, were observed between sites primarily affected by input from the sub-estuaries (sites 1–4; Fig. 2a) with lower minima and medians, vs those primarily affected by wave-driven resuspension events (sites 6–8; Fig. 3). Differences were also observed between these two groups of sites in the organic content of sediment settling fluxes (sediment collected in traps)

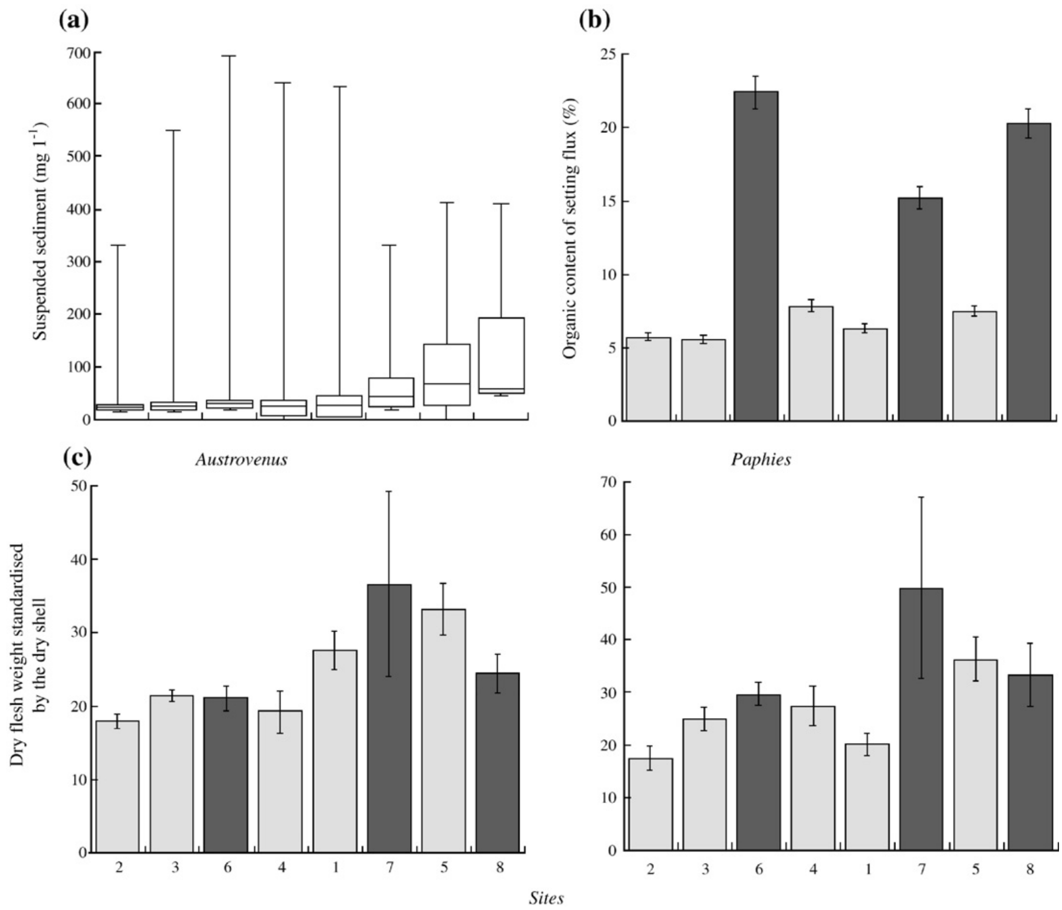

Fig. 2. Variation between sites in (a) suspended sediment concentrations, calculated from OBS data, measured over a 1-mo period, (b) organic content of the settling flux measured three times, and (c) standardised biomass from all transplanted individuals. Box plots show minimum, lower quartile, median, upper quartile and maximum. Sites are arranged in order of increasing upper quartile suspended sediment concentrations. For b–d, sites nearest to sub-estuaries are light shaded and sites that are wave-exposed are dark shaded.

(Fig. 2b) suggesting that this may be important in explaining differences in biomass between sites.

