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An investigation of the relationship between sediment particles size and the development of green algal mats (*Ulva prolifera*) on the intertidal flats of Muan, Korea

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Abstract The relationship between median grain size of sediments and the abundance in the wild of green algal mats (*Ulva prolifera*) on the intertidal flats of Muan, Korea, were investigated. The impact of substratum particle size on the growth and survival of germlings was examined in the laboratory. In the wild, the average annual density of algal mats was 7,950 ind m^{-2}. The algal mats mainly occurred in sands and exhibited patchy distribution. Statistical analysis indicates significant spatial analysis differences and a significant relationship between density and the ratio of sands to silts, suggesting that the distribution and density of this species were related to particle size. In laboratory experiments, the survival rate of *U. prolifera* germlings was the lowest value (22%) on sediments with a median grain size of 63–125 µm. Laboratory experiments have generally shown a positive relationship between attachment or survival of the alga and substratum particles size. Our laboratory results indicate a clear link between germling settlement/survival and substratum particle size. These results explain the spatial differences in abundance observed in the field in relation to the distribution and ratio of sands to silt on the Muan flats.

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Introduction

Ulva prolifera O.F. Müller is an edible green alga that grows in almost every bay, intertidal flat, and river mouth in Korea. In 2005, the production of *U. prolifera* as food was approximately 2,500 tonnes wet weight (Informatization officer 2006). Because of the demand for this seaweed and the need to increase biomass, there have been many efforts to harvest this alga on an industrial scale, but there are few places in Korea where *U. prolifera* production in the wild is adequate for commercial exploitation, and consequently, the opportunity for increasing production through stock enhancement is being investigated (Yoon et al. 2003).

Tidal flats show a marked longitudinal gradient in environmental factors (temperature, salinity, light, sediment, etc.) and biological factors (herbivory and competition with other intertidal organisms) from the land to the sea (Buschmann et al. 1997). Generally, salinity and wave action decrease, whereas silt, turbidity, light extinction, and nutrient concentrations all increase along this gradient. Consequently, tidal flat macroalgae communities typically exhibit spatial zonation and low species diversity. Attached species such as *Ulva* spp. often form the dominant algal species in warm intertidal mudflat environments.

Sediment dynamics significantly influence benthic macroalgal distribution patterns on both rocky shores (Seapy and Littler 1982; Kendrick 1991; Renaud et al. 1997; Airoldi and Cinelli 1997; Umar et al. 1998) and soft sediments (Albrecht 1998; Chapman and Chapman 1999) in the coastal environment. On rocky shore habitats, it has been demonstrated for a range of algal species that sediment deposition can interfere with the attachment of microscopic stages of seaweeds (Norton 1978; Littler et al. 1983; Arakawa and Matsuike 1992). In addition to impairing the initial attachment process, burial under sediment may significantly reduce growth and impair the regeneration ability of adults (Lyngby and Mortensen 1996). Scour through sediment movement removes small life stages of macroalgae from the substratum and hence reduces successful recruitment (Devinny and Volse 1978).

Recruitment of seaweeds through small reproductive stages is limited on sediment-inundated rocky shores and largely unsuccessful in soft sediment environments. Burial in sediment has several potentially negative effects for seaweed propagules. Sediment dynamics on intertidal flats may alter ecological assembly composition because species shifts occur in consequence to differential sediment susceptibility and life history responses (Airoldi 1998). In soft sediment-dominated coastal environments (e.g., tidal flats), the effects of dynamic sediments on marine macroalgae are more fundamental than other stable attachment substrate. However, in nature, soft sediment environments with organically enriched muds (e.g., tidal flats and salt marshes) represent habitats that are favorable for colonization through small reproductive stages of seaweeds.

Whereas the effects of sediment depositions on growth and survival of adult seaweeds have been tested experimentally for a number of species (Umar et al. 1998) as well as for species assemblages (Airoldi and Cinelli 1997), direct evidence for the mechanisms by which sediment burial reduces survival and/or growth of macroalgal recruits, especially after settlement, remains scarce.

Investigations of *U. prolifera* have been mainly carried out on the pattern of distribution on rocky shore habitats, morphology (Pang et al. 2010), physiology (Runcie et al. 2003), and growth (Sfriso and Marcomini 1996). To date, there have been no studies that examine the distribution and population dynamics of *U. prolifera* on intertidal flats.

