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NOTE

Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*

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ABSTRACT: Sediments are likely to influence the distribution of limpets and dominant sessile species on intertidal rocky shores by smothering and interfering with feeding activity. This hypothesis was tested by field observations and laboratory experiments in which the effects of different amounts and grain sizes of sediments on the grazing and survival of the limpet *Patella vulgata* L. were measured. On rocky shores close to Plymouth (south-west UK), natural patchiness of sediment deposits was related to the distribution of *P. vulgata* and macroalgae. Sediments severely impaired *P. vulgata*. Even a ~1 mm thick layer of sediment (equivalent to 50 mg cm^{-2}) decreased grazing activity by 35%, with total inhibition and mortality at loads of 200 mg cm^{-2} of fine sediments. Coarse sediments had less severe effects than fine sediments.

KEY WORDS: Sedimentation · Grazing · *Patella vulgata* · Grain size · Rocky shores

INTRODUCTION

The nature and amount of sediment that occurs on rocky shores either naturally or as a consequence of human activities is highly variable, resulting in a variety of possible effects on biota. Recent experiments have made substantial progress in detecting the effects of sedimentation on rocky coast assemblages (reviewed by Airoldi 2003), but our ability to generalise these effects is restricted.

Herbivorous organisms, including limpets, are often scarce in areas with high sediment loading (Airoldi & Virgilio 1998, Airoldi 2003, Pulfrich et al. 2003, Schiel et al. 2006). This effect of sediment is particularly important because grazing is a key process controlling algal vegetation on rocky shores (Southward 1964, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Benedetti-Cecchi et al. 2001). Direct evidence of the negative effects of sediments on limpets is limited. Following the flooding of the Orange River in South Africa, different assemblages developed in areas most affected by water dilution and high loads of sediments, and the shore changed from being dominated by patellid limpets to being dominated by ephemeral algae (Branch et al. 1990). Experiments in which limpets were transplanted to areas buried or not buried by shifting sands (Robles 1982), or in which they were exposed to burial conditions in the laboratory (Marshall & McQuaid 1989), showed that some species of limpets suffer mortality under severe burial by sand. However, there has been no research designed to identify sub-lethal effects arising from less extreme but possibly frequent sedimentation events, and eventual critical levels of perturbation by sediment are not known.

The limpet *Patella vulgata* L. forms high-density populations on rocky intertidal shores along the coasts of north-west Europe (Hawkins et al. 1992). This

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limpet is an important macroalgae grazer, controlling the abundance and distribution of macroalgae (Southward 1964, Hawkins 1981, Jenkins et al. 2005). Circumstantial observations suggest that this species may be affected negatively by sediment, because its density tends to decline with shelter (presumably associated with an increase in sediment), and its grazing activity is limited by the presence of turf-forming algae that typically trap sediment (Jenkins et al. 1999). The biology and ecology of *P. vulgata* have been studied extensively, but little is known about its responses to different amounts and types of sediments. We analyzed the relationships between the distribution of sediments, *P. vulgata* and dominant sessile species on rocky shores in the south-west UK, and tested the hypothesis that sediments negatively affect the grazing rate and survival of *P. vulgata* in the laboratory. Responses of *P. vulgata* to different amounts and grain sizes of sediments were quantified, with the aim of identifying the critical levels above which detrimental effects of sediments become manifest.

MATERIALS AND METHODS

Field observations. Field observations were made in April and May 2002 at 4 moderately exposed rocky platforms (Looe, Cawsand Bay, Heybrook Bay and Wembury) and a sheltered one (Cremyll) in the south of Devon, UK. One mid-shore site (~20 m^2) with patchy distribution of sediments was selected on each shore with the exception of Wembury, where 2 sites about 500 m apart were selected. At each of these 6 sites, cover (%) of sessile species and sediment (both on rock and entrapped in turfs) and number of limpets, mainly represented by *Patella vulgata*, were estimated visually in 10 replicate 20 × 20 cm plots.

The relationships between the patchy accumulations of sediment and the distribution of species were examined by superimposing the cover values of sediments onto a non-metric multi-dimensional scaling (MDS) ordination of benthic species (Clarke 1993). The MDS was based on Bray-Curtis dissimilarities from a matrix of 4th root-transformed abundances of 11 species. The correlation between abundance of *Patella vulgata* and sediment was also calculated.