Differences in organic content were incorporated in the multiple regression analysis both by calculating suspended organic concentrations from the OBS suspended sediment concentrations and percent organic content and using the average organic settling flux. The variables useful for predicting biomass were the same for both species, the median and upper quartile suspended sediment concentrations and the average organic settling flux. Temperature, salinity, current velocity, wave height and average energy expended on the bed were not useful predictors ($p > 0.5$, Pearson's $r < 0.3$). These results suggest that the transplant results were not being affected by site differences in hydrodynamics or location within the estuary, except as those affected suspended sediment concentrations and organic content.

Biomass of both *Austrovenus* and *Paphies* increased with increases in the median suspended sediment concentrations and the average organic content of the settling flux, but decreased with the upper quartile of suspended sediment concentration (Table 3), resulting in a peak at intermediate to high concentrations of suspended sediment. Maximum biomass of both *Austrovenus* and *Paphies* were found at the same site (Fig. 2c). This site had a median and upper quartile suspended sediment concentration of 39 and 70 mg l^{-1} respectively and was wind-exposed with suspended sediment comprised of resuspended marine sediment with an organic content of around 15%. However, examination of plots of predicted biomass vs upper quartile or median suspended sediment concentration suggested that maximum biomass for *Austrovenus* would occur at higher suspended sediment concentrations than the maximum biomass for *Paphies*,

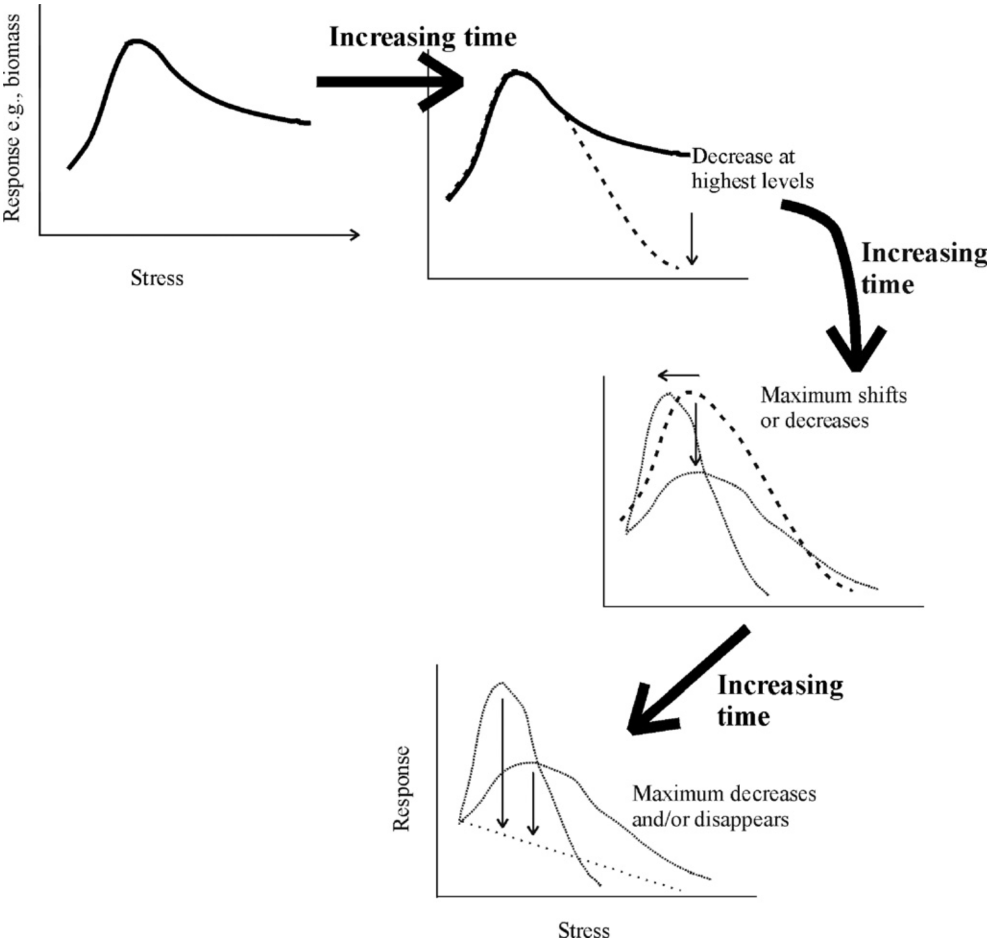

Fig. 3. Conceptual model of feeding or biomass responses to increasing time-scales of stress.