In this study, we investigated the relationship between distributions of *U. prolifera*, a representative species of a dominant intertidal group of seaweeds with a wide distribution in soft sediment environments. The spatial and temporal variation in density and structure of *U. prolifera* were investigated from Muan intertidal flats and the influence of substrate heterogeneity on its distribution.

Materials and methods

Sampling and measurement

The density of *U. prolifera* in the wild was tested by collecting samples of *U. prolifera* from the intertidal flats of Muan, Korea (Fig. 1). Three replicate quadrat samples of 400 cm^2 (20 cm in width×20 cm in length) were taken from five stations spaced at a 50-m interval distance on an orthogonal line to the shore. Sampling was undertaken once a month at low tide between October 2006 and September 2007. In each sample, the total number of individuals of >1-mm thalli length was recorded. This helped remove the bias in density within a given sampling period, caused by recruitment to the sampled population. The maximum thallus length was measured to the nearest 0.1 mm using digital Vernier calipers.

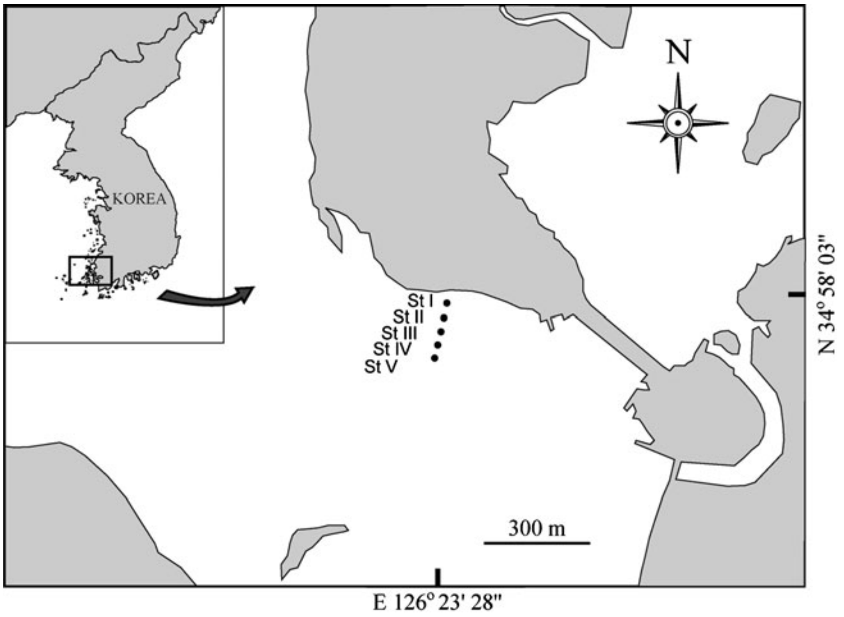

Fig. 1 Map showing the location of the five sampling sites along the Muan intertidal flat in the southwest coast of Korea

Sampled thalli were dried for 24 h at 60°C, and thallus dry weight determined to the nearest 0.1 g using an electronic digital balance.

A crust sample of substratum (500-g wet weight of <5 cm in depth) was taken adjacent to each station for particle size analysis. Fine and coarse grain sizes represented lower and upper limits of size ranges from tidal flats known to support macroalgal populations. Dry weight in each particle grade was measured using Sedigraph 5100 (Micromeretcs, Australia). Classification of particle size and grade were adopted from Friedman and Sanders (1978). Environmental factors, water temperature, salinity, and conductivity were measured by a logging multiparameter probe (YSI-85, USA) at the experimental site. Triplicate samples for the particle size analysis were taken at January 2007 during the peak growing season for the alga.

Zoospore release, settlement, and growth in the laboratory

For the laboratory experiments, *U. prolifera* thalli were collected at low tide between October and November 2006 from the intertidal flats of Muan, on the Southwest coast of Korea. *U. prolifera* thalli were placed in filtered seawater, and were allowed to release zoospores at 15°C and 16:8-h L/D cycle (approximately 100 μmol photons $m^{-2}s^{-1}$). The solution of suspended zoospores was checked by means of counting the number of zoospore individuals under a microscope, and the concentration of the solution was adjusted to 1,000 individuals mL^{-1} (Chapman and Fletcher 2002).