Laboratory experiments. Experiments were run using a tidal tank system with direct daylight illumination, running seawater and a semidiurnal cycle, situated in the Seawater Yard at the Marine Biological Association of the UK. The system consisted of 6 tanks (28 × 36 × 30 cm) filled with ca. 25 l water at 'high tide'. 'High' and 'low tide' were achieved through a system of pumps that allowed tanks to be either filled or emptied simultaneously in about 45 min. Each tank contained 5 flat, smooth, large boulders (about 140 to 170 cm^2), each drilled with two 14 mm diameter holes to accommodate wax discs to quantify the grazing activity of limpets (see below). The boulders were in contact with each other to allow movements of limpets, while the bottom of the tank was filled with coarse fragments of shells and the sides were covered with a metal mesh to prevent limpets from escaping.

Small cobbles with *Patella vulgata* (average length 36 ± 10 mm) were collected at the beginning of each experiment from the shore at West Hoe. Relocation of limpets onto the test boulders in experimental tanks was achieved by removing the cobbles once limpets moved from them onto the test boulders. This operation continued until a total of 5 limpets per tank had moved onto the test boulders, which took up to 20 d.

Experiments tested the effects of different amounts and grain sizes of sediment. Amounts of sediment were 50, 100 or 200 g dry wt (50 g being equivalent to about 2 g dry wt l^{-1}, 50 mg dry wt cm^{-2} and a 1 mm thick layer; these increased proportionally for 100 and 200 g). These amounts mimicked a wide range of sediment deposits likely to occur on rocky coasts close to urban areas (e.g. Airoldi et al. 1996, Connell 2005). Sediment was collected in April 2002 from a tidal flat in the nearby Plym Estuary. Sediment was oven-dried and manually sieved through wire meshes of 500 and 250 µm in order to separate a 'coarse' fraction (retained on the 250 µm sieve) from a 'fine' fraction (passing through the 250 µm sieve). Although the site where sediment was collected is not considered particularly polluted, duplicate samples of each fraction were analyzed for contents of metals and tributyltin (TBT). Triplicate samples of each fraction were also analyzed for grain size distributions by using a laser particle sizer (Malvern Instruments).

It was too difficult to set up enough replicate 'tidal' tanks to simultaneously test the effects of different amounts and grain sizes of sediments in orthogonal combination. Because feeding activity of limpets varies seasonally (e.g. Jenkins et al. 2001), comparison of results from experiments run at different times would have also proved impractical, requiring great temporal replication of the experiments. Therefore, we tested the effects of different combinations of sediment amounts and grain sizes during 6 independent experiments, run from April 2002 to February 2003. In each experiment, 5 new limpets were used per tank. At the beginning of each experiment, treatments (sediment addition vs. unmanipulated control) were each assigned at random to 3 tanks. Responses of *Patella vulgata* to sediment were quantified as differences in rates of grazing and mortality among treatments. Rates of grazing were estimated by using the method described by Thompson et al. (1997), which relies on distinctive radular marks that are left by grazing limpets on the surface of dental wax cast into small discs and placed into pre-formed holes in the rock surface. Ten wax discs were placed in each tank into the pre-formed holes just before sediments were added to the treatment tanks as a fine 'rain'. The behaviour of the limpets was regularly observed during the experiments, which lasted 8 to 12 d. At the end of the experiments the wax discs were retrieved and the health of limpets checked. Wax discs were examined under a binocular microscope. Grazing rate was estimated by counting the number of marks in contact with a transparent grid of 25 dots regularly spaced over the surface of the disc.

Effects of sediment on grazing rates were analyzed separately for each experiment by 2-way ANOVAs, with treatment (sediment addition vs unmanipulated control) as a fixed factor and tank (3 levels) as a random factor nested in treatment. Homogeneity of variance was assessed by Cochran's C-test ($p > 0.05$).

