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High amplitude tides that result in floating mats decouple algal distribution from patterns of recruitment and nutrient sources

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ABSTRACT: Three processes that may facilitate proliferation of *Ulva intestinalis* blooms in eutrophic estuaries include: rapid growth in response to nutrient enrichment, the capacity for biweekly sexual recruitment, and the ability to transition from attached benthic stages to floating mats. We conducted field surveys and *in situ* experiments to evaluate whether these 3 processes affect spatial and temporal distribution of *U. intestinalis* biomass within a eutrophic California (USA) estuary. We sampled environmental variables (sediment redox potential, organic content, total nitrogen, and total phosphorus; water column nitrate, ammonium, and dissolved organic nitrogen) and algal biomass and cover at 2 to 4 mo intervals over 15 mo at 3 permanent sites at the head, middle, and mouth of the estuary. Principal component analysis demonstrated significant yet weak relationships between macroalgal abundance and water and sediment N concentrations. Recruitment was abundant throughout the estuary (76.1 ± 22.8 spores cm^{-2}), with little spatial pattern. Thus, we hypothesized that water flow may affect distribution by causing size-dependent detachment of benthic filaments. In 2 experiments on different substrata (tiles and sediment cores), 2 lengths of *U. intestinalis* filaments were exposed to accelerated and ambient water flow during flood tides. On both substrata, there was greater removal at high flow compared to ambient flow and greater removal of tall filaments. Pull tests confirmed that tall filaments required less force to break. Together, these experiments demonstrated that rapid water flow during high amplitude tides caused transitions between attached and floating stages and at least partially decoupled distribution from recruitment patterns and nutrient sources.

KEY WORDS: Green macroalgae · Estuaries · Eutrophication · Habitat expansion · *Ulva* · Soft-bottom intertidal · Recruitment

INTRODUCTION

The distribution and abundance of bloom-forming macroalgae influence the physical, biological, and community structure of shallow coastal habitats (Astill & Lavery 2001, Osterling & Pihl 2001). Many studies have demonstrated that nutrients stimulate algal blooms in coastal estuaries (e.g. Raffaelli et al. 1989, Valiela et al. 1992, Hernandez et al. 1997). However, recent studies have also suggested that there are numerous mechanisms that may influence distribution patterns, including physical processes such as recruitment (Johnson & Brawley 1998, Lotze et al. 2000) and detachment (Granhag et al. 2007). In addition, while many physiological traits that enable opportunistic green algae to proliferate in shallow estuaries have been well studied (rapid nutrient uptake rates: Naldi & Viaroli 2002, Kennison et al. 2011; temperature tolerance: Fong & Zedler 1993; salinity tolerance: Kamer & Fong 2000), to our knowl-

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edge, no studies have addressed the mechanisms whereby shifts from attached to floating stages may expand habitat usage.

Many bloom-forming macroalgae progress through various life stages, including settling as single-celled recruits, growing into attached forms, and ultimately transitioning into free-floating mats (Flindt et al. 2007). The process of transitioning from benthic to floating stages can have dramatic impacts on community composition and structure in coral reefs (Stewart 2006) and shallow bays and lagoons (Cummins et al. 2004, Irlandi et al. 2004, McGlathery et al. 2007). For example, Stewart (2006) found that changes in buoyancy and morphology increased dispersal capabilities of *Turbinaria ornata*, thus potentially contributing to a phase shift from coral- to algal-dominated reefs. In Sweden, shifting from attached to floating mats was advantageous to *Sargassum muticum* as habitats were extensively expanded (Karlsson & Loo 1999). Community and ecosystem level effects of drift algae include the potential destruction of seagrass beds (Kopecky & Dunton 2006) and consequent negative impacts on estuarine ecosystems (Cummins et al. 2004, Canal-Vergés et al. 2010). To date, most investigations of algal detachment processes have been done in high-energy environments and in members of the Orders Laminariales, Fucales, and Gigartinales (see Thomsen & Wernberg 2005 for review). Therefore, a key to understanding spatial patterns of green macroalgal blooms in estuaries is to evaluate the factors affecting early life stages as well as detachment and formation of floating mats.

Understanding interactions between recruitment and hydrodynamics may be essential to evaluating distribution patterns of macroalgae (Lotze et al. 2000, Granhag et al. 2007, Martins et al. 2008). Previous investigations of early life stages have mainly focused on the biotic and abiotic factors that influence early survivorship of recruits (Lotze et al. 2000, Lotze & Worm 2002). However some recent studies suggest that there may be a link between hydrodynamics, recruitment, and adult distribution. For example, propagule banks that consist of microscopic life stages were an important source of *Enteromorpha* recruits in a field experiment, suggesting that recruitment may be localized to areas where 'seed banks' occur (Lotze et al. 2000). Further, in their model, Martins et al. (2008) found that in high hydrodynamic conditions (frequent winter storms), adults were removed and blooms were generated from dormant spores occurring in the summer and fall, whereas low hydrodynamic conditions contributed to overwintering of adults and higher biomass in spring and summer. In small, shallow estuaries such as those in southern California (USA) where flow is channelized, tidal flushing is vigorous, and distance for recruits is small relative to the open ocean (Kennison 2008), it is likely there will be a relationship between algal biomass, water flow, and recruitment.

In estuaries around the world, it has been well-established that macroalgal blooms are stimulated and maintained by nutrients supplied from both the water column (Valiela et al. 1992, Hernandez et al. 1997) and the sediments (McGlathery et al. 1997, Tyler et al. 2001). Variability in nutrient supply to the water has been related to precipitation and runoff from the watershed that may drive spatial and temporal patterns of biomass accumulation in some systems (Martins et al. 2001). Nutrients may be stored in sediments during times of high supply and act as a nutrient source supporting macroalgal blooms when water column supplies decline (McGlathery et al. 1997, Kamer et al. 2004). Flux of nutrients from sediments is affected by mineralization associated with low redox potential (Koch et al. 1992), high organic matter (Dong et al. 2000), and increased salinity (Hopkinson et al. 1999). Although stimulation of macroalgal blooms by both water column and sediment sources of nutrients has been well studied in many estuarine types (e.g. Schramm 1999, Sundbäck et al. 2003), less attention has been focused on Mediterranean climate systems, especially those in southern California (but see Page et al. 1995, Fong & Zedler 2000, Kamer et al. 2001).