The zoospores were inoculated to settle onto sterilized disposable plant culture dishes (SPL310100, 100×40 mm), each containing one of the experimental sediment types and Provasoli's PES culture medium. The sediments were collected from the study area and represented a range of particle size classes (Table 1). For the selection of treatment levels, we used conditions within the range encountered in Muan intertidal flat sediment environments studied previously (size range of grain sizes; Ryu et al. 2000; Kang et al. 2008). A glass slide (used as the control substratum) was placed at the bottom of each culture dish and left for 24 h to allow time for zoospores of *U. prolifera* to attach to the slide. The number of zoospores attached to each slide was counted under a microscope. The experiment was repeated ten times and the values of zoospores attaching to the glass slides are given as the mean value of the ten replicate trials.

Culture conditions for on-growing the germlings were 15°C at 12:12-h L/D cycle (approximately 50 μmol photons $m^{-2}s^{-1}$). The survival rate of germlings was obtained from the following equation: $S_r = N_{final}/N_{control} \times 100$ (%), where S_r is the survival rate of germlings, N_{final} is the number of germlings after 30 days of cultivation, and $N_{control}$ is the mean number of germlings in the control. After 30 days of cultivation, the number of germlings and young thalli attached to each substrate were counted under a Stereomicroscope and with the naked eye. To avoid systematic error, all experiments were carried out for one set of replicates first then for the second set of replicates.

Statistical analysis

The differences in density of *U. prolifera* between monthly samples were tested by an analysis of variance (ANOVA). The differences in density of *U. prolifera* between stations were analyzed by Kruskal–Wallis test, and subsequent a posterior comparisons between all pairwise stations were tested by Tukey's honestly significant difference test (Sokal and Rohlf 1995) in SigmaStat, version 2.0. The differences in survival rate of zoospores were expressed as a percentage of the control in

Table 1 Mean percentage of each particle size group at the five stations in the intertidal flats of Muan, Korea

Size		Size classification[a]	Stations				
(μm)	(Ø)		I	II	III	IV	V
1,000–2,000	−1–0	Very coarse sand	0.235±0.112[b]	0.033±0.014	0.022±0.018	0.094±0.072	0.035±0.024
500–1,000	0–1	Coarse sand	0.133±0.059	0.128±0.026	0.029±0.016	0.216±0.148	0.109±0.071
250–500	1–2	Medium sand	3.064±1.276	4.531±1.872	1.074±0.291	2.598±1.275	3.872±0.795
125–250	2–3	Fine sand	20.298±7.149	33.784±6.387	10.873±5.285	9.863±4.019	15.474±4.683
63–125	3–4	Very fine sand	61.459±9.623	54.112±7.582	65.363±8.027	51.954±6.436	24.549±7.876
<63	>4	Silt	14.811±4.811	7.412±2.693	22.639±5.251	35.275±5.977	55.961±7.442
Ratio (sand/silt)			5.757	12.492	3.417	1.835	0.791

[a] Size classification of particle is adopted from Friedman and Sanders (1978)

[b] Mean ± SD represents the average of triplicate data

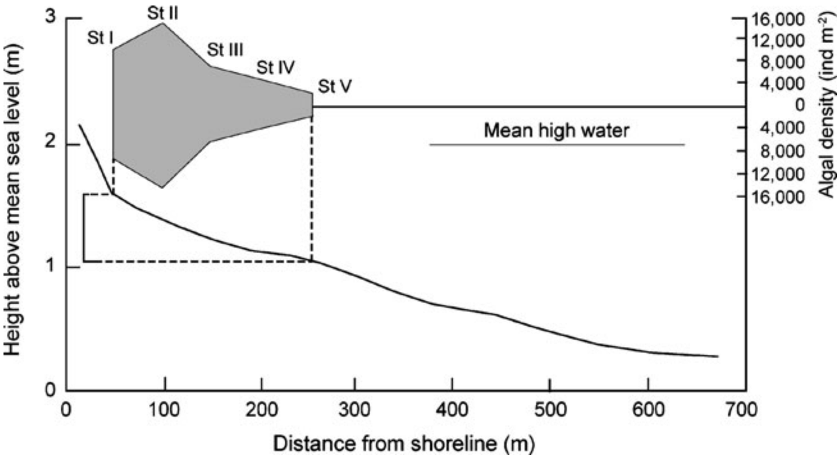

Fig. 2 *Ulva prolifera*: kite diagram of the distribution along a transect of the Muan intertidal flats superimposed upon a diagram of the intertidal area

each of replicate culture dishes. These data were normalized by arcsine transformation before statistical analysis.