matching field observations on abundances of the two species. *Austrovenus* biomass was predicted to increase with median and upper quartile concentrations up to 40 and 75 mg l^{-1} respectively, above which it would decrease, while *Paphies* was predicted to have lower thresholds around 28 and 58 mg l^{-1} respectively.

4. Discussion

In the area of resource management, failure to consider the effect of duration on responses to stressors can be particularly problematic (Innes, 1998). This study found two results of particular importance in such situations: (1) the comparison of thresholds of response

Table 3
Factors useful in predicting differences in biomass

	Austrovenus laboratory	*Austrovenus* field	*Paphies* laboratory	*Paphies* field
Model *p*-value	0.0305	0.0237	0.0071	0.0479
Model R^2	0.91	0.88	0.83	0.81
Mean laboratory SSC	$+0.045x+0.0001x^2+0.0005x^3$		$-3.39\ \ln(x)$	
Median field SSC		+1.78		+3.35
Average organic field settling flux		+0.023		+0.048
Upper quartile field SSC		−0.70		−1.37

+ = increases growth rates, − = decreases growth rates. SSC = suspended sediment concentrations derived from OBS measurements.

over time; (2) and the effect of temporal variability of intensity in the field situation.

4.1. Comparison of thresholds of response over time

Specifically, this study asks the question, are short-term experiments enough to indicate thresholds of responses? The study results suggest the answer is 'no', short-term feeding responses (2 days) did not reflect feeding or biomass responses over slightly longer time-scales (8–14 days) and biomass responses measured over three months in the field suggested increased sensitivity to suspended sediment concentrations.

Clear changes in both clearance and filtration rates occurred for both species, with responses to suspended sediment concentrations observed on the second day being markedly different from those on the 14th day. Initially, unimodal responses to suspended sediment concentrations with maxima around 200–400 mg l^{-1} were observed. Changes were becoming apparent by the 8th day, and slowly continued over the duration of the experiment, with responses moving towards a monotonic decrease. These temporal changes were most marked for filtration rates and, particularly for *Austrovenus*, may well have continued had the experiment lasted longer. Changes over time in feeding responses to stressors have also been observed by Ellis et al. (2002) for the response of *Atrina zelandica* to suspended sediment concentrations. Some studies on feeding rates have been carried out after an acclimation period of a number of days (12–15 days, (Ren et al., 2000), 1 week (Riisgard, 1988)). Our results emphasise the need to consider duration of elevated stress explicitly in experiments and that, for shellfish, 14 day experiments may not be long enough.

As none of the co-variables (temperature, salinity, current velocity, wave height nor average energy expended on the bed) were useful predictors in the transplant experiment, comparing the biomass responses observed for the laboratory and field experiments is relatively straight forward. Although the maximum field-observed suspended sediment concentrations were similar to those in the laboratory, it is probably more sensible to compare the laboratory concentrations with the upper quartiles of the field-observed concentrations as these conditions would have lasted for ~19 days. The field experiment observed decreases in biomass with increased upper quartile suspended sediment concentrations. It is tempting to conclude that the longer duration of the field transplant had, thus, resulted in an increased response, changing the unimodal response of *Austrovenus* to a wholly negative one, and strengthening the decrease for *Paphies*. However, the complicated relationship between organic content of the sediment and median and upper quartile effects precludes this simple comparison. Even so, for *Austrovenus*, the suspended sediment threshold at which the maximum biomass occurred was less in the field transplant, and a larger decrease in biomass relative to low suspended sediment concentrations was observed. These differences are unlikely to be caging artefacts as cages did not cause sediment deposition, nor did they affect the biomass of animals at the donor sites. It also seems unlikely that the differences were due to better food quality in the laboratory as biomass in the controls did not increase during the laboratory experiment. For *Paphies*, the effect of higher organic content of sediments at sites with the higher median suspended sediments resulted in an initial increase in biomass with increased suspended sediment concentrations, unlike the laboratory experiment, where organic content was lower.