RESULTS

Field observations

On all shores, sediment occurred as scattered patches (several mm to several cm thick) of fine to medium sand, either in depressions and crevices or trapped by turf-forming algae. Despite differences in the composition of benthic assemblages both among

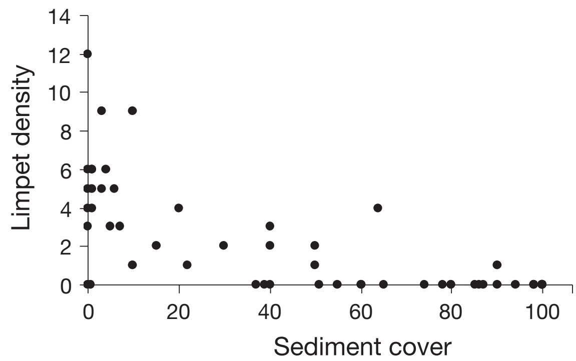

Fig. 2. *Patella vulgata.* Relationship between limpet density (no. ind. 400 cm^{-2}) and sediment cover (%). Points represent 60 plots (10 from each of 6 sediment-impacted sites)

and between sites, plots with no or low cover of sediments tended to group (Fig. 1) and were characterized by high densities of *Patella vulgata* and low cover of fleshy macroalgae. Conversely, plots where sediments were present had more heterogeneous distributions of macroalgae and were dominated by either turf-forming algae *Fucus vesiculosus* or *Ulva* spp., depending on the shore.

Coverage of sediment and density of *Patella vulgata* were negatively correlated ($r = -0.68$, $p < 0.01$). Limpets were clearly most abundant in plots with least amounts of sediment, and were locally absent when sediment covered more than 50 to 65% of the substratum (Fig. 2).

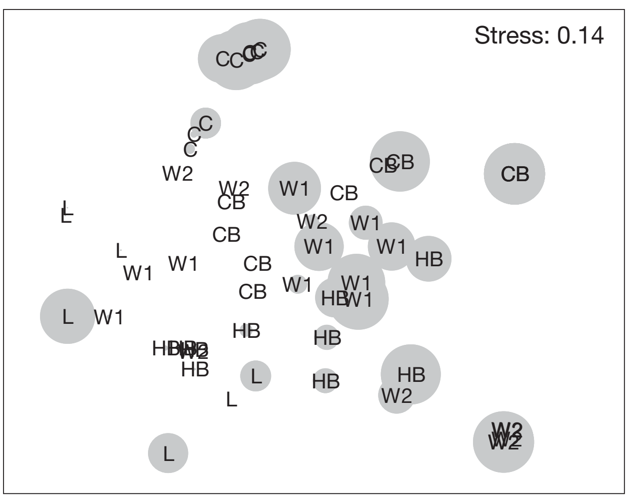

Fig. 1. MDS ordination of 4th root transformed covers of sessile species and density of limpets (mainly *Patella vulgata*) at the 6 study sites (L = Looe, HB = Heybrook Bay, W1 and W2 = Wembury 1 and 2, CB = Cawsand Bay, C = Cremyll). Superimposed grey circles represent sediment cover (%). Points represent 10 plots per site except for L (7 plots) and CB (9 plots) (4 empty plots were excluded from the analysis)

Laboratory experiments

The particle size distribution and chemical characteristics of the sediments used in experiments are summarized in Table 1. Coarse sediment was dominated by sands (58%), whereas fine sediment was dominated by silt (67%). The sediments, particularly the fine fraction, contained concentrations of As, Ag, and Cu and, to a lesser extent, Pb and Zn that exceeded threshold guidelines levels (CCME 1999). Direct, short-term toxic effects were unlikely (W. J. Langston pers. comm.), but such contamination is typical of urban areas where sedimentation is increased by human activities.

In all 6 experiments, rates of grazing were lower in treatments with sediments than in unmanipulated controls (Fig. 3). The effects of additions of fine sediment were always significant, whereas effects of coarse sediment were significant only with the addition of 200 mg cm^{-2} (but note $p = 0.07$ for 50 and 100 mg cm^{-2} of coarse sediment, Table 2). Overall, additions of 50, 100 and 200 mg cm^{-2} of coarse sediment decreased rates of grazing by 35, 45 and 50%, respectively (Fig. 3),

Table 1. Average characteristics of sediment particles used in experiments (n = 3 for grain size distributions, n = 2 for metals). Mean, mode, median, sorting, skewness and kurtosis expressed as Φ-values; abundance of sand, silt and clay expressed as %; abundance of metals expressed as μg g^{-1} dry wt; TBT (tributyltin) expressed as μg Sn g^{-1} dry wt

Sediment	Mean	Mode	Median	Sorting	Skewness	Kurtosis	Sand	Silt	Clay
Coarse	3.09	1.22	2.16	2.4	0.59	0.79	58.07	38.93	3
Fine	5.01	4.68	4.91	1.89	0.11	1.06	29.48	67.12	3.4