Results

Spatial and temporal variation in distribution and biomass

Water temperature varied from 5°C to 25°C during the experimental period. Maximum water temperature was recorded in September 2007 and the minimum in February 2007. Salinity ranged between 29.2 and 32.5 ppt.

The average annual density of the whole *U. prolifera* population was 7,950 ind m^{-2}. Density ranged from 1,950 ind m^{-2} at station V (lowest mean density) to 15,475 ind m^{-2} at station II (highest mean density; Figs. 2 and 3). There was a significant difference in mean density between stations ($p<0.001$), with the greatest density being >87% of that at the station with the lowest mean density. The density distribution of the algal population relative to the profile of the Muan intertidal flats is presented as a kite diagram in Fig. 2.

The mean thallus length (TL) and dry weight per square meter (DW) of *U. prolifera* ranged from 25 to 141 mm and 5.0 to 1,307.5 g m^{-2}, respectively. It spatially ranged from 25 mm in station IV (lowest mean TL) to 141 mm in station II (highest mean TL) and 5.0 g m^{-2} in station V (lowest mean DW) to 1,307.5 g m^{-2} in station II (highest mean DW; Table 2). The period of minimal growth of *U.*

Table 2 Mean in length and biomass of *U. prolifera* between October 2006 and September 2007 on the intertidal flats of Muan, Korea

Month	Stations (distance from shore)									
	I (50 m)		II (100 m)		III (150 m)		IV (200 m)		V (250 m)	
	Frond length (mm)	Biomass (g dry wt m^{-2})	Frond length (mm)	Biomass (g dry wt m^{-2})	Frond length (mm)	Biomass (g dry wt m^{-2})	Frond length (mm)	Biomass (g dry wt m^{-2})	Frond length (mm)	Biomass (g dry wt m^{-2})
Oct 2005	35±16	295.0±57.5	41±25	307.5±47.5	38±19	267.5±57.5	34±18	112.5±17.5	31±13	87.5±20.0
Nov	48±21	327.5±47.5	53±31	587.5±52.5	49±21	295.0±77.5	51±29	227.5±57.5	42±19	115.0±30.0
Dec	109±37	395.0±52.5	112±42	1,160.0±65.0	98±32	312.5±70.0	96±33	257.5±62.5	102±31	182.5±57.5
Jan 2006	125±43	465.0±60.0	130±35	1,307.5±77.5	115±28	352.5±72.5	121±42	292.5±72.5	123±28	105.0±35.0
Feb	137±36	355.0±47.5	141±41	1,262.5±92.5	123±36	292.5±55.0	126±36	242.5±60.0	135±36	95.0±22.5
Mar	104±22	262.5±55.0	112±28	492.5±62.5	92±24	220.0±47.5	98±24	140.0±52.5	105±31	60.0±12.5
Apr	53±31	202.5±40.0	71±27	315.0±45.0	51±31	180.0±27.5	62±21	80.0±45.0	49±25	52.5±15.0
May	46±25	162.5±57.5	58±16	272.5±35.0	42±28	117.5±20.0	38±15	67.5±27.5	38±14	35.0±10.0
Jun	41±28	157.5±45.0	51±15	290.0±22.5	38±17	87.5±10.0	32±11	62.5±15.0	29±13	32.5±12.5
Jul	35±22	185.0±37.5	43±12	235.0±40.0	31±12	80.0±15.0	26±12	55.0±12.5	31±15	30.0±7.5
Aug	28±13	107.5±7.5	36±21	227.5±20.0	30±11	75.0±12.5	33±7	40.0±10.0	28±10	20.0±2.5
Sep	34±18	80.0±5.0	38±22	212.5±12.5	26±12	55.0±7.5	25±9	22.5±5.0	30±11	5.0±2.5

prolifera occurred during the summer and autumn, and the period of maximal growth occurred during winter. The biomass of *U. prolifera* varied between sites, with the deepest (seaward) site recording the least (5.0 g m^{-2}) biomass and site II recording the highest biomass (1,307.5 g m^{-2}) values. The mean length of *U. prolifera* was not significantly different between sites, but the mean density of *U. prolifera* varied significantly between sites both spatially ($p<0.001$) and temporally ($p<0.001$).