Summarising over both feeding and biomass results, even where shorter-term experiments correctly predicted the functional form of the biomass response of the species, similar to Hofmann and Powell (1998) delayed reactions altered responses and the threshold was not accurate. That is, with increased time, thresholds, with the exception of *Paphies* biomass, moved to a lower level of suspended sediment concentrations, suggesting a general form for time scaling an energy-related response to a stressor (Fig. 3). Initially, there is a unimodal response of some form, although only a part of the curve may be observed, with the biological response (e.g., biomass, mobility, feeding etc.) exhibiting a maximum at some point along the gradient of stress. With increasing exposure time, levels will firstly decrease at higher levels of stress. As exposure time lengthens, the position of the maximum will slide towards the lower levels of the stressor, and/or the height of the maximum will decrease. It seems most likely that the time scaling function will be logarithmic, with greater changes observed as durations increase from small to medium time scales than from medium to large time scales. Obviously, the more sensitive the species to the stressor, the more quickly the response will change.

4.2. Quantifying and investigating the effect of temporal variability of intensity

The most interesting information gained from the field that could not be gained in the laboratory experiments was the effect of temporal variability in suspended sediment concentrations. Natural fluctuations are extremely hard to replicate in laboratory situations and are generally ignored in experiments, with the exception of the more predictable daily fluctuations of light, temperature and water depth. Measurements of variables over the duration of field experiments offer a way of deciphering effects of discontinuous and fluctuating conditions.

Differences between the effect of the median, upper quartile and maximum of suspended sediment concentrations indicate whether an effect is related to duration and/or frequency of high concentrations, as for example, with the macrofaunal changes observed by Peterson (1985). When concentrations are high for brief periods, both the median and upper quartile will be low. When high concentrations persist for >25% of the time, whether this time is contiguous or not, the maximum and upper quartile will be elevated although the median will remain low. As the period of time over which high concentrations exist increases, or the frequency of high concentrations increases, the median will slowly increase. In this study, both the median and upper quartile of suspended sediment concentrations were important, and operated in different ways. Thus, for our two species, high suspended sediment concentrations, 100 and 70 mg l^{-1} for *Austrovenus* and *Paphies* respectively, with high organic content, can be beneficial, unless they persist for >25% of the time, which for this study would be 19 days. This study could not determine how important consecutive days of high suspended sediment concentrations were, compared to single tides. Suspended sediment concentrations were generally high for 1–3 days only, i.e., there were not 19 days of consecutively high suspended sediment levels. However, it is likely that when high suspended sediment levels occur for >25% of the time, regardless of how many events are contained therein, there is not sufficient time to recover condition and biomass is lost.

5. Conclusions

This study confirms the importance of considering temporal scales of responses and suggests that temporal variability in stressors is also important. In a real system, variations in suspended sediment concentrations occur as events of differing intensity and duration. Use of average concentrations can result in observing a dampened response, and thus an underestimation of maxima. This may be compounded by other factors, including exposure history (Boesch and Rosenberg, 1981; Rapport et al., 1985; Hewitt and Pilditch, 2004), leading to problems in extrapolating process measurements from one biological scale to another (Innes, 1998). Field surveys and transplants offer a way to integrate over co-occurring factors and investigate the effect of temporal variability in duration and intensities of a stressor. Combining field experiments with laboratory experiments, which offer a mechanism for the field-observed response and the ability to control actual levels of stress, results in better knowledge than is available from either method alone.

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