	Ag	Cd	Co	Cr	Cu	Fe	Mn	Ni	Pb	Zn	As	Hg	TBT
Coarse	0.43	0.35	3.24	10.89	86.9	6.34	74.5	6.93	30.3	77.2	39	0.14	0.0014
Fine	0.82	0.58	5.26	18.32	233.3	11.56	146.4	9.4	56.5	160.3	102.7	0.34	0.0029

Table 2. ANOVA results: effects of combinations of sediment amount and grain size on grazing rate (% wax disk scraped per day) of limpets. Cochran's *C*-test was always non-significant except under a load of 200 mg cm^{-2} fine sediment ($C = 0.3908$, $p < 0.05$). Significant p-values in **bold**; T = treatment

	df	50 mg cm^{-2}			100 mg cm^{-2}			200 mg cm^{-2}		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Fine										
T	1	192.8	9.57	**0.036**	374.9	110.1	**<0.001**	447.9	22.87	**0.009**
Tank (T)	4	20.2	1.17	0.333	3.4	0.6	0.69	19.6	4.32	**0.004**
Residual	54	17.2			6.0			4.5		
Coarse										
T	1	154.0	5.91	0.072	124.5	5.61	0.077	262.9	10.02	**0.034**
Tank (T)	4	26.0	1.69	0.164	22.2	1.93	0.118	26.2	2.83	**0.034**
Residual	54	15.4			11.5			9.3		

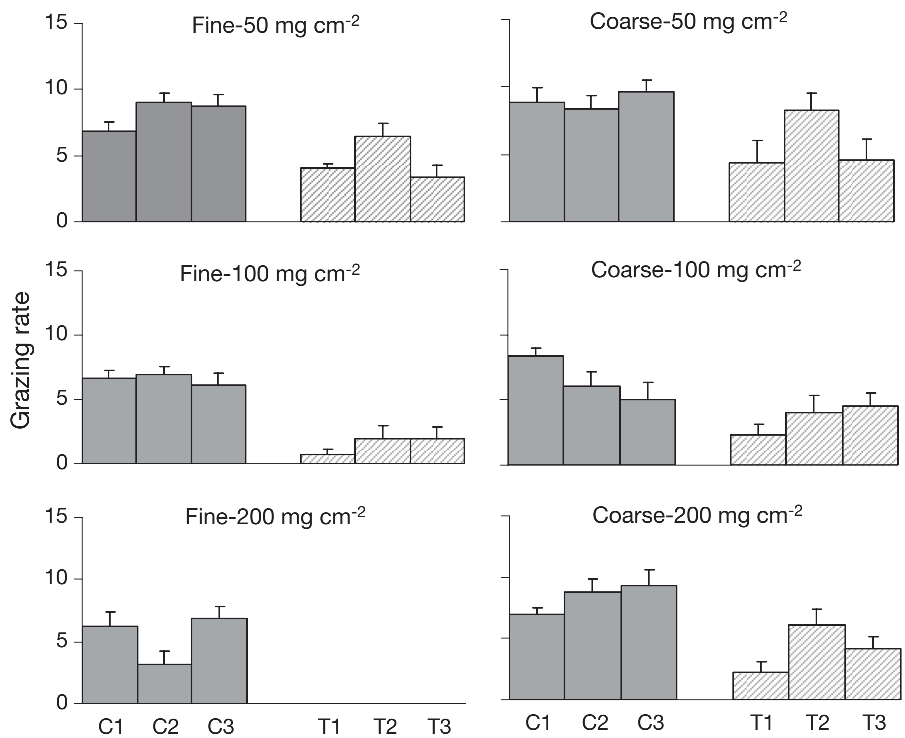

Fig. 3. *Patella vulgata.* Grazing rate (% wax disk scraped per day) measured in 3 sediment-addition treatment (T) and 3 unmanipulated control (C) tanks during 6 experiments testing combinations of sediment amount (50, 100 and 200 mg cm^{-2}) and grain size (fine and coarse). Grazing rate was 0 in all treatment tanks containing 200 mg cm^{-2} fine sediment. Data are mean ± 1 SE

whereas additions of 50 and 100 mg cm^{-2} of fine sediment decreased rates of grazing by 40 and 77%, respectively (Fig. 3). When 200 mg cm^{-2} of fine sediment was tested, grazing was totally inhibited (Fig. 3): limpets initially tried to escape sediments but lost attachment after a few days, and subsequent mortality was observed.