Substratum heterogeneity

An analysis of particle size class from substratum samples shows a varied composition and a variable ratio of sand to silt, dominated by fine sands in the study area at the Muan intertidal flats (Table 1). In all the stations, very fine sands (3–4Ø) outweighed coarse sands (0–1Ø). From station I through station V, the percentage of sand decreased, with fine sand (2–3Ø) outweighing coarse sands (0–1Ø), while that of silt (>4Ø) increased. Consequently, this led to the increased ratio of silt to sand. The ratio appeared to correspond closely with the population density of *U. prolifera*. Thus, when the relationship between *U. prolifera* density and ratio of sand to silt was investigated, by plotting logarithm of density against ratio, a significant relationship was obtained ($p<0.001$, Fig. 4). The regression equation is: $\log_e$ density$=0.7869x+7.2247$ $\log_e$ ratio ($r^2=0.6597$).

Growth and survival of *U. prolifera* in the laboratory

Ulva prolifera zoospores were allowed to germinate during exposure to the experimental conditions. Survival of *U. prolifera* zoospores was calculated from the number of germlings present in each culture dish after 30 days (Fig. 5). Survival rates ranged from 0% in the <63 μmØ (silt) to a maximum of 88% in the 500–1,000 μmØ (coarse sand) substrates (Table 3). Three of the four sediment types (very fine sand, fine sand, coarse sand) generally supported high survival rates of zoospores. The density of *U. prolifera* on the experimental culture dish ranged from 0 to 15±6 ind cm^{-2}. One-way ANOVA showed significant differences in density between the four sediment treatment groups ($F_{3,12}=35.429$, $p<0.001$), with the coarse sediment exhibiting the highest density.

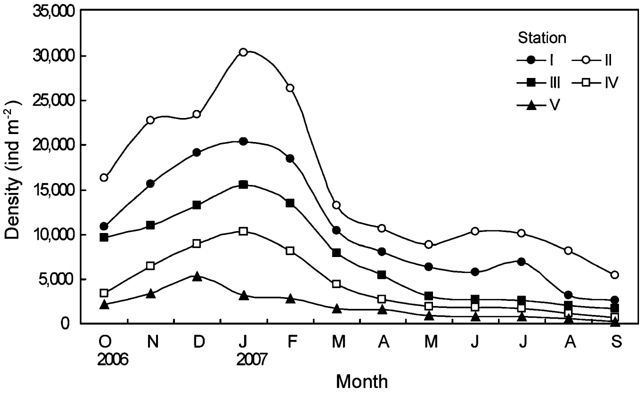

Fig. 3 Mean in spatial and temporal density (ind m^{-2}) of *U. prolifera* during the study period between October 2006 and September 2007 on the intertidal flats of Muan, Korea. Legend from *I* to *V* represents stations in Fig. 2

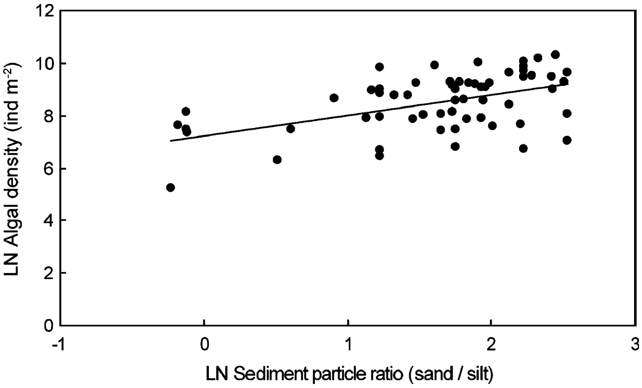

Fig. 4 *Ulva prolifera*: regression of $\log_e$ density on $\log_e$ median diameter (mm) of the substratum particles

Discussion

The density of *U. prolifera* plants on the intertidal mudflat shows a significant spatial and temporal variation, with peak density in station II. In the study area, *U. prolifera* inhabits a wider range of substrata containing from 44% to 93% sand (>2.0 mm) to 7–56% silt (<0.063 mm), suggesting that the *Ulva* occurred in sediment dominated by coarse particles. It has been observed for *Ulva* at Kochi, Japan (Ohno and Miyanoue 1980).

Studies on sediment dynamics in seaweed beds have focused mainly on depositional processes (Madsen et al. 2001). It has been shown that sediments may reduce survival and growth of seaweed propagules after settlement through the processes of scour and burial (D'Antonio 1986). Few studies describe the influence of substrate particle size on seaweeds without the smothering effects of sediment deposition. On the Muan flats, the population density of *U. prolifera* shows significant spatial variation, with the highest density occurring at station II, which also had the coarsest substrate (Fig. 2). However, the algal population inhabits a wide range of substrata containing from 54% to 93% sand (>0.063 mm) to 7% to 56% silt (<0.063 mm). The interaction between sediment dynamics, hydrodynamics, and macrophytes is complex. By a multitude of interactions, the sedimentary environment and hydraulic environment affect macrophytes, which in turn

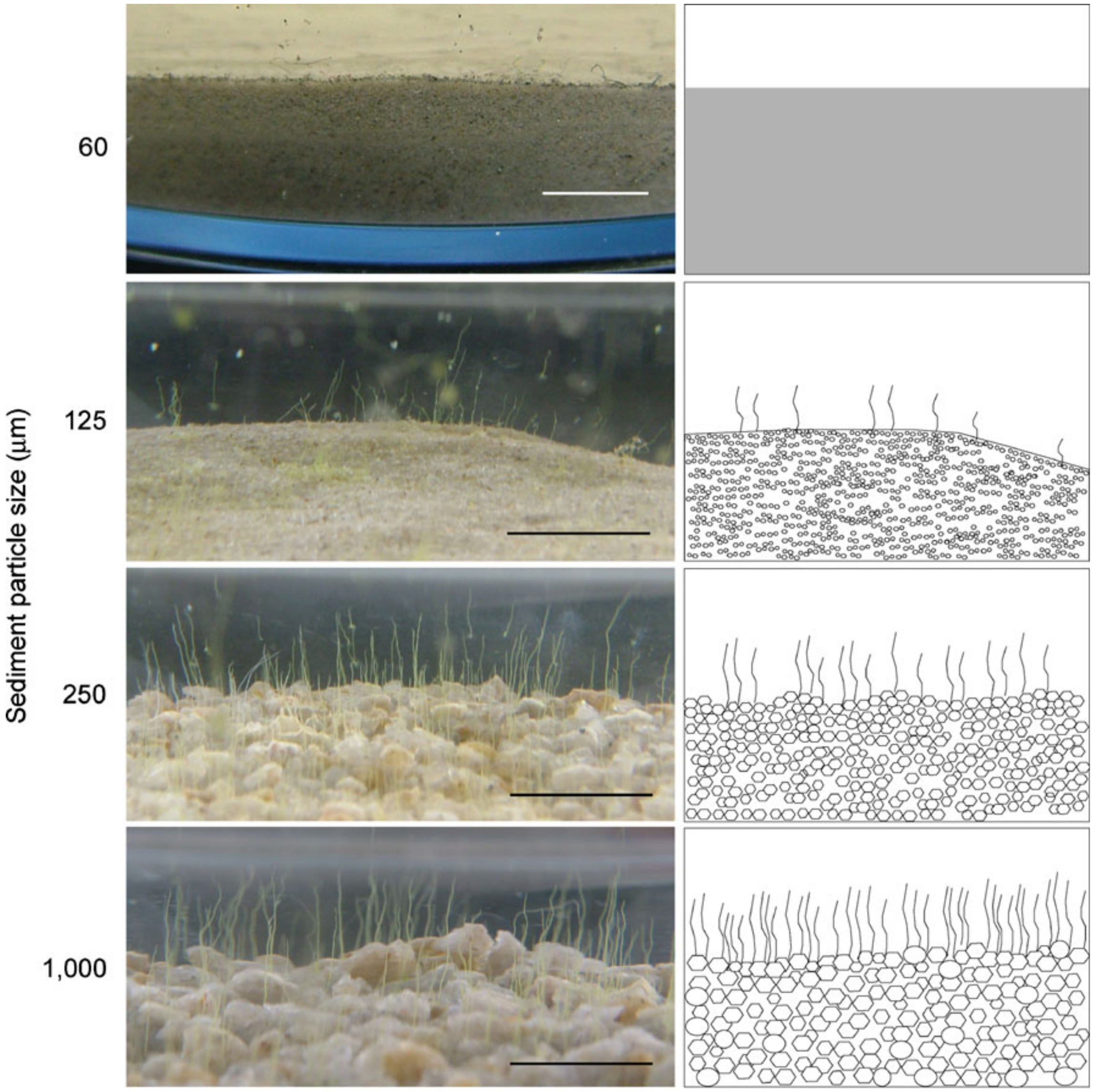

Fig. 5 Survival of *U. prolifera* according to different sediment particle sizes after a 30-day culture period. Diagram illustrates the algal density on the different substrata (n=4). All culture conditions are 15°C, 50 µmol photons $m^{-2}s^{-1}$ and 12:12-hL/D cycle. Culture medium is PES. *Scale bar* is 1 cm

have direct effects on the physical environment (Best et al. 2001; Van Duin et al. 2001). Despite this complexity, most of the basic interactions have at least been conceptualized at both the individual plant and stand levels. However, there are only limited studies that provide numerical data to quantify the conceptual relationships. In several instances, results from field or laboratory are not only disparate in numerical value, but also often contradictory in result.

The laboratory experiments demonstrated that the granular composition of sediments affected the survival of *U. prolifera* germlings: Germlings did not survive in the fine silt treatment, which may be because the fine sediments

Table 3 Mean density and survival rates of *U. prolifera* in experimental treatments with four sediment types after 30 days culture period[a]

Content	Sediment type (µm)			
	Silt (<63)	Very fine sand (63–125)	Fine sand (125–250)	Coarse sand (500–1,000)
Mean density (ind/cm^2)	0	3±1[b]	11±3	15±6
Survival rate (%)	0	22±9	67±15	88±21

[a] Culture condition is in Fig. 5

[b] Mean ± SD represents average of four replicate data

used in this experiment had particle sizes on the same scale or smaller than the germlings and were so densely packed that few interstices remained in which the germlings could establish. In contrast, grains of coarse sand sediments (500–1,000 μm) were significantly larger than germlings at the beginning of the experiment and, even when compacted, which led to a structure rich in interstitial spaces. Sediments in the Petri dishes were not subjected to resuspension, and therefore, survival rates were not affected by burial or scouring effects that plants may be subject to in the wild. The fact that macroalgal assemblages can spatially dominate sediment-influenced rocky shore habitats despite such negative effects has been attributed to specific morphological and life cycle features, to life history strategies, and to indirect advantages in the presence of herbivores (Chapman and Fletcher 2002).

Regression analysis for *U. prolifera* survival indicated a significant inverse relationship between $\log_e$ ratio of sand to silt and $\log_e$ density in the field (Fig. 4). This confirmed the preference of sandy substrata with a ratio of sands to silt in favor of sand. Other *in situ* studies of *U. prolifera* have also shown that community biomass increases with increasing substratum particle size (Ohno and Miyanoue 1980). *Undaria pinnatifida* and *Ecklonia cava* exhibited a 50% reduction in settlement efficiency when a very thin (0.008 mm) layer of fine sediment was present (Arakawa 2005; Arakawa and Matsuike 1992). Devinny and Volse (1978) reported that *Macrocystis* spores, which were released into a Petri dish together with fine sand filtered through a 74-μm mesh strainer, hardly attached when sand was deposited at 10 mg cm^{-2}. Our results show that benthic macroalgae distribution patterns in soft bottom coastal environments influenced at least one of two categories. First, sediment deposition on settlement surfaces may prevent the attachment of propagules. Second, sediments may reduce survivorship and growth of seaweed propagules after settlement through the processes of scour and burial (D'Antonio 1986).

Marked differences on survival rate of the algal zoospores were apparent among the experimental sediment types having different particle sizes (Table 3). The survival rate of the zoospores decreased with decreasing particles size, falling to 67% when the particle size was 125–250 μm and 22% at 63–125 μm. In silt treatments with a mean particle size <63 μm, no growth was observed after30 days of culture.

The ability of seaweed spores to attach to a substrate has been shown to vary depending on the particle size on the substrate. The study has demonstrated that attachment and survival of zoospores of *U. prolifera* is dependent on particle size. By analyzing the quality of sediment in the intertidal flats, it should therefore be possible to estimate the potential for successful stock enhancement of this species within a given estuary.

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