The objectives of this study were: (1) to quantify and link spatial and temporal patterns of macroalgal biomass and sediment and water column nutrients; (2) to investigate the effect of water flow on spatial patterns of recruitment and early survivorship; and (3) to investigate the relationship between water flow and transitions from benthic to floating stages. First, we hypothesized that if the watershed is the main source of nutrients, macroalgal biomass would be associated with high concentrations of water column and sediment nutrients at the head of the estuary, near freshwater inflow. Second, we evaluated whether recruitment was related to water flow (more flow resulting in higher supply of recruits) or would be localized to areas of high algal biomass. Last, we tested whether flow affected detachment of attached filaments, and whether filaments were more difficult to remove when shorter and/or intercalated into soft sediments.

MATERIALS AND METHODS

Study organism

Ulva intestinalis progresses through 4 life stages. Recruits are defined as single-celled zoospores that settle on the substratum and grow first into germlings (>200 µm in length, 7 to 14 d of growth, Lotze et al. 2000), then into filaments (>3 cm in length), and ultimately form floating mats. Germlings and filaments are intercalated into the sediments, whereas mats detach, float throughout the estuary, and can form extensive rafts up to 30 cm thick (Astill & Lavery 2001).

Study site

Spatial and temporal patterns of water column and sediment characteristics and algal cover and biomass were evaluated during a 15 mo field survey, and processes resulting in these patterns were investigated through *in situ* field experiments at Carpinteria Salt Marsh Reserve (CSMR). CSMR is a 93 ha estuary located approximately 21 km east of Santa Barbara, California (34° 24′ N, 119° 32′ W; Fig. 1a). California's climate is Mediterranean, characterized by warm dry summers (May–October) and cooler wet winters (November–April). Most rainfall occurs during discrete storm events within the wet season, and the frequency and magnitude of these events is tremendously variable both within and among years (Zedler 1982). The watershed drains approximately 2600 ha of the foothills of the Santa Ynez Mountains, is developed by agriculture and urbanization, and has 2 major inflowing streams, Santa Monica and Franklin Creeks, the lower reaches of which are channelized (Page et al. 1995). Multiple smaller-flow channels drain 283 ha of the adjoining watershed (Page et al. 1995). Sampling sites were located along a dredged channel west of Santa Monica Creek that was modified from a natural drainage in the 1960s. The channel is shallow (1–2 m depth), narrow (3–6 m), and relatively straight with steep banks from the middle of the estuary to the mouth, making tidal flushing rates rapid in that area. Toward the head (upstream), the channel broadens and shallows, and water flow speeds are reduced.

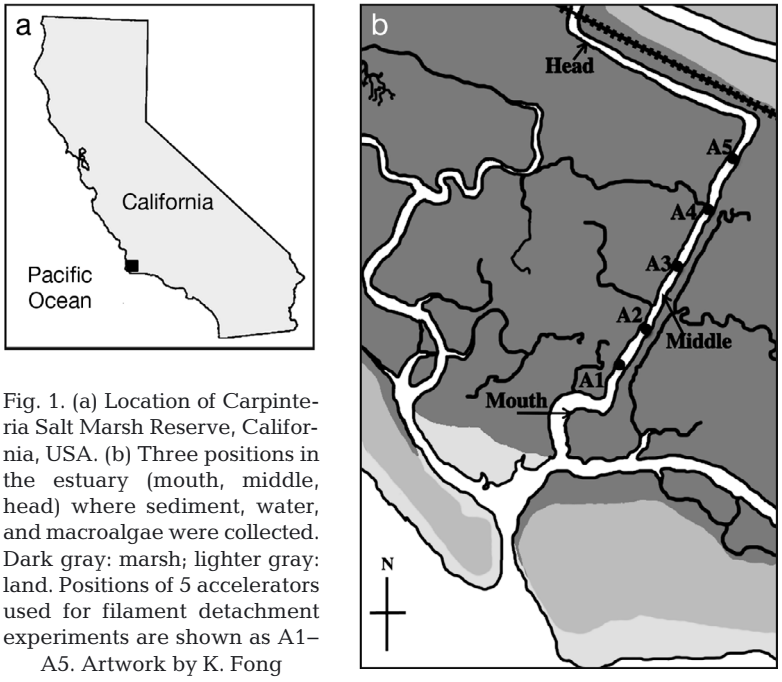

Fig. 1. (a) Location of Carpinteria Salt Marsh Reserve, California, USA. (b) Three positions in the estuary (mouth, middle, head) where sediment, water, and macroalgae were collected. Dark gray: marsh; lighter gray: land. Positions of 5 accelerators used for filament detachment experiments are shown as A1–A5. Artwork by K. Fong

Sampling protocol for field survey

Sampling was conducted in December 2001, February, June, September, and December 2002, and February 2003 at 3 permanently established sites: the head where 2 drainage channels enter the estuary, the mouth near the ocean inlet, and the middle midway between the 2 (Fig. 1b). December and February were in the wet season while June and September were in the dry season. During low tide, 3 water samples were collected at each site, placed in a dark cooler on ice, returned to the laboratory within 6 h, filtered (Whatman GF/C), frozen, and sent to the University of California Analytical Laboratory for analysis of NO_3^-, NH_4^+, total Kjeldahl nitrogen (TKN), and total phosphorus (P). NH_4^+ and NO_3^- were measured by the diffusion-conductivity method (Carlson 1978). TKN was measured using the Kjeldahl method (Bremner & Mulvaney 1982) and does not include N from heterocyclic or oxidized forms. Dissolved organic nitrogen (DON) was calculated as TKN – NH_4^+. Total P was determined by atomic emission spectroscopy following microwave acid digestion (APHA et al. 1998). The method detection limits were 3.57 µM for all forms of N and 3.226 µM for total P.

We sampled intertidal macroalgae and sediments at each site along a 30 m transect parallel to the waterline and 1 m downslope from the vascular vegetation. We estimated macroalgal

abundance as both algal biomass and percent cover, as cover is a more sensitive measurement at low abundance when detached mats are absent and filaments are intercalated in the sediment and cannot be collected quantitatively. At 5 randomly chosen 0.25 m^2 quadrats along each transect, percent cover (top layer of algae) was estimated using the point-intercept method (Kamer et al. 2001). Quadrat location was re-randomized in each sampling period. We only found *Ulva intestinalis* at CSMR. When present in sufficient abundance, algae were collected from a 530.9 cm^2 area circumscribed by a plastic cylinder at the same location as cover was estimated. Each sample was placed in an individual Ziploc bag in a cooler, transported to the laboratory, and refrigerated. Algae were cleaned of macroscopic debris, mud, and animals, placed in a nylon mesh bag, spun in a salad spinner for 1 min, and wet weighed. Biomass was normalized to area (g wet wt m^{-2}).

In the same quadrats, we measured sediment oxidation-reduction potential (redox), organic content, and nutrient content. In order to minimize disturbance to the sediment, sediment measures were taken after water samples but before algal samples. Redox was measured with 6 brightened platinum electrodes and a calomel reference electrode at 5 cm depth into the sediment with a portable pH/millivolt meter. To quantify sediment organic and nutrient content, we collected 3 cores (5 cm diameter, 5 cm depth) from each of the 5 quadrats after macroalgae were removed. Cores were composited, placed in a dark cooler on ice, returned to the lab within 6 h, dried at 60°C to a constant weight, ground with mortar and pestle, and sieved to less than 2 mm. Organic content was determined after ignition in a 400°C muffle furnace for 10 h. At the University of California Davis Analytical Laboratory, total N was quantified by the combustion gas analyzer method and total P by ascorbic acid reduction of phosphomolybdate complex and flow injection analysis (Olsen & Sommers 1982). These automated methods have detection limits of 0.04% for sediment total N and 0.01% for sediment total P.

To assess the relationship between the structure of the environmental data (water column DON, NO_3^-, NH_4^+, and sediment total N, total P, organic content, and redox) and biomass (as wet wt m^{-2}), a principal component analysis (PCA) was performed. The PCA was performed on the correlation matrix of the means for each sampling date, thus standardizing data to 0 mean and unit variance, giving them the same scale. Locations in the estuary (head, middle, mouth) were superimposed on the PCA plot in order to assess patterns visually but were not included in the statistical analysis. Biomass as wet wt m^{-2} was $\log(x + 1)$ transformed, and sediment N and water column nitrate were log transformed to correct for unequal variances.

Two-factor analysis of variance (ANOVA), with factors of location and season, was used to test for differences in mean algal biomass and percent cover. To correct for unequal variances, biomass and percent cover were $\log(x + 1)$ transformed. Means reported throughout the text were generated from untransformed data. Effects were considered significant if $p < 0.05$.

Experiments investigating process

Recruitment

We investigated relationships between recruitment, water flow (advective supply of zoospores), and algal biomass (zoospore source). To measure recruitment, on 27 May 2005, at low tide, unglazed ceramic Saltillo tiles (Lotze et al. 2000) sterilized with alcohol and heated in a 60°C oven for 24 h (Worm et al. 2001) were attached with Velcro to a metal shelf bracket and pushed into the sediment until they lay flat on the benthos at 28 sites along the main channel 10 m apart. Concurrently, percent cover of algae was measured adjacent to the tiles using the point-intercept method.

Tiles were removed after 24 h and transported to the lab at UCLA within 4 h in individual containers holding filtered seawater (10 µm) enriched with nitrogen and phosphorus (concentrations were comparable to the field survey, Table 1) with GeO_2 (0.5 mg l^{-1}) added to inhibit diatom growth (Lotze et al. 2000). Each container was placed outdoors in a temperature-controlled water bath (20 ± 2°C) and covered with 1 layer of window screening to reduce incident light (2200–2500 µmol m^{-2} s^{-2} at mid-day) by ~30% (1405–1956 µmol m^{-2} s^{-2}) which simulated local cloud-covered conditions of coastal areas (Arnold & Murray 1980). Filtered seawater was replaced every 2 to 3 d. After 10 to 14 d, attached filament abundance was determined in 2 ways. First, individual filaments were counted on a subsection of the 10 × 10 cm tile through a dissecting microscope (Lotze et al. 2000), and density was calculated as number of spores cm^{-2}. In order to make sure that an adequate sub-sample was counted, fields of view were counted and the running mean of the number

Table 1. Spatial and seasonal patterns of water column NO_3^-, NH_4^+, total phosphorus (µM) and sediment nitrogen and phosphorus concentrations (% dry wt) for Carpinteria Salt Marsh Reserve. Values are means ± SE and sample size = 3 unless otherwise indicated. For water column total phosphorus, SE or sample size are in parentheses and if n < 3, remainder are below detection limit (BDL) of 3.226 µM. Positions in the estuary: H, head; Mid, middle; M, mouth

Date	Site	NO_3^-	NH_4^+	Total P	Sed N	Sed P
Dec 2001	H	420.71 ± 63.39	5.71 ± 0.41	6.45 (0.0)	0.21 ± 0.01	0.06 ± 0.00
	Mid	272.14 ± 10.21	11.91 ± 0.24	3.23 (n = 2)	0.18 ± 0.02	0.08 ± 0.01
	M	107.38 ± 1.04	12.14 ± 0.41	BDL	0.03 ± 0.01	0.06 ± 0.00
Feb 2002	H	1044.05 ± 52.52	12.38 ± 0.24	3.23 (n = 2)	0.21 ± 0.03	0.06 ± 0.00
	Mid	573.81 ± 15.62	18.20 ± 1.26	BDL	0.15 ± 0.02	0.07 ± 0.01
	M	173.57 ± 15.36	27.14 ± 4.76	BDL	0.08 ± 0.00	0.07 ± 0.00
June 2002	H	80.95 ± 4.76	17.38 ± 0.48	3.23 (n = 2)	0.20 ± 0.02	0.06 ± 0.00
	Mid	11.91 ± 2.38	18.33 ± 1.67	BDL	0.11 ± 0.01	0.06 ± 0.00
	M	9.52 ± 2.38	11.43 ± 0.71	BDL	0.06 ± 0.00	0.07 ± 0.00
Sept 2002	H	333.33 ± 4.95	16.91 ± 1.95	BDL	0.25 ± 0.04	0.06 ± 0.00
	Mid	142.62 ± 1.72	25.24 ± 1.56	BDL	0.15 ± 0.01	0.06 ± 0.00
	M	15.24 ± 0.95	16.91 ± 1.95	BDL	0.06 ± 0.02	0.07 ± 0.00
Dec 2002	H	171.67 ± 3.56	17.86 ± 0.83	3.23 (n = 1)	0.16 ± 0.04	0.06 ± 0.00
	Mid	100.48 ± 3.15	13.81 ± 1.86	BDL	0.17 ± 0.02	0.07 ± 0.01
	M	40.48 ± 1.26	20.95 ± 0.63	BDL	0.06 ± 0.01	0.07 ± 0.00
Feb 2003	H	380.95 ± 20.30	7.38 ± 1.33	6.45 (0.0)	0.29 ± 0.02	0.07 ± 0.00
	Mid	230.71 ± 14.05	18.10 ± 0.24	3.23 (0.0)	0.07 ± 0.00	0.06 ± 0.00
	M	104.05 ± 1.26	15.00 ± 0.71	3.23 (0.0)	0.03 ± 0.00	0.07 ± 0.00

of spores was graphed; counts were continued until the mean stabilized. Second, concentration of chlorophyll *a* (chl *a*) was measured. Tiles were scraped in a darkened room using a razor blade, biomass was ground in a mortar for 3 min, and chlorophyll was extracted using ethanol (Sartory & Grobbelaar 1984). A spectrophotometer was used to measure absorption at 664 and 750 nm before and after acidification, and chlorophyll concentration was calculated using standard methods (Jeffrey et al. 1997). Chl *a* was normalized to area (µg chl *a* cm^{-2}).

Relative water motion was measured using clod cards (see Doty 1971 for methods) glued to plastic sheets secured flat on the sediment surface with 5 inch (~12.7 cm) nails. Clod cards were dried for 24 h at 65°C, weighed, and placed in CSMR adjacent to the tiles when tiles were deployed. Clod cards remained *in situ* for 3 d, were removed, rinsed of salts, redried, and reweighed (Doty 1971, Thompson & Glenn 1994). Relative water movement was calculated as:

$$\text{Dissolution rate (g d}^{-1}) = \frac{(\text{initial weight of clod card} - \text{final weight})}{\text{no. of days}} \quad (1)$$

Data met assumptions with no transformations. Non-linear regression (best fit) was used to quantify the relationship between recruitment (no. of spores and chl *a*) and relative water flow as well as algal biomass (percent cover).

Detachment

To investigate the effects of water flow on transitions from attached to floating stages of macroalgae, we conducted 2 field experiments. One quantified detachment of *Ulva intestinalis* filaments from tiles, and the other assessed detachment from sediment cores. Both substrata were used to evaluate whether substratum type influenced detachment rate as both rocky and soft substrata can be found in many estuaries. In each experiment, 2 filament lengths (short and tall) were subjected to 2 water flow regimes (accelerated and ambient). The tile experiment was conducted on 4 days (June 20 and June 21, July 16, and September 8, 2006) on a total of 80 tiles, and the core experiment was conducted on 2 days (September 9 and 10, 2006) on 40 cores. Both experiments were conducted during relatively high amplitude flood tides and were terminated at slack high tide. Days were chosen based on the closest matches of tidal ranges. However, there was some variability. For the first 3 days of the tile experiment, the tidal range was 0.0 to 1.3 m, while on the last it was 0 to 1.8 m (http://tidesonline.nos.noaa.gov/). For both days of the core experiment, the tidal range was 0 to 1.8 m. Thus, ambient tides in each experiment represented conditions that occurred repeatedly each month, while accelerated treatments were representative of the highest 3 to 4 tides of each month.

Algal spores were collected on tiles (see recruitment methods above). Sediment cores were collected using 6.3 cm height × 7.6 cm diameter PVC pipe from a mudflat where filaments (~0.5 cm tall) were intercalated in the sediment. Pipes were inserted into the sediment until flush with the top of each pipe. Window screening was secured to the bottom of the pipe in order to prevent the core from sliding out of the PVC. Filaments on cores and tiles were cultivated by the same methods as in the recruitment experiment until lengths were >15 cm. On the day of each experiment, attached filaments on 10 experimental units (tiles or cores) were trimmed to 3–5 cm and 10 were trimmed to 10–15 cm lengths.

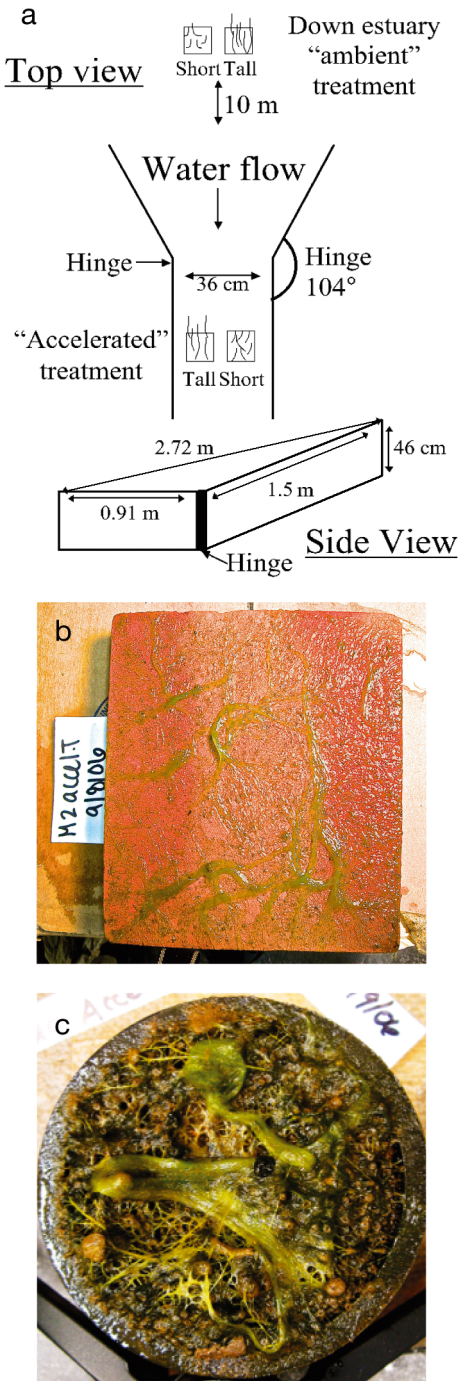

Fig. 2. (a) Schematic representation of accelerator. Top and side view. A pair of tiles (short and tall) were placed 10 m down estuary of the unit (ambient treatment) and within the unit (accelerated treatment). Photos of tall *Ulva intestinalis* filaments grown on (b) tile and (c) core

Five water flow accelerators were constructed by attaching 2 acrylic sheets (2 cm thick) with an acrylic hinge to make each side of the accelerator (Fig. 2a). Accelerators were placed in the center of the main channel and secured with 4 wooden stakes driven into the benthos and attached to each panel with acrylic wing nuts and bolts. Dye studies were used to ensure that eddies caused by the walls of the accelerator did not interfere with unidirectional water flow over the experimental units (tiles or cores) inside the accelerator. Ambient flow experimental units were placed at least 10 m away from each accelerator and accelerators placed at least 20 m apart to ensure that eddies formed did not interfere with unidirectional water flow of accelerators. Accelerators were left in place for the duration of all experimental runs.

Prior to deployment, experimental units (tile/core) were removed from the culture water and photographed (Fig. 2b,c). At slack low tide, pairs of experimental units (1 with short filaments, 1 with tall) were placed both on the inside of the 5 accelerators and in the 5 ambient flow positions. During each flood tide, flow velocities were measured 3 to 5 cm above the benthos using a Marsh-McBirney portable Flow-Mate adjacent to all experimental units. Velocities were measured for 10 min at each position during the flood tide midway between slack tides, as synoptically as possible, and on average, were higher in the core experiments than in the tile experiments for both accelerated and ambient flow stations (Table 2). For both tile and core experiments, water flow velocities were significantly higher (paired *t*-test, p = 0.0001) in the

Table 2. Average water flow velocities (mean ± SE) for both experiments on tile and core substrata for accelerated and ambient flow, demonstrating higher velocities in the core experiment

Substratum	Flow (m s^{-1})	
	Accelerated	Ambient
Tiles	0.21 ± 0.01	0.15 ± 0.01
Cores	0.29 ± 0.01	0.24 ± 0.01

accelerator than in the ambient flow stations. Experimental units were removed during slack high tide, placed in low-nutrient seawater, and returned to the laboratory within 4 h to be re-photographed.

To quantify algal density, percent cover of tiles and cores was measured using a point-intercept method (see Kamer et al. 2001) by superimposing dots onto each photograph (PhotoStudio 4). In order to test for replicability in the method, 15% of the photographs were randomly selected, re-analyzed, and compared to the original analysis; differences were <5%. Percent removal was calculated by subtraction (initial % cover –final % cover).

For each substratum, we investigated variation in percent removal of algal filaments by using a 2-factor nested ANOVA. Water flow type (ambient and accelerated) was treated as the fixed main factor, and filament size (short and tall) was treated as the fixed nested factor. Data in all analyses were balanced, and prior to statistical analyses, normality and homogeneity of variance were assessed, and no transformations were necessary.

Tensile strength

We estimated the force required to detach both tall and short *Ulva intestinalis* filaments on tiles and cores to evaluate whether substratum and size changes the force needed for removal. As in the detachment experiments, filaments were collected, grown, and trimmed on tiles (n = 5) and cores (n = 5). Five short and 5 tall filaments were tested on each tile/core. The end of each filament was wrapped in a paper towel to avoid damage, clamped to a spring device (Pesola scale 0–10 g), and pulled vertically downward until it broke (Anderson et al. 2006). Weight (g) required to break a filament was recorded and multiplied by gravitational acceleration, 9.81 m s^{-2}, to calculate force (N). Means for each tile/core were used to test differences in force required to break algal filaments in a 2-factor ANOVA. Data were log transformed to meet assumptions.

RESULTS

Eutrophic conditions

Spatial and seasonal patterns of water column nutrients suggest the watershed as a source of nitrogen throughout the year, likely associated with storm flows in the wet season and agricultural runoff in the dry season (Table 1). Overall, water column NO_3^- was extremely high, with the maximum mean value exceeding 1000 µM. Concentrations were below 100 µM only in June 2002 (all sites) and in September and December 2002 (mouth sites only). Highest NO_3^- was found at the head decreasing to the mouth in all seasons. Water column NH_4^+ showed an opposite pattern from NO_3^- in December 2001, February 2002, and February 2003, with the lowest values at the head and higher values in the mouth and middle. There was some indication that water column total P was entering the estuary from the watershed because, when detectable, it was highest at the head. Sediment N showed a consistent pattern with highest values at the head and middle decreasing to the mouth in all seasons, in general mirroring spatial patterns of water column NO_3^-. Sediment P values were similar between sites and seasons.

Relating environmental data to biological responses

Almost 80% of the variance in the environmental and biological data was explained by the first 3 principal components (Fig. 3, Table 3). Sediment total N, organic content, and water column NO_3 as well as macroalgal biomass increased along PC1, and explained 43% of the variance. Biomass, NO_3, sediment N, and organic content were all grouped toward the

Table 3. Principal component analysis (PCA) using environmental variables (sediment redox, organic content, and N and P content; water column dissolved organic nitrogen [DON], NH_4, and NO_3) and biomass as wet wt m^{-2}. The eigenvectors making up each PC axis are highlighted in **bold**

Eigenvalues			
PC	Eigenvalues	%variation	Cum. %variation
1	3.42	42.7	42.7
2	1.54	19.3	62.0
3	1.20	15.0	77.0
Eigenvectors (coefficients in the linear combinations of variables making up PCs)			
Variable	PC1	PC2	PC3
Biomass	**0.478**	0.011	0.084
NO_3	**0.356**	–0.036	–0.109
Sed N	**0.456**	–0.165	–0.340
Organic	**0.462**	–0.310	–0.231
Sed P	–0.233	**–0.642**	–0.160
DON	0.158	**0.508**	–0.441
Redox	–0.286	–0.292	**–0.573**
NH_4	–0.250	0.346	**–0.515**

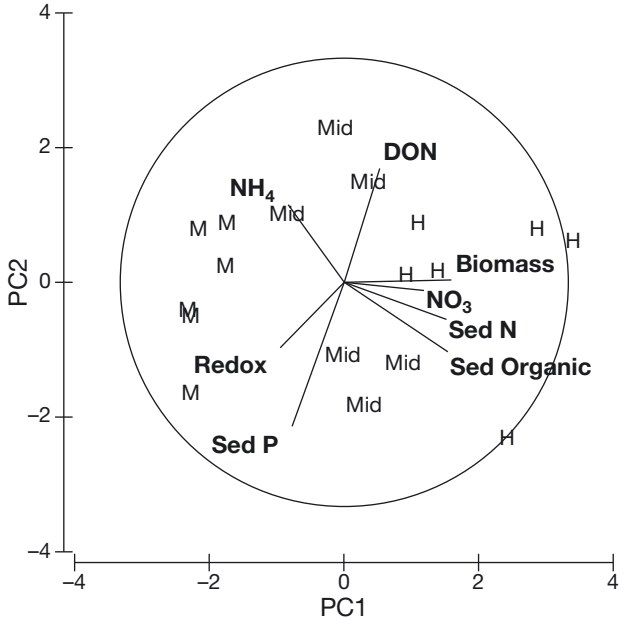

Fig. 3. Principal component analysis (PCA) of environmental data (water column dissolved organic nitrogen [DON], NO_3, and NH_4; sediment total N, total P, organic content, and redox) and biomass (wet wt m^{-2}) over all sampling dates. The location of the sampling points is superimposed by PRIMER on the graph (M: mouth, Mid: middle, H: head). Maximum mean ± SE water nitrate was 1044 ± 53 µM NO_3 in February 2002 at the head

head of the estuary. This suggests that runoff high in nutrients may have been enriching the water and sediment and fueling algal blooms. The PC2 axis independently explained 19% of the variance, which was comprised of sediment total P and water column DON, which were negatively correlated. One possible explanation for the negative correlation is that sediment P is deposited at the head, decreasing down estuary, while water column N enters the estuary as inorganic N and is transformed into organic N as it moves down estuary. Water column NH_4^+ loaded on PC3 axis along with sediment redox potential. It appears that in CSMR, where sediments were generally anoxic (< +400 mV during our daytime sampling), mineralization and subsequent release of NH_4^+ from the sediments may contribute to eutrophication, although the link is not as direct as it is with watershed inputs of NO_3.

Spatial and temporal patterns of algal biomass and cover

Overall, temporal and spatial patterns of biomass and percent cover of algae demonstrated that abundance was higher in the wet seasons (December and February) and toward the head of the estuary (Fig. 4). Maximum values in both biomass (1760 ± 452 SE g wet wt m^{-2}) and cover (99 ± 1%) occurred at the head in December 2001. This supports the implications of the PCA that blooms were fueled by winter rains that transported N into the estuary. However, these patterns were not always consistent over space or time. For example, while in general, maximum values of biomass were recorded in the wet season and minimum in the dry season (Fig. 4a), an exception was in December 2002, when biomass was relatively low. This may be explained by 6 inches (~15 cm) of rain that occurred 2 wk before sampling (Santa Barbara County Flood Control District, Carpinteria Fire Station) that may have resulted in macroalgae being scoured and washed into the ocean. Overall, detached mats occurred at the head at every sampling time, in the middle only twice, and never at the mouth. At 1 sampling time (June), biomass at the middle exceeded that at the head. Such variability implies that processes other than watershed nutrient

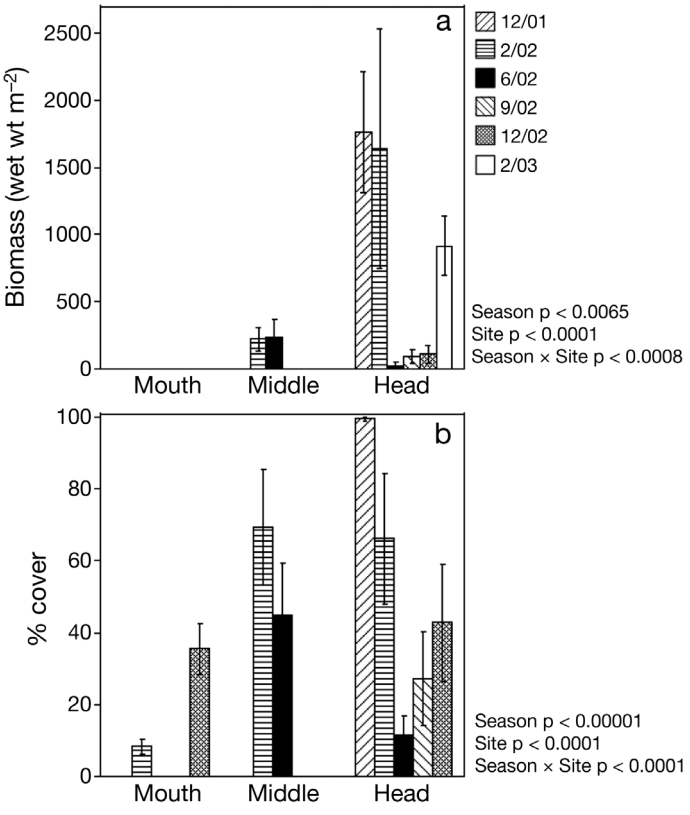

Fig. 4. Spatial and seasonal variation of (a) algal biomass and (b) algal percent cover in Carpinteria Salt Marsh Reserve during December 2001, February, June, and September 2002, and February 2003. Error bars are ±1 SE. Summary statistics for 2-factor ANOVA next to each panel

supply may have affected spatial and temporal patterns in algal biomass.

Patterns in cover and biomass did not always correlate, providing some insight into transitions from attached to floating stages. Attached filaments (Fig. 4a) occurred more consistently than detached mats (Fig. 4b) among sites and seasons but did not always proliferate into mats within the same sites they recruited. For example, while attached filaments covered portions of the benthos at the mouth in February and December 2002, this never resulted in formation of mats at this site. In addition, at the middle site the relatively high cover of attached filaments in both wet and dry seasons (February and June 2002) resulted in only modest accumulations of mats. This suggests that although nutrients were relatively lower in June 2002, dry season inputs were sufficient to stimulate growth of filaments even though they did not transition to the detached and floating mat stage.

Experiments investigating process

Recruitment

Overall, recruitment rates of macroalgal zoospores, measured as filament density and chl *a*, increased across the range of water flow speeds experienced in the channel (Fig. 5, maximum = 534 spores cm^{-2}). Although this relationship only explained 16 to 30% of the variability, it suggests that spore supply was important in enhancing recruitment. In contrast, there was no relationship between percent cover of algae and recruitment (data not shown) across the spatial scale of this estuary.

Detachment

Accelerated water flow significantly increased removal of filaments attached to tiles compared to those subjected to ambient flow (Fig. 6a). Overall, there was 2-fold more removal in accelerated versus ambient flow treatments. In addition, tall algal filaments subjected to increased water flow had higher removal than short filaments in both flow treatments.

Removal of filaments in the experiment conducted on cores was almost double that on the tiles (Fig. 6b); however, the tidal amplitude was also higher and water velocities faster than in the tile experiment. There was significantly higher filament removal on the cores subjected to accelerated water flow than on those subjected to ambient flow. Overall, tall algal filaments subjected to increased water flow had higher removal than short algal filaments, especially in the accelerated treatment.

Tensile strength

Overall, less force was required to break tall versus short filaments, and this difference was far greater for filaments intercalated into sediment cores than for those attached to tiles, resulting in an interaction between substratum and size (Fig. 7). These results

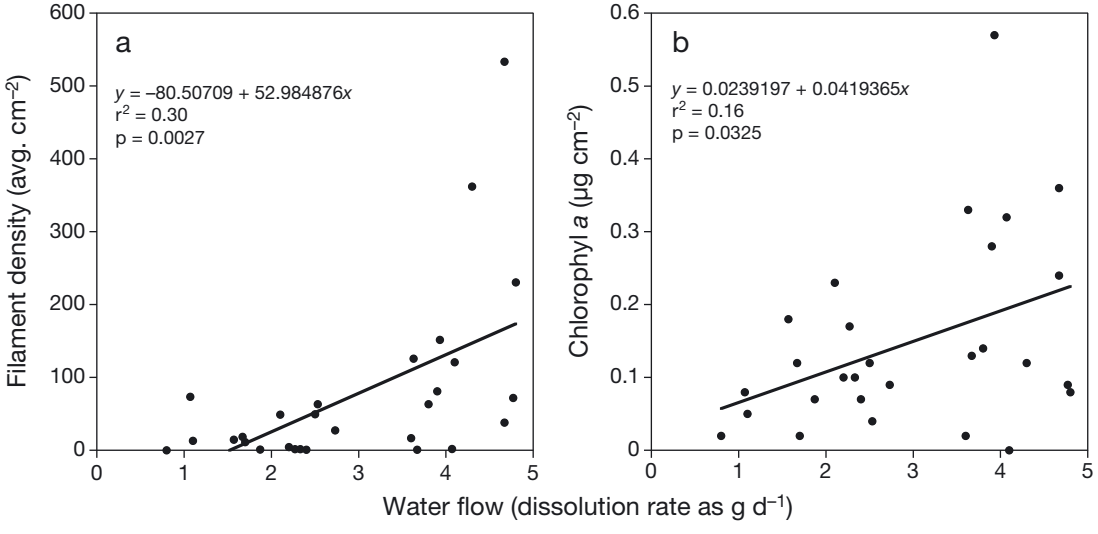

Fig. 5. Effect of water flow on spore recruitment rates. Water flow as dissolution rates (g d^{-1}) and (a) density of spores in no. of *Ulva intestinalis* filaments cm^{-2}, (b) density of spores as chlorophyll *a* in µg cm^{-2}

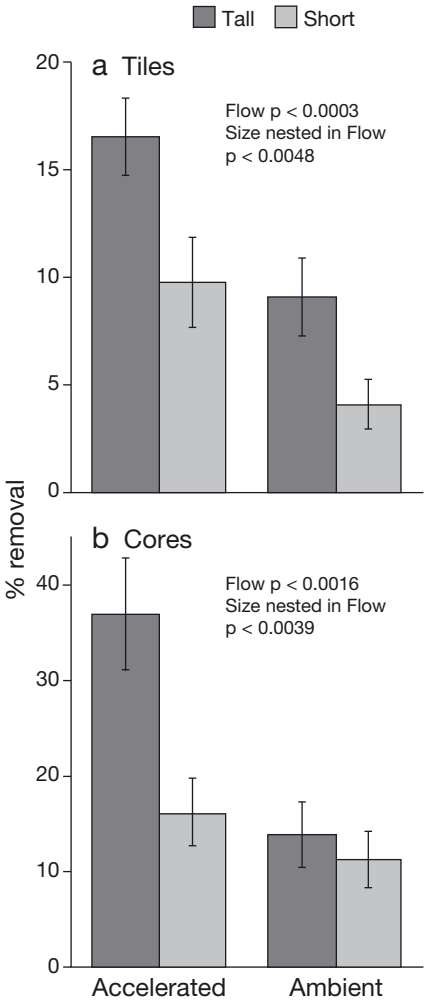

Fig. 6. Effects of water flow treatments (ambient and accelerated) on percent removal of *Ulva intestinalis* algal filaments grown on (a) tiles and (b) cores. In both experiments, for accelerated water flow and ambient water flow there was a significant effect of filament size (tall and short). Error bars are ±1 SE

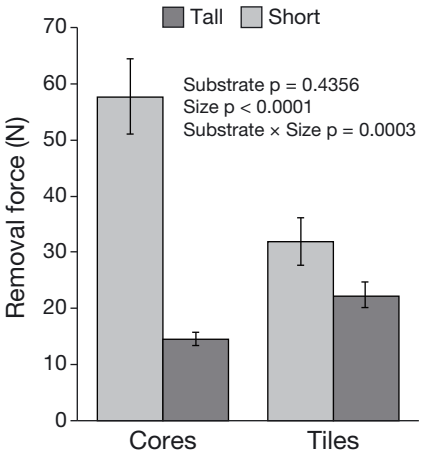

Fig. 7. Effect of substrate (core vs. tile) and size of *Ulva intestinalis* filaments (tall vs. short) on force (N) required to remove filaments. Error bars are ±1 SE. Summary statistics for 2-factor ANOVA are given in the panel

help explain our trend of a greater difference in removal of tall compared to short filaments, especially on cores in the *in situ* experiments.

DISCUSSION

We found that watershed nutrient sources were linked to higher overall macroalgal biomass, a finding that supports evidence from many eutrophic estuaries throughout the world (e.g. Flindt et al. 1997, Hauxwell et al. 1998). However, our study also demonstrated that patterns in nutrients alone did not explain much of the variance in the distribution and abundance of macroalgal blooms within estuaries. Although elevated nutrient supply and storage in sediments have clearly impacted estuarine water quality by increasing macroalgal abundance, the distribution patterns of these blooms can only be comprehensively understood through shifts in habitat usage via detachment and formation of floating mats. These shifts provide an additional mechanism by which macroalgae may be affecting trophic linkages across habitat types (Vanderklift & Wernberg 2008) and resultant widespread impacts on estuarine flora and fauna (Cummins et al. 2004, Green 2011).

Transitions between benthic and floating stages of *Ulva intestinalis* driven by high amplitude tides may facilitate the widespread proliferation of macroalgal blooms in eutrophic estuaries. These shifts may expand habitat usage as benthic stages are restricted to shallow (<0.5 m) intertidal mudflats, while floating mats may also occupy deeper subtidal areas (Kopecky & Dunton 2006, Britton-Simmons et al. 2012). In our study, hydrodynamic processes likely removed portions of attached filaments from mudflats in high-flow environments such as the estuary mouth; this removal may provide a continuous source of regenerative material to mats floating to lower-flow areas up estuary. Hydrodynamics play an important role in the removal of algal thalli in both rocky high-energy temperate (Milligan & DeWreede 2004) and tropical environments (Anderson et al. 2006), but in these cases removal may be a disadvantage as biomass is lost from these systems. In contrast, by detaching and rafting as mats, estuarine algae can relocate to lower-energy, deeper, subtidal areas taking advantage of the whole euphotic zone and facilitating distribution throughout the entire estuary (Kopecky & Dunton 2006, Thomsen et al. 2006, Britton-Simmons et al.

2012). For example, in a study in Hog Island Bay, Thomsen et al. (2006) found that green algal biomass was highest in the deeper lagoon area, although present in both intertidal and shallow subtidal elevations, indicating that the mobility of the algae allowed them to occupy these different locations in the bay. Although they did not directly measure the relationship between water flow and biomass, Merceron & Morand (2004) found blooms of *Ulva* in both intertidal and subtidal habitats and hypothesized that, due to their mobility, the subtidal stock may be providing a source to intertidal biomass in the spring while the opposite may be true later in the season. Our study demonstrated that the spatial distribution patterns of detached mats may be controlled, at least in part, by hydrodynamic processes including removal and redistribution, and consequently, this might expand the habitat available for macroalgal proliferation.

Removal processes may also be advantageous to attached filaments that remain on mudflats. 'Pruning' (the fragmentation of thalli) rather than complete dislodgement may be an adaptive mechanism to disturbance from hydrodynamic forces. Partial removal may act to increase recovery potential via rapid regrowth (Thomsen 2004) as well as provide a mechanism to deter self-shading. This may explain why we found only attached filaments at our highest water flow location. In a study of the effects of water motion on *Fucus gardneri*, pruning yielded a maximum sustainable plant size and maximum reproductive output (Blanchette 1997). In a field experiment, biomechanical pull-tests determined that *Ulva curvata* fragmented rather than dislodging completely, and this resulted in higher recovery rates than for algae with more complex structures that completely dislodged (Thomsen 2004). In soft-bottom lagoons, the polychaete *Diopatra cuprea* attaches macroalgae to hard tube caps with mucous secretions (Berke 2012) and was shown to facilitate distribution of *U. curvata* by retaining fragments and reducing storm-induced biomass removal (Thomsen & McGlathery 2005). *Ulva* spp. can reproduce by fragmentation, so the partial removal of attached filaments may be an adaptation to accelerated water flow and enhance macroalgal accumulation throughout an estuary by reducing shelf-shading and subsequent rapid re-growth from basal cells and/or persistent holdfasts.

The size of attached filaments as well as the substratum they were attached to regulated the habitat shift from attached to floating stages. Both the core and tile experiments provided evidence that removal increased with size of filaments, particularly when exposed to accelerated flow. The effect of drag may have reduced the force needed to detach the tall filaments independent of substratum. This suggests that once algal filaments grew to 5 to 15 cm they were vulnerable to removal from the substratum during high amplitude tides. In a flume experiment, Flindt et al. (2007) found that sloughing of 7% *Enteromorpha* and *Ulva* attached to small shells or bivalves occurred at current speeds of 10 to 15 cm s^{-1} and up to 40% at 30 cm s^{-1}. These speeds are similar to removal of attached filaments in the range of 15 to 28 cm s^{-1} found in our experiment; however, they did not compare filament sizes or substrate types. In an estimation of mean water velocities at which *U. lactuca* would detach, a model predicted that thallus sizes >50 cm may detach at lower speeds than thalli <24 cm (Hawes & Smith 1995), although thallus sizes and velocity ranges were greater than those used in our study. In addition, we found that soft sediment substrata appeared to be more effective for persistent attachment. To our knowledge, all previous studies investigating the relationship between algal detachment and water velocity either made comparisons between different hard substrata (Thomsen 2004) or only considered a single hard substratum (Flindt et al. 2007, Granhag et al. 2007). Our study's unique comparison between soft and hard substrata indicated that not only does size matter, but substratum matters, suggesting that for early life stages, intercalated growth into sediments might be an adaptation to higher flow.

While transitioning to floating mats may be an advantage to the alga, the net ecosystem impact of very high abundances may be negative, as deposition of drifting algal mats is known to stress benthic infauna, resulting in changing species composition, and to create hypoxic conditions throughout the estuary (Norkko et al. 2000). Thomsen & McGlathery (2006) found that high abundances of drift algae had a negative impact on invertebrate recruitment, reducing species abundance and richness of reef-building oysters. In contrast, more modest accumulations of drift algae transported a high diversity of macrofauna and juvenile macroinvertebrates and provided additional food and habitat resources (Norkko et al. 2000, Vandendriessche et al. 2006). The effects of drift algae in tidal creeks or other areas where flow is muted or restricted, like the head site in CSMR, may include increased decomposition rates, further increasing the oxygen demand for biogeochemical processes and potentially interfering with important estuarine functions such as nutrient processing (Valiela et al. 1992).

Although we found that recruitment was abundant throughout the estuary, higher recruitment was not related to the distribution of algal biomass and was only weakly related to water flow. This contrasts with prior studies showing that recruitment was localized to areas where there were adults and/or propagule banks providing a source of recruits (Lotze et al. 2000, Martins et al. 2008). In a laboratory experiment with *Enteromorpha* spores exposed to glass slides, Granhag et al. (2007) found an inverse relationship between spore settlement and water flow velocities. However, our study allowed recruits to settle over a 24 h period in the field with variable water velocities, and spore settlement could have occurred anytime throughout the tidal cycle. Previous studies have shown that the interaction between multiple factors including nutrients, grazing, light, and the presence of a dormant source of spores affected distribution patterns of algal biomass (Lotze et al. 2000, Worm et al. 2001, Martins et al. 2008). Our study demonstrated that in this small and relatively well-flushed estuary, neither the presence of a local source of recruits nor water motion had strong effects on the spatial pattern of recruitment.

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