DISCUSSION

We observed that *Patella vulgata* was generally absent from rocky shores near Plymouth when sediments covered more than 50% of the rock. This distribution can be accounted for by the low tolerance of *P. vulgata* to sediments. In the laboratory, the grazing activity of *P. vulgata* was severely inhibited by the presence of a sediment layer that was only ~1 mm thick (equivalent to 50 mg cm^{-2}), and mortality was recorded under loads of 200 mg cm^{-2} fine sediment.

It is possible that the effects of sediments under natural field conditions may be less severe than those observed in our experiments: firstly, because limpets can respond to patchy accumulations of sediments by moving out of disturbed areas; secondly, because laboratory conditions are likely to impose additional stress on organisms; and thirdly, because waves in the field will tend to re-suspend deposited sediments. Nevertheless, it is clear that the presence of sediments per se is an important source of stress for *Patella vulgata*. Furthermore, a broad spectrum of land- and ocean-based human activities (Airoldi 2003, Ahrens & Morrisey 2005) is likely to result in large-scale and persistent loads of thin layers of sediments. These layers will resemble those of experimental conditions of the present study, rather than the dynamic and patchy accumulations of sediments in naturally sand-impacted shores, and will negatively affect limpets.

Fine sediments affected *Patella vulgata* more severely than coarse sediments, particularly when they formed thicker deposits. Indeed, grain size composition greatly influences the effect of sediments (Airoldi 2003), but generalizations are difficult. For example, during a laboratory experiment, fine sediments had more detrimental effects than coarse sediments on the survivorship and growth of embryos of *Fucus serratus* (Chapman & Fletcher 2002), which was attributed to higher diffusion barriers. Conversely, during a field experiment, coarse sediments had more negative effects than fine sediments on the biomass of subtidal turf-forming algae (Airoldi & Virgilio 1998), which was attributed to greater scour. Our experiments simulated water movements related to tidal regimes rather than to wave action, which is a common condition in sheltered environments. It is possible that effects of coarse sediments would be more significant under more dynamic flow conditions.

A number of studies have shown distinct spatial and temporal variations in the feeding activity of limpets, including *Patella vulgata* (Thompson et al. 1997, Jenkins & Hartnoll 2001). Proposed explanations have focussed on the roles of sea temperature, wave action, slope of the rock, reproductive activity and food supply (Della Santina et al. 1994, Jenkins & Hartnoll 2001, Santini et al. 2004). We showed that even a thin layer of sediment may severely reduce the grazing rate of *P. vulgata*. Thus, spatial and temporal variations in sediment loads could influence the grazing activity of limpets. For example, accumulation of sediments, especially the finest fractions, is in general most pronounced at sheltered locations (Airoldi 2003), which could at least in part explain the differences in grazing activity of *P. vulgata* between exposed and sheltered shores (Jenkins & Hartnoll 2001).

Future work should attempt to clarify the mechanisms by which sediments impair *Patella vulgata.* These could include the clogging of gills, thereby reducing oxygen availability and leading to physiological stresses, or interference with attachment, movements or feeding activities, or a combination of these factors. Possible harmful effects resulting from the presence of contaminants should also be considered. Although acute toxic effects were unlikely under the present experimental conditions, contaminants are often present in sediments — especially along urbanized coastlines — and could exert adverse chronic effects on top of those resulting from the particulates themselves (Ahrens & Morrisey 2005).

Any physical and biological processes affecting the feeding and distribution of limpets will have consequences for the organization of intertidal rocky shore assemblages (Jenkins et al. 2005). We have shown that sediments have direct negative effects on the limpet *Patella vulgata*: even a thin layer of sediment may impair this species and significantly decrease its grazing activity. Because sediment deposition on rocky shores is a highly dynamic process, it is clear that the effects of sediments will ultimately be related to their spatial and temporal distribution. Indeed, on rocky shores close to Plymouth, the natural patchiness of sediments was related to the distribution of *P. vulgata* and macroalgae, thereby generating spatial heterogeneity. Any change in sedimentation regime that results in a persistent alteration of the characteristics and distribution of sediment particles could, therefore, pose a serious threat to the diversity and function of rocky shore assemblages through the inhibition of grazing by limpets, in addition to direct effects such as smothering or scouring.

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