

# Spatial variation in recruitment of native and invasive sessile species onto oyster reefs in a temperate soft-bottom lagoon

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## Abstract

Although spatial variability in recruitment is a strong force structuring many marine communities, relatively few data exist on recruitment variability in sessile oyster reef communities. In a soft-bottom lagoon in Virginia, we tested if recruitment differed among three reefs situated across a mainland-lagoon-barrier-island transect and among elevations (>90–80, >80–70, >70–55 and >55–20 cm below MSL) on the lagoon reef. The most abundant taxa (the invasive algae *Gracilaria vermiculophylla* and *Codium fragile* and the indigenous oyster *Crassostrea virginica* and algae *Ulva curvata*) had highest recruitment at the lagoon reef, where propagule supply was likely highest. The mainland reef had lowest algal richness (1.4–3.1 panel<sup>-1</sup>) and abundances (<4% cover) compared to lagoon and island reefs (3.3–6.5 panel<sup>-1</sup>, 14–20%), but there were no differences between sites for animals. Overall, animals and algae were equally dominant at the mainland reef, whereas algae dominated at lagoon and island reefs. High water turbidity and suspended solids are typical algal stressors at mainland reefs, and these may account for the low algal abundance in that region. For many species (at least 9 out of 14) differences in recruitment success were observed over elevation differences as small as 10–30 cm, e.g. *G. vermiculophylla* and *C. fragile* mainly recruited up to >70–55 and >80–70 cm respectively (probably limited upward by desiccation), *U. curvata* down to >70–55 cm (probably limited downward by grazing or competition), whereas *C. virginica* recruited at all elevations. Animal richness was highest at the two lowest elevations (2.0–2.5 vs. 1.1–1.8 panel<sup>-1</sup>), but there was no effect of elevation on algae (3–6 panel<sup>-1</sup>) because of species substitutions between elevation levels. Thus, as in rocky intertidal systems, spatial variability in recruitment is important for community structure on oyster reefs, and if biodiversity is considered an important reef conservation goal, managers should focus conservation and restoration on locations and elevations that support successful recruitment and survival of many different species.

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## 1. Introduction

Recruitment is fundamental to the structure of marine communities, as recognized by a renewed interest in “supply-side ecology” (Lewin, 1986; Underwood and Keough, 2001). The importance of recruitment in regulating community organization is particularly well established for sessile rocky intertidal

species (e.g. Connell, 1961; Caffey, 1985; Menge, 1991; Menge et al., 1993; Underwood and Keough, 2001; Bellgrove et al., 2004; Forde and Raimondi, 2004). In rocky systems, recruitment can vary dramatically at many spatial scales, e.g. between nearby localities with different wave exposure levels, across large spatial scales in upwelling vs. downwelling regions, or between slightly different elevation levels (Caffey, 1985; Menge, 1991; Menge et al., 1993). Such spatial variability ultimately sets the baseline conditions for what species are found at a location, the abundance of those species, and what interactions may be of importance to community organization.

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As analogues to rocky bottom systems, oyster reefs in soft-bottom lagoons provide similar hard substratum for development of sessile animal and algal assemblages (Bahr and Lanier, 1981; Grizzle, 1990). Thus, oysters act as habitat-formers or foundation species in “a sea of soft substratum” by creating and maintaining patchy reefs for attachment of sessile species. In this way oysters are similar to corals and seagrasses in that a few key organisms facilitate the distribution of a range of associated species (Bruno et al., 2003). In comparison to the rich literature on community recruitment of sessile species onto rocky systems, there are fewer studies of recruitment of sessile species onto oyster reefs (but see Rhodes, 1970; Connor, 1980; Bahr and Lanier, 1981; Ortega and Sutherland, 1992; Underwood and Anderson, 1994; Anderson and Underwood, 1997; Anderson, 1998, 1999; Coen and Luckenbach, 2000; Mazouni et al., 2001; Soniat et al., 2004; Thomsen and McGlathery, 2006). However, many of these oyster reef studies only (a) described recruited assemblages qualitatively (e.g. Rhodes, 1970; Connor, 1980; Bahr and Lanier, 1981), (b) measured recruitment at a single spatial location and elevation level (e.g. Bahr and Lanier, 1981; Underwood and Anderson, 1994; Anderson, 1998; Thomsen and McGlathery, 2006), or (c) measured assemblages on recruitment panels facing downward or elevated from the bottom (e.g. Ortega and Sutherland, 1992; Underwood and Anderson, 1994; Anderson and Underwood, 1997; Anderson, 1998). This panel placement could result in differences in the levels of light, sedimentation, re-suspension, grazing and geotaxis compared to upward facing panels positioned directly on oyster reefs (Glasby, 2000; Glasby and Connell, 2001). Quantitative data on spatial variability in recruitment of sessile assemblages onto oyster reefs are therefore still needed, in part because this information is critical for oyster reef conservation and restoration (Lenihan and Peterson, 1998; McCormick-Ray, 1998; Coen and Luckenbach, 2000; Mann, 2000; Lenihan et al., 2001). Our objective in this study was to quantify variability in recruitment between locations and elevation levels in Hog Island Bay, a shallow, turbid and tidal lagoon in Virginia using upward facing panels positioned directly on the reef surface. We hypothesized that recruitment (settlement and post-settlement survival and growth, terminology as in Thomsen and McGlathery, 2006) would be highest (1) in the mid-lagoon region, where reefs are largest and adjacent mud-flat macroalgae are most abundant (Thomsen et al., 2006b), making propagule supply likely highest, and (2) at intermediate elevations where grazing, desiccation, light and sedimentation stress are intermediate (Connell, 1961; Lenihan and Peterson, 1998; Bartol et al., 1999; Lenihan, 1999).

## 2. Methods

### 2.1. Study locations

Hog Island Bay is a ca. 100-km<sup>2</sup> shallow soft-bottom lagoon situated in the Virginia Coast Reserve on the Delmarva Peninsula. The lagoon is characterized by high turbidity, high sedimentation (Lawson, 2003), and a tidal prism of 1 m

that creates large intertidal mudflats. There are numerous oyster reefs (typically 10–1000 m<sup>2</sup>, generally positioned 10–90 cm below MSL) that provide islands of hard substrata; these reefs are largest in the mid-lagoon region. Drift algae (unattached or attached to single shells) can be found in high but patchy abundances and with high spatio-temporal variability, since they are transported and deposited by currents and storms (McGlathery et al., 2001; Thomsen, 2004). The lagoon is well mixed both vertically and horizontally due to frequent shallow-water waves and semi-diurnal tides (Lawson, 2003). Water and sediment properties differ along the mainland-lagoon-barrier-island transect, with highest turbidity ( $k = 0.9, 1.5, 1.8 \text{ m}^{-1}$ ), dissolved inorganic nitrogen (4.4, 2.3, 1.2  $\mu\text{M}$ ) and sediment organic matter (3.8%, 2.1%, 0.5% DW) (McGlathery et al., 2001) in mainland regions, intermediate in mid-lagoon regions and lowest in island regions.

### 2.2. Recruitment panels

Recruitment was measured on clay bricks (20 × 8 × 6 cm). Preliminary experiments showed that sessile species found attached to oysters recruited onto the bricks without exception. Abundance was estimated by the visual percentage cover method (Dethier et al., 1993; Thomsen and McGlathery, 2006). A quadrat divided into 20 rectangles facilitated cover estimations. Percentage cover of all organisms combined could exceed 100% if organisms occupied different vertical layers or covered more than the brick-area (Lenz et al., 2004).

### 2.3. Location and elevation panels

Bricks were positioned around reefs at three locations in April, 2001: a “mainland” reef near the Delmarva peninsula (–75.801828 W, 37.463313 N), a larger “lagoon” reef in the center of Hog Island Bay (–75.767928 W, 37.417413 N), and an “island” reef on the lagoonal side of Hog Island near the inlet to the Atlantic ocean (–75.727248 W, 37.374213 N) (for a map of sample locations and Hog Island Bay on the Delmarva Peninsula, see McGlathery et al., 2001). Each brick was separated by a minimum of 1 m to reduce small-scale spatial non-independence, such as that related to grazing patterns by low-mobility abundant mollusks (e.g. *Astytis lunata*) or algal propagule settlement patterns (Kendrick and Walker, 1991; Bellgrove et al., 2004). Twenty bricks were incubated at the mainland reef, 100 at the lagoon reef and 20 at the island reef, but some were lost in storms. At each reef bricks were positioned haphazardly at each of two elevation intervals; half 90–75 cm below MSL (low) and half 75–20 cm below MSL (high). Thus, bricks were allocated in proportion to the extent of the reef structure, i.e. more at the lagoon-reef and at lower elevations, as reefs are largest at their base. Bricks were positioned at the “interior” of the reefs, i.e. no bricks were positioned directly on the crest top or on the lower mudflat–oyster interface. The exact elevation of each brick within each elevation interval was measured to cm-precision with a kinematic Trimble 4000SE GPS, using

a mainland benchmark (to obtain vertical precision of 3–5 cm, P. Smith, personal communication).

The three localities have different distances to the Delmarva Peninsula watershed (ca. 0.5, 5, and 15 km) and therefore different levels of suspended solids, light extinction, nutrients, water residence time and salinity fluctuations (highest at mainland, intermediate at lagoon, lowest at island, cf. method section, McGlathery et al., 2001). Bricks were on average positioned at similar elevations between the three locations ( $F_{2,126} = 2.46$ ,  $p = 0.10$ , homogeneous variances, mainland =  $68 \pm 3$  cm below MSL, lagoon =  $70 \pm 1$  cm, island =  $62 \pm 4$  cm, data variability refers to standard errors), i.e. statistical tests between locations were not confounded by elevation (cf. Section 2.5; Data analysis). Percentage cover of recruited sessile species was measured in spring 2002 (March 10–15), early summer 2002 (June 1–5, only mid-lagoon bricks) and late summer 2002 (July 25–30).

#### 2.4. Transplantation panels

To test if post-recruitment processes could also influence variation in community structure on oyster reefs, we transplanted entire identical assemblages to different locations and elevations. To obtain the identical assemblages, an additional 55 bricks were incubated in April 2001, but positioned in close proximity to each other (<20 cm between bricks) at the lagoon reef, 80–70 cm below MSL. On June 14, 2002, 11 bricks were transplanted to the mainland reef, 11 to the island reef and 11 back-transplanted to the lagoon reef (to same elevation levels). To ensure that the manipulation (1 h transport in wet and dark coolers) did not affect assemblages differentially, bricks that were back-transplanted to the lagoon reef underwent similar treatment. Transplanted bricks were sampled on June 30, July 30, and November 2, 2002, corresponding to 0.5, 1.5 and 4.5 months after transplantation. Of the remaining transplantation bricks, 11 were moved to deeper elevations (180–150 cm below MSL, in a channel) and 11 to higher elevations (20–10 cm below MSL, on the top of reefs). Elevation transplants were only sampled in November 2002, but because of the loss of several bricks due to storms and a near 100% mortality on remaining bricks, these results are only discussed briefly without statistical analysis.

#### 2.5. Data analysis

We initially aimed to conduct two types of tests: (a) 2-factorial tests including both location (3 levels) and elevation (2 levels), using a random subset of the 100 bricks allocated at the lagoon reef (10 low and 10 high) to obtain a balanced design, and (b) an elevation-correlation analysis, only on the lagoon bricks (unpublished data). However, this approach was changed, partly because of the loss of replicate bricks, particularly at the mainland reef, and partly because recruitment variability was higher than expected. The 2-factorial test was changed to a 1-factorial test of location effects, including all lagoon bricks and pooling across elevation levels ( $n = 14, 96, 19$ ), as this data set provided more “true” mean

recruitment values, and the 2-level vertical classification was too coarse to detect many elevation effects. It should be noted that elevation means and variances were similar between locations (cf. Section 2.3) and results were generally similar between 2- and 1-factorial ANOVAs, i.e. with the same location effects. Secondly, the correlation analysis (with very scattered patterns) was changed to a 1-factorial test for elevation effects on 4 levels that reflects the vertical range found on most reefs in Hog Island Bay: low (<90–80 cm below MSL,  $n = 21$ ), low–mid (<80–70 cm,  $n = 49$ ), mid–high (<70–55 cm,  $n = 16$ ) and high levels (<55–20 cm,  $n = 10$ ). These levels were chosen as an *a priori* compromise of obtaining a minimum of 10 replicates and having vertical intervals of a minimum 10 cm.

Since bricks were resampled on several occasions (cf. Section 2.3), and therefore were not independent in time (Underwood and Anderson, 1994; Anderson and Underwood, 1997), tests were conducted on each sample occasion separately. One-way ANOSIM was used to test for differences between entire assemblages and 1-way ANOVA for differences in animal and algal richness, total animal and algal cover, and cover of the four most abundant recruiters (see Table 1) (Anderson and Underwood, 1997; Glasby, 2001; Lenz et al., 2004). Data were  $\text{Log}(x + 1)$  transformed before the ANOSIM test to downplay the importance of dominant species (Clarke and Warwick, 1994) and of univariate variables with variance heterogeneity. A few variables remained with variance heterogeneity, even after transformation (in a few instances we still conducted the transformation, i.e. if we achieved a large reduction in heterogeneity). In these tests, insignificant results are still valid whereas significant results should be interpreted to be either due to different means and/or different variances (Anderson, 2000). Significant results from ANOVA and ANOSIM were followed respectively by SNK-tests and permutation *R*-tests (Clarke and Warwick, 1994; Underwood and Anderson, 1994; Anderson and Underwood, 1997; Glasby, 2001). The SNK test was chosen over other posterior group tests because our data are more likely to be low in power (low replication) than suffer from excessive type I error (Underwood, 1981). We did not apply corrections for multiple testing, but acknowledge that because all tests are ultimately based on a single large species-sample dataset, 1 out of 20 tests will be significant by chance (Anderson, 2000; Anderson et al., 2005). We emphasize that the location test is unreplicated on the watershed level and the elevation test is unreplicated between reefs. Thus, causation linkages to environmental variables that vary along the horizontal and vertical gradients should be interpreted with caution (cf. discussion). Clearly, future oyster reef recruitment studies should implement balanced orthogonal and nested designs that allow for loss of replicates, test of interaction effects, and should include more levels of spatial variability and independent time sampling, thereby facilitating more robust causation linkages (for examples, see Michener and Kenny, 1991; Anderson and Underwood, 1997; Lenihan, 1999; Thomsen and McGlathery, 2006).

Table 1  
Average cover of the most common species, constituting >99% of the assemblage abundances (pooling time, elevation and location bricks). The “Abbreviation” column corresponds to taxonomic abbreviations used on x-axis in Figs. 2, 4 and 6

Taxa	Abbreviation	Group	%	SE
<i>Gracilaria vermiculophylla</i> <sup>a</sup> (Ohmi) Papenfuss	GRA	Rhodophyta	10.17	0.95
<i>Crassostrea virginica</i> (Gmelin) (eastern oyster)	CRA	Mollusca	5.08	0.72
<i>Ulva curvata</i> (Kutzing) De Toni	ULV	Chlorophyta	1.95	0.36
<i>Codium fragile</i> <sup>a</sup> ssp. <i>tomentosoides</i> (van Goor)	COD	Chlorophyta	1.75	0.25
<i>Enteromorpha</i> <sup>b</sup> spp.	ENT	Chlorophyta	1.55	0.21
<i>Fucus vesiculosus</i> Linnaeus	FUC	Phaeophyta	1.53	0.36
<i>Ectocarpus</i> spp.	ECT	Phaeophyta	1.27	0.18
<i>Agardhiella subulata</i> C. Agardh Kraft et Wynne	AGA	Rhodophyta	0.98	0.33
<i>Scytosiphon lomentaria</i> Lyngbye Link	SCY	Phaeophyta	0.53	0.13
<i>Amathia vidovici</i> Heller	AMA	Bryozoa	0.49	0.13
<i>Punctaria latifolia</i> Greville	PUN	Phaeophyta	0.24	0.05
<i>Balanidae</i> <sup>c</sup> spp.	BAL	Crustacea	0.20	0.06
<i>Ralfsia verrucosa</i> Aresch. J. Ag.	RAL	Phaeophyta	0.13	0.03
<i>Hydroides dianthus</i> Verrill	HYD	Polychaete	0.12	0.02

<sup>a</sup> Non-native species from the West Pacific.  
<sup>b</sup> A mixture of *E. intestinalis* (L.) Link, *E. linza* (L.) J. Agardh and *E. prolifera* (Muller) J. Agardh.  
<sup>c</sup> A mixture of *Chthamalus fragilis* Darwin, and *Balanus improvisus* Darwin. In addition, we observed in minute quantities: Phaeophyta: *Leathesia difformis* (Linnaeus) Areschoug, *Lomentaria baileyana* (Harvey) Farlow, Rhodophyta: *Ceramium strictum* Harvey, *Ceramium rubrum* (Hudson) C. Agardh, *Polysiphonina nigrescens* (Hudson) Greville, *Polysiphonia denudata* (Dillwyn) Greville ex Harvey, *Grinnellia Americana* (C. Agardh) Harvey, *Dasya bailouviana* (Gmelin) Montagne, *Champia parvula* (C. Agardh) Harvey, *G. tikvahiae* McLachlan, *Hypnea musciformis* (Wulfen) Lamouroux, Chlorophyta: *Cladophora* sp., *Bryopsis plumosa* (Hudson) C. Agardh, Bryozoa: *Bugula turrita* Alder, *Membranipora* sp., Porifera: *Halichondria bowerbanki* Burton, *Cliona* sp., *Microciona* sp., Hydrozoa: Hydroids spp., Tunicata: *Molgula manhattensis* (DeKay, 1843), tunicata indet., Polychaeta: *Polydora* spp., Mollusca: *Geukensia demissa* (Dillwyn), and *Anadara* sp.

### 3. Results

#### 3.1. Location panels

There were significant effects of location on the entire assemblages in both March and July. In each month, each location had a unique assemblage (ANOSIM, *R*-test, Tables 2 and 3), demonstrating a high sensitivity of assemblage level tests. There was a tendency for animal richness to be higher at the mainland and lagoon reefs compared to the island reef, although this trend was insignificant in March and not detected by the SNK-test in July (Tables 2 and 3, Fig. 1). Similarly, the percentage cover of animals seemed highest at the lagoon reef, although this trend was again not detected by the SNK test. In contrast to the animal variables, both algal richness and cover were clearly and significantly higher at the lagoon and island reefs compared to the mainland reef in both March and July. Single species analyses of the four

Table 2  
Tests results: Assemblages (ANOSIM), animal and algal richness and cover and cover of *G. vermiculophylla*, *C. virginica*, *U. curvata* and *C. fragile* (ANOVA), (log) = Log(x + 1)-transformed. Cf. Table 3 for abbreviations and results from permutation-*t*-tests (ANOSIM) and SNK-tests (ANOVA). Degrees of freedom: Location-March<sub>2,126</sub>, Location-July<sub>2,116</sub>, Transplant<sub>2,30</sub>, Elevation-March<sub>3,90</sub>, Elevation-June-July<sub>3,83</sub>. The *F*-column for the Assemblage test corresponds to the global *R*-value. Asterisks indicate large (\*\**p* < 0.01) and small (\**p* > 0.01) variance heterogeneity (Levine's test)

	Location bricks						Elevation bricks						
	March		July		June		March		June		July		
	SS	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	SS	<i>F</i>	<i>p</i>	SS	<i>F</i>	<i>p</i>		
Assemblage	0.42	0.001	0.33	0.001	0.21	0.001	0.41	0.001	33.7	0.000	0.14	0.002	
ANIRIC	2.989	1.38	0.254	6.834	3.62	0.030	1.879	0.60	47.091	1.515	0.93	2.94	0.038
Error	136.05	29.43	0.000	39.109	11.57	0.000	1.515	0.35	100.74	24.364	0.815	2.94	0.038
ALGRIC	99.726	29.43	0.000	39.109	11.57	0.000	1.515	0.35	100.74	24.364	0.815	2.94	0.038
Error	213.50	3.56	0.031	0.428	1.39	0.253	65.455	0.29	61.273	18.242	4.46	1.80	0.151
ANICOV	0.679	3.56	0.031	0.428	1.39	0.253	16.572	0.29	134.84	3094.8	3.35	5.91	0.001
Error	12.028	33.20	0.000	7.279	23.49	0.000	858.75	0.55	7.930	13843	6.70	13.867	**
ALGCOV	5.340	10.132	3.67	0.028	780.08	3.27	1349.4	0.55	7.930	13843	6.70	13.867	**
Error	1684.18	28922.6	*	13817	*	0.041	36832	1.11	1536.5	19851	7.023	7.023	0.75
GRA	82.103	2.39	0.096	317.53	0.75	0.477	8.402	0.35	1536.5	2430.9	4.81	0.015	4.26
Error	2162.19	6.74	0.002	28.451	0.75	0.475	4.839	0.26	1060.4	7584.5	2.19	6.98	0.000
CRA	0.533	4.987	18.802	4.69	0.011	0.020	0.060	0.11	1060.4	7584.5	2.19	6.98	0.000
Error	143.14	2042.7	**	2042.7	**	2042.7	8.108	0.11	1060.4	7584.5	2.19	6.98	0.000
ULV	18.802	4.69	0.011	0.020	0.020	0.020	0.060	0.11	1060.4	7584.5	2.19	6.98	0.000
Error	252.50	252.50	**	2042.7	**	2042.7	8.108	0.11	1060.4	7584.5	2.19	6.98	0.000
COD	18.802	4.69	0.011	0.020	0.020	0.020	0.060	0.11	1060.4	7584.5	2.19	6.98	0.000
Error	252.50	252.50	**	2042.7	**	2042.7	8.108	0.11	1060.4	7584.5	2.19	6.98	0.000

Table 3

Permutation-*t*- (Assemblage, ANOSIM) and SNK- (other, ANOVA) test results. N.S., not significant; N.D., not detected, i.e. significant ANOVA test, but no distinct group differences. ANIRIC, ALGRIC, animal, algal richness; ANICOV, ALGCOV, GRA, CRA, ULV, COD, cover of animals, algae, *G. vermiculophylla*, *C. virginica*, *U. curvata*, *C. fragile*; LOC, location; TRA, transplants; ELE, elevation; M, mainland; L, lagoon; I, island. a = >90–80, b = >80–70, c = >70–55, and d = >55–20 cm below MSL

	LOC <sub>March</sub>	LOC <sub>July</sub>	TRA <sub>June</sub>	TRA <sub>July</sub>	TRA <sub>Nov.</sub>	ELE <sub>March</sub>	ELE <sub>June</sub>	ELE <sub>July</sub>
Assemblage	M ≠ S ≠ I	M ≠ L ≠ I	N.S.	M ≠ L = I	M ≠ L ≠ I	a = b = c ≠ d a ≠ c	a = b = c ≠ d a ≠ c	a = b ≠ c ≠ d
ANIRIC	N.S.	N.D.	N.S.	N.S.	N.S.	N.D.	a = b > c = d	a = b > c = d
ALGRIC	M < L < I	M < L = I	N.S.	N.S.	N.D.	N.S.	N.S.	N.S.
ANICOV	N.D.	N.S.	N.S.	N.S.	M < L = I	a > b = c = d	N.S.	N.S.
ALGCOV	M < L = I	M < L = I	N.S.	N.S.	M < L = I	N.S.	N.S.	N.S.
GRA	M = I < L	M < L = I	N.S.	N.S.	N.D.	N.S.	a = b = c > d	a = b = c > d
CRA	N.D.	N.S.	N.S.	N.S.	N.S.	a = b > c = d	N.D.	N.S.
ULV	M = I < L	N.S.	N.S.	N.S.	N.S.	N.S.	a = b < c = d	N.S.
COD	M = I < L	M = I < L	N.S.	N.S.	N.S.	N.D.	a = b > c = d	a = b > c = d

most abundant recruiters (*Gracilaria vermiculophylla*, *Crasostrea virginica*, *Ulva curvata*, *Codium fragile* ssp. *tomentosoides*, cf. Table 1) showed a significant pattern with highest recruitment at the lagoon reef (March, Tables 2 and 3, Fig. 2), although this was less clear in July, when there were only insignificant trends for *C. virginica* and *U. curvata*, and when the island reef had similar cover to the lagoon reef (for *G. vermiculophylla* and *C. fragile*). Of the less dominant recruiters (cf. Table 1), one group was most abundant at the lagoon reef (*Agardiella subulata*, *Punctaria latifolia*, and *Amathia vidovici*), whereas another group had low abundance at the mainland, intermediate at the lagoon and high abundance at the island reef (*Enteromorpha* spp., *Fucus vesiculosus*, *Ectocarpus* spp., *Scytosiphon lomentaria*). In contrast, *Balanus*

spp. was most abundant at the mainland reef whereas *Ralfsia verrucosa* and *Hydroides dianthus* showed no clear pattern (but were only found in very low abundances). In short, animals were relatively more important at the mainland reef, whereas algae dominated at the island and lagoon reefs.

### 3.2. Location transplant panels

No response variables (assemblages, cover values, richness) showed any short-term effects of relocation (0.5 month after the transplantation, Tables 2 and 3). However, after 1.5 months the mainland assemblage was significantly different from lagoon and island assemblages. Still, no univariate response variables were significant, although *F*-statistics increased for

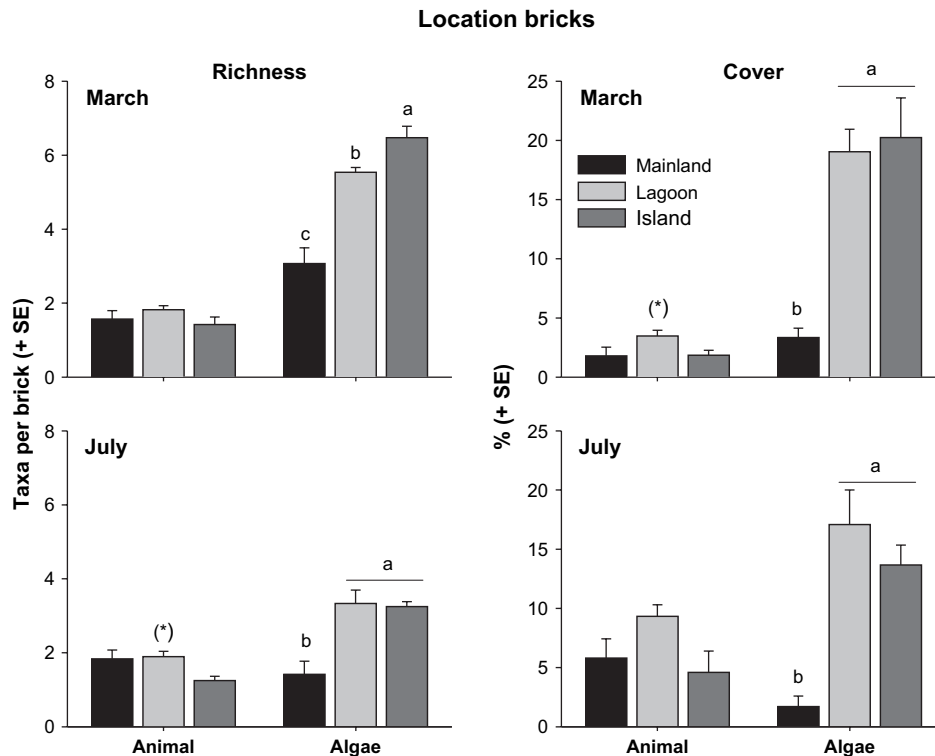


Fig. 1. Richness and cover of animals and algae at three locations in March and July. Letters designate statistically different groups (based on SNK tests), whereas asterisks indicate significant ANOVA effects but with no significant differences between groups (also based on SNK).

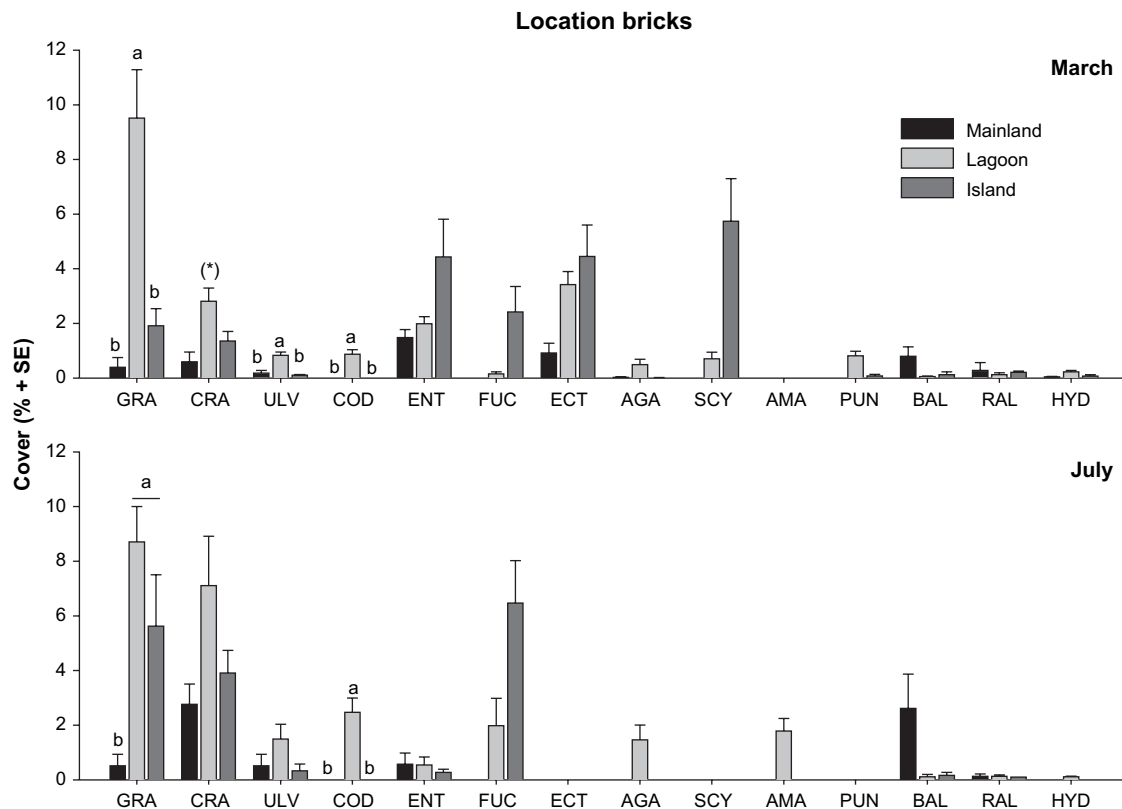


Fig. 2. Abundances of the 14 most common taxa at three locations in March and July. Taxonomic nomenclature, corresponding to abbreviations shown on x-axis, is listed in Table 1. Letters designate statistically different groups (based on SNK tests), whereas asterisks indicate significant ANOVA effects but with no significant difference between groups (also based on SNK).

most variables (but not for *Crassostrea virginica* or *Ulva curvata*), typically in the direction that later showed to be significant for animal and plant cover. After 4.5 months, the transplanted bricks had unique assemblages at each reef (Tables 2 and 3), and animal and algal cover were significantly higher at the lagoon and island reefs compared to the mainland reef. There was a similar trend for algal richness, although this was not detected by the SNK-test (Fig. 3). Patterns were less clear for the single species tests, and only showed one significant effect (*Gracilaria vermiculophylla*, but the SNK-test did not detect any different groupings). Thus, *G. vermiculophylla* (Fig. 4) had a tendency for highest cover at the island reef, similar to many other algae, and was the only transplanted algae to survive and grow well at the mainland reef. In contrast, *Codium fragile* transplants survived at both the lagoon and island reefs, but died when transplanted to the mainland reef (Fig. 4), whereas *U. curvata* likely disappeared in November after 4.5 months at all locations due to ontogenetic causes (an ephemeral life strategy). Finally, *C. virginica* also showed a tendency for highest survival and growth at the lagoon and island reefs, although still with the ability to survive at the mainland reef (in contrast to *C. fragile*). Thus, in less than 5 months bricks diverged to follow patterns similar to bricks originally positioned at the respective locations, i.e. with relatively more abundant animals at the mainland reef, and dominance of algae at the lagoon and island reefs. Note also that most species

were present with low cover in July (late summer), potentially due to heat stress or a recent storm disturbance event.

### 3.3. Elevation panels

The recruited reef assemblages were significantly different between elevation levels in each month, generally with one assemblage type at the two lower levels (i.e. <90–80 ≈ <80–70 cm) and distinct assemblages at each of the two higher levels (<70–55 and <55–20 cm, Tables 2 and 3). A similar pattern was observed for animal richness, where the two low levels had significantly more taxa per brick than the two high levels (Tables 2 and 3, Fig. 5). In contrast, there were generally no significant effects on either algal cover or algal richness (the latter with a weak significant effect in March). However, this lack of significance was caused by species replacement between levels, rather than the same species being equally abundant at all levels (Fig. 6). Of the individual species, *Gracilaria vermiculophylla* had significantly highest cover at the three lowest elevations (<0.55 cm) in both June and July (but not significant in March, Tables 2 and 3, Fig. 6), a pattern relatively similar for *Codium fragile*, although the latter species had a more distinct lower threshold (<70 cm, and again only significant in June and July). In contrast, the ephemeral *Ulva curvata* had significantly higher cover at the two high elevations, but only in June (but with

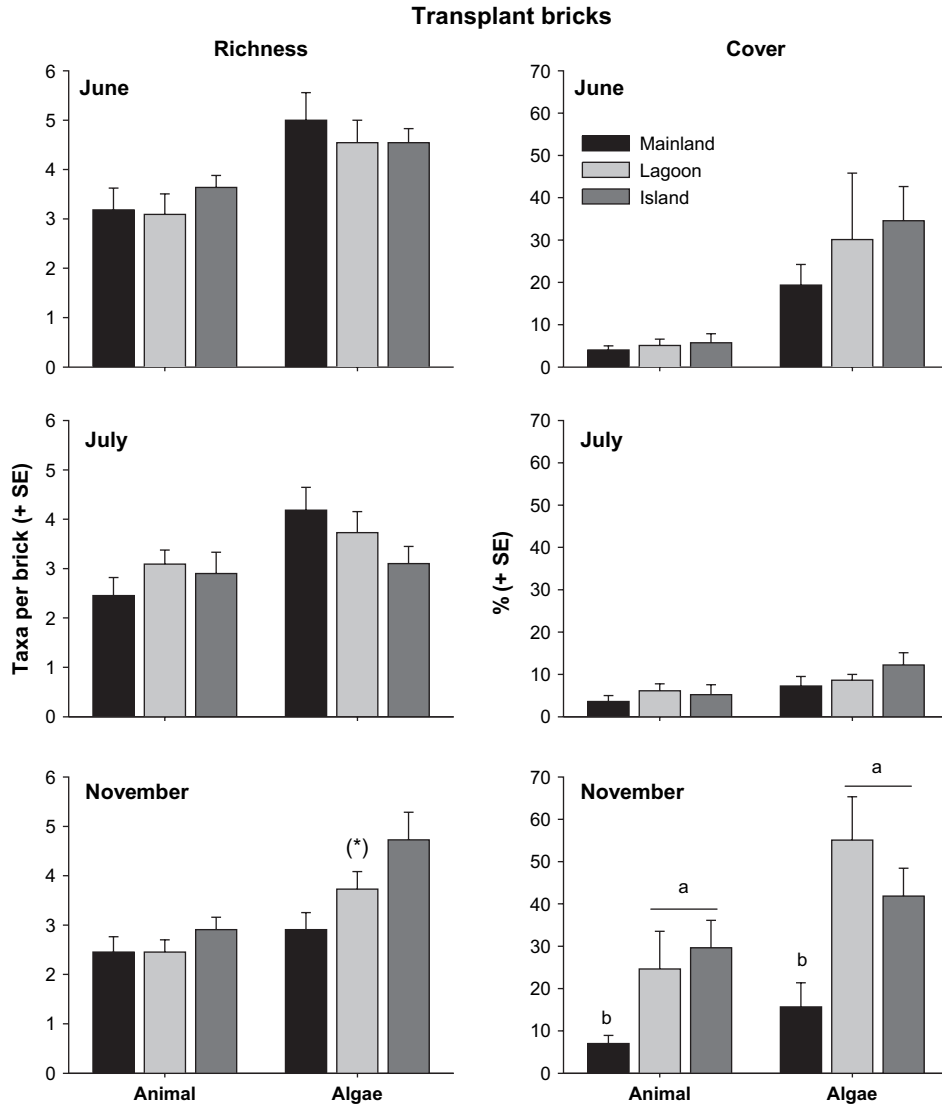


Fig. 3. Richness and cover of animals and algae at three locations in June, July and November (0.5, 1.5 and 4.5 months after transplant from lagoon, all elevations 75 cm below MSL). Letters designate statistically different groups (based on SNK tests), whereas asterisks indicate significant ANOVA effects but with no significant difference between groups (also based on SNK).

similar trends in March and July). *Crassostrea virginica* showed no obvious pattern, with significantly different recruitment between alternating elevation levels in March, a significant effect but no SNK-grouping in June, and no effect at all in July (Fig. 6). Observations on the less common species also documented strong differences in recruitment between elevations. For example, *Fucus vesiculosus* and *Scytosiphon lomentaria* mainly recruited successfully >55 cm, *Enteromorpha* spp. recruited successfully >70 cm, whereas *Agardhiella subulata*, *Punctaria latifolia* and *Amathia vidovici* primarily recruited <70 cm (similar to *C. fragile*). The remaining species were either too rare to suggest any patterns or were not affected by elevation levels (e.g. a spring bloom of the epiphytic *Ectocarpus* spp.).

### 3.4. Elevation transplant panels

All bricks that were moved down to 150 cm below MSL were buried in sediments and no sessile species were observed

in November 2002. Of the bricks moved up to 20 cm below MSL which were not lost in storms, most algae died (mainly *Gracilaria vermiculophylla*, *Codium fragile*, and *Agardhiella subulata*). Only a few small oysters, barnacles, *Enteromorpha* spp. and *Fucus vesiculosus* were observed alive.

## 4. Discussion

The importance of spatial variability in recruitment of sessile marine species is well established in rocky intertidal ecosystems (e.g. Menge, 1991; Menge et al., 1993; Underwood and Keough, 2001; Forde and Raimondi, 2004). In comparison, few studies have quantified spatial variability in recruitment and survival of sessile assemblages onto hard-substratum oyster reefs within soft-bottom ecosystems (Ortega and Sutherland, 1992; Coen and Luckenbach, 2000; Thomsen and McGlathery, 2006). The presence of a species-rich and abundant sessile reef community (including the macroalgal component) has rarely been identified

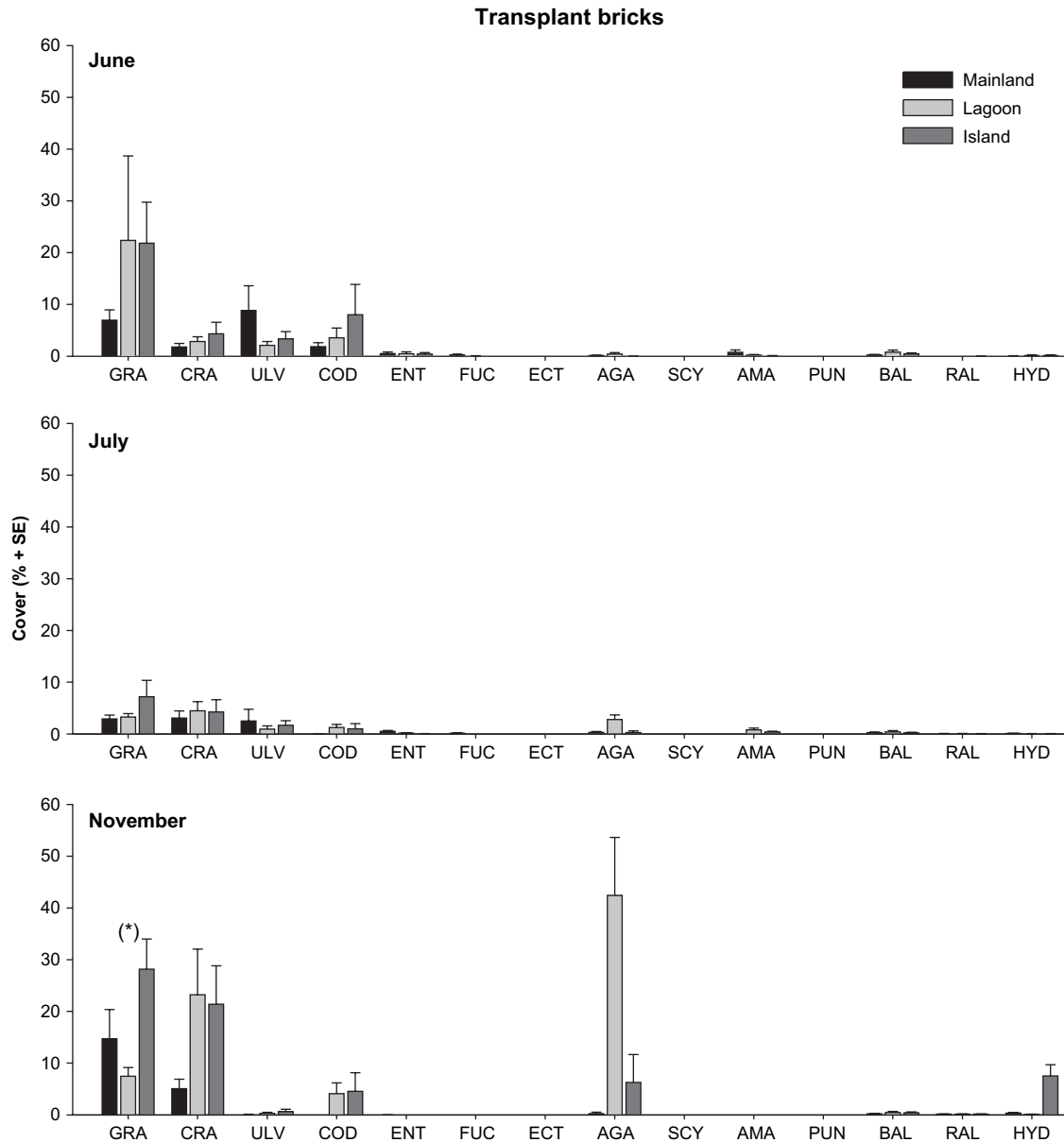


Fig. 4. Abundances of the 14 most common taxa at three locations in June, July and November (0.5, 1.5 and 4.5 months after transplant from lagoon, all elevations 75 cm below MSL). Taxonomic nomenclature, corresponding to abbreviations shown on x-axis, is listed in Table 1. The asterisk indicates statistical significant effects based on ANOVA, but without statistical group separation based on SNK test.

as a specific oyster restoration goal, in contrast to ecosystem properties such as oyster filtration capacity, benthic-pelagic coupling, or trophic linkages to mobile crustaceans and fishes (e.g. Breitburg et al., 2000; Coen and Luckenbach, 2000; Mann, 2000; Peterson et al., 2003). However, we argue that because biodiversity per se is a main conservation goal (Jeffries, 1997; Soule et al., 2005) and because the entire sessile community contributes to filtration and benthic-pelagic coupling processes (Mazouni et al., 2001) and provides additional shelter, spawning ground and food sources for higher trophic levels (cf. references in Peterson et al., 2003), knowledge of recruitment patterns of the entire oyster-associated sessile community should be included in reef conservation evaluation schemes. Here we document that recruitment of sessile oyster reef species varies significantly on both large horizontal (km) and small

vertical (cm) scales in a well-mixed soft-bottom lagoon. Thus, when feasible, spatial variation in recruitment should be addressed in oyster reef community structure studies. Our hypothesis was supported that there would be highest recruitment on mid-lagoon reefs where drift-algal assemblages are abundant. However, our hypothesis that recruitment was highest at intermediate elevation levels with intermediate grazing, desiccation, light and sedimentation stress was not supported because different species, likely with different susceptibilities to these stressors, substituted for one another.

#### 4.1. General patterns

We observed distinct spatial patterns on the recruitment bricks, as has been shown for rocky ecosystems (Caffey,



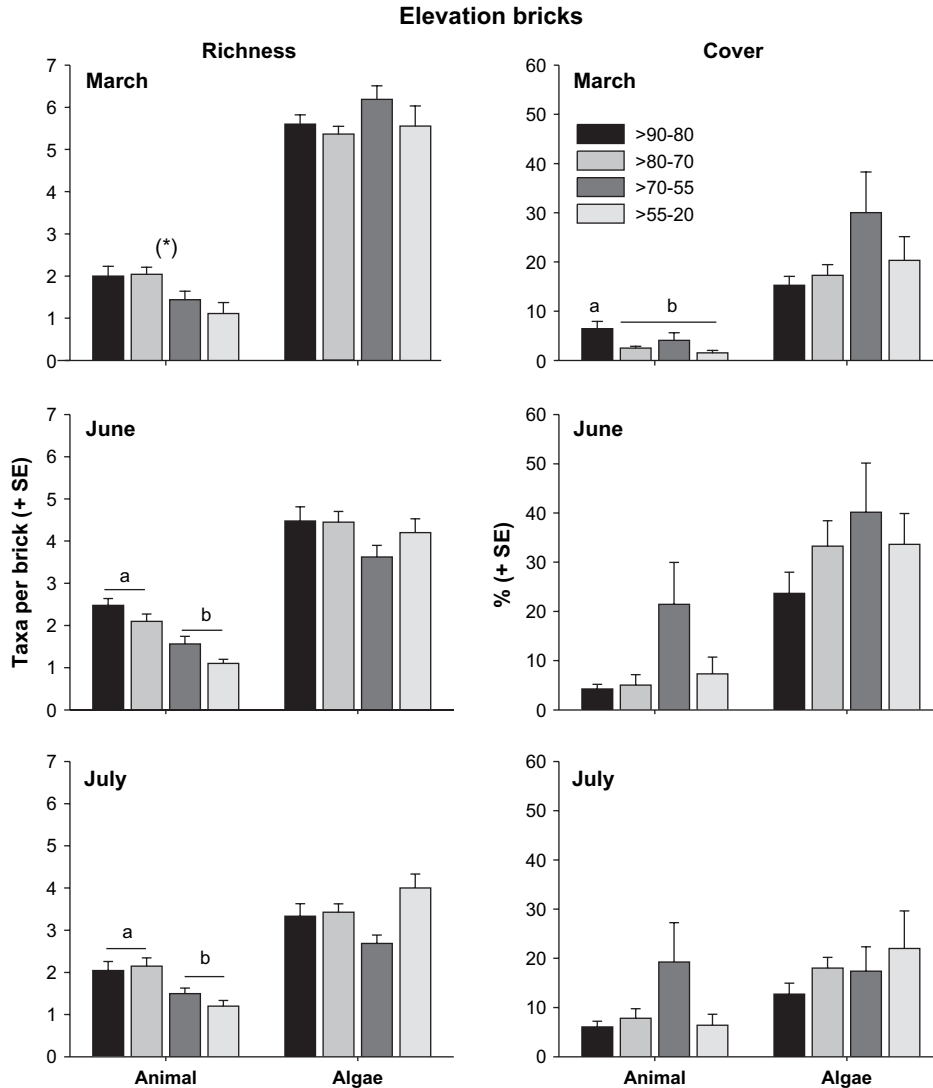


Fig. 5. Richness and cover of animals and algae at four elevations in March, June and July (Lagoon location). Letters designate statistically different groups (based on SNK tests), whereas asterisks indicate significant ANOVA effects but with no significance between groups (also based on SNK).

1985; Bellgrove et al., 2004; Forde and Raimondi, 2004). Algae were more species rich and abundant than animals, in contrast to previous oyster-recruitment studies that reported the dominant species to be filter feeders (Ortega and Sutherland, 1992; Underwood and Anderson, 1994; Anderson and Underwood, 1997; Anderson, 1999). This difference is probably attributed to (a) our panels were incubated facing upward and directly on the substratum, and therefore received more light and passive algal propagules, (b) our panels were incubated at higher elevations where light for photosynthesis is adequate, and/or (c) other studies were conducted in algal-poor ecosystems with a low algal propagule supply. However, it is also possible that the choice of substrate influenced the results, as bricks are more structurally simple (with smooth horizontal surfaces and vertical sides), bigger, chemically different, and likely more stable and stronger than oyster shells, which could potentially affect both settlement and early post-settlement survivorship.

The non-native alga, *Gracilaria vermiculophylla*, which was introduced from the West Pacific, was the most abundant species. This invader was able to colonize free space more efficiently than any of the native species, which is an important trait for establishing permanent populations in newly invaded habitats (Thomsen and McGlathery, 2006; Thomsen et al., 2006a,b). The other non-native species, *Codium fragile*, had previously been suggested to be an abundant recruiter onto oyster reefs (Fralick and Mathieson, 1973; Malinowski and Ramus, 1973), and our study confirmed this, although its recruitment was limited to lower tidal levels and reefs some distance from the mainland. Given the widespread and high abundance of *G. vermiculophylla* on oyster reefs and mudflats (this study, Thomsen and McGlathery, 2006; Thomsen et al., 2006b), its associated epibiotic community structure (Thomsen and McGlathery, 2005), and its contribution to biogeochemical transformation processes (McGlathery et al., 2001; Tyler et al., 2003), this non-native is likely to have altered ecosystem properties throughout Hog Island Bay. Other abundant

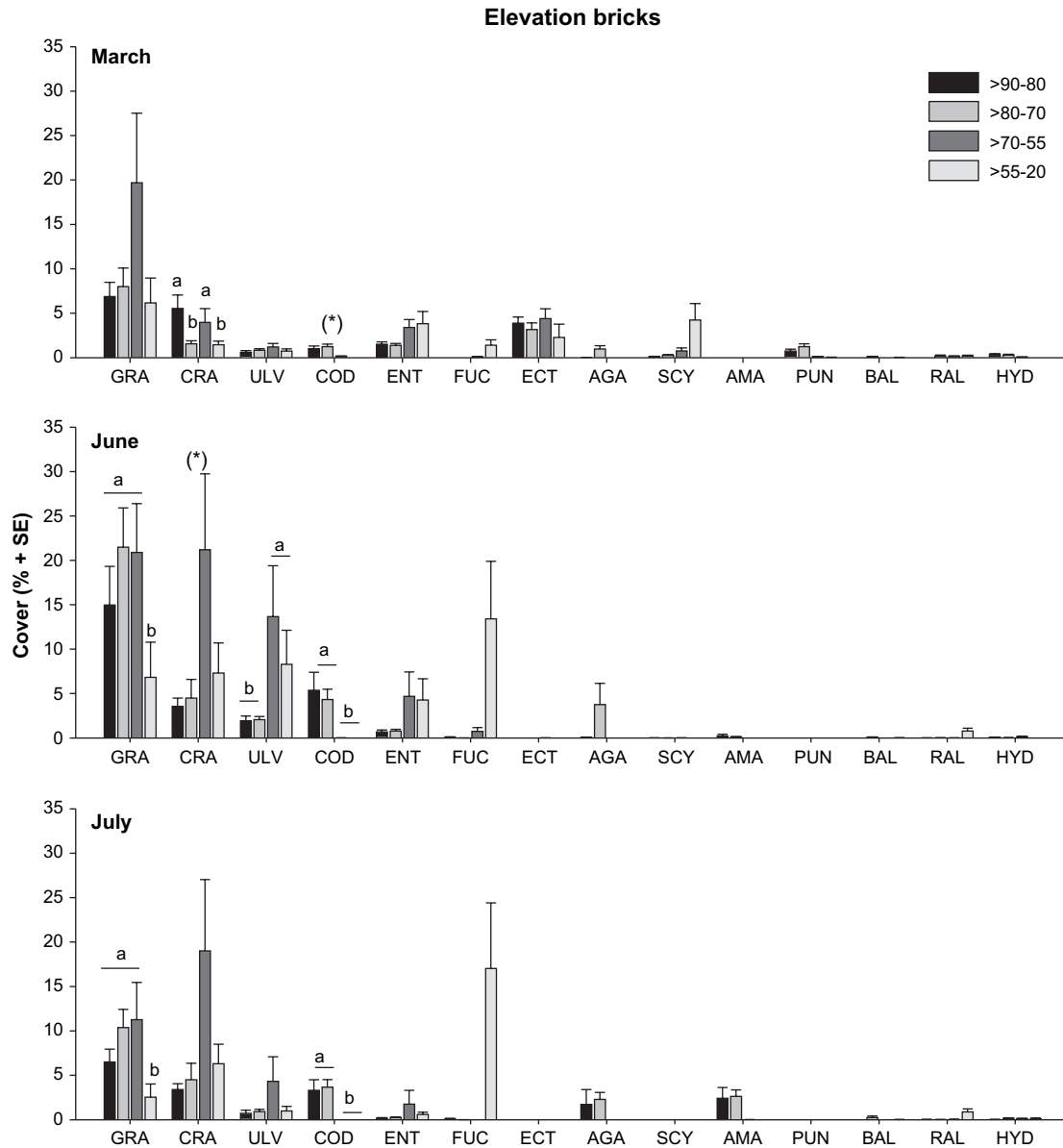


Fig. 6. Abundances of the 14 most common taxa at four elevations in March, June and July (Lagoon location). Taxonomic nomenclature, corresponding to abbreviations shown on x-axis, is listed in Table 1. Letters designate statistically different groups (based on SNK tests), whereas asterisks indicate significant ANOVA effects but with no significant differences between groups (also based on SNK).

algae included *Ulva curvata*, *Fucus vesiculosus*, *Agardhiella subulata*, *Scytosiphon lomentaria* and *Punctaria latifolia*. These species can grow in a few months into large individuals (this study, Wallentinus, 1984) that are susceptible to dislodgment and pruning (Denny et al., 1985; Thomsen, 2004; Thomsen and Wernberg, 2005). Thus, peak currents and storm waves probably transport algal fragments to the adjacent soft-bottom drift assemblages on a regular basis, thereby minimizing the risk of local mud-flat extinction (Thomsen, 2004; Thomsen and McGlathery, 2006). In comparison, *Enteromorpha* spp. was found as a small turf and *Ralfsia verrucosa* as a crust and these low-drag species are unlikely to dislodge and have not been found in the drift assemblages (Thomsen and McGlathery, 2005). Clearly, algal recruitment onto hard substratum can be common, even though asexual vegetative

growth of unattached fragments likely dominate on large scales within soft-bottom systems (Norton and Mathieson, 1983).

The most abundant animal recruiter was the oyster *Crassostrea virginica*, as has been shown by other oyster-reef recruitment studies (Ortega and Sutherland, 1992; Underwood and Anderson, 1994; Anderson, 1999; Lenihan, 1999). We noted that a large proportion of the recruited oysters died within a few months, possibly due to predation by mud crabs and oyster drills, or diseases (Bahr and Lanier, 1981; O'Beirn et al., 1996; Lenihan, 1999). The remaining empty oyster shells still increased topographic complexity on the panels (by projecting hard substratum upward) and therefore also available space for recruitment (Connor, 1980; Bahr and Lanier, 1981; Soniat et al., 2004). Other common filter feeders included *Amathia vidovici*,

*Balanidae* spp. and *Hydroides dianthus*, typical “fouling” organisms that perform well in high depositional environments (Dean, 1981).

#### 4.2. Location patterns

Species richness and assemblage structure varied between locations, where the mainland reef had lowest algae richness and cover. Most large conspicuous algae (*Fucus vesiculosus*, *Agardhiella subulata*, *Codium fragile*, *Scytosiphon lomentaria*, *Punctaria latifolia*) did not recruit at the mainland reef, probably due to a combination of low propagule supplies and low survival and growth rates. However, because Hog Island Bay is well mixed with a long residence time (Lawson, 2003) and large amounts of drifting unattached algae (Thomsen and McGlathery, 2006), we expect that propagules, given time, will eventually reach mainland reefs. Thus, on a long time-scale (months-years) we believe that post-settlement mortality excludes most algae from mainland reefs. The transplantation bricks supported this hypothesis as it took less than 5 months to cause identical mid-lagoon assemblages to diverge to local reef assemblages. Adverse conditions at the mainland reef likely include high sedimentation, turbidity and salinity fluctuations (McGlathery et al., 2001), conditions that are more stressful to primary producers than filter feeders. Both the non-native *Gracilaria vermiculophylla* and *Crassostrea virginica* were among the few species that recruited and survived at all locations, showing a broad tolerance to all lagoon sub-environments.

Linking recruitment patterns to specific processes is complicated by the fact that many of the variables co-vary along the distance-from-mainland gradient (cf. Section 2.1), making it nearly impossible to single out specific factors. Many other studies have sampled along similar gradients, and have also typically been unreplicated at the watershed level (e.g. Castel et al., 1996; Flindt and Kamp-Nielsen, 1997; Tyler et al., 2003). Most of these studies link patterns to nutrient and eutrophication effects, and have quantified highest levels in close proximity to the watershed. However, we prefer a more conservative approach, emphasizing that several environmental factors likely are of importance (e.g. nutrients, light/water clarity, salinity fluctuations, hydrodynamics, water residence time, sedimentation, anoxia, available substratum and propagule supply). Clearly, manipulative experiments (e.g.  $\pm$ shading,  $\pm$ sediment addition/removal,  $\pm$ nutrient additions) repeated at the watershed level are needed to address these shortcomings. To support the generality of our data we emphasize that (a) macroalgal samples from mudflats adjacent to reefs from replicated watersheds also contained fewest species and low biomass at mainland locations (similar to this study, Thomsen et al., 2006b), (b) qualitative observations on oyster reef communities from the adjacent watersheds indicated similar diversity and biomass patterns, and (c) densities and diversity of mobile invertebrates from sediment cores and drift-algal traps were also lowest at mainland locations (Rosinski, 2004).

#### 4.3. Elevation patterns

The elevation bricks were analyzed from a single location, and although settlement can vary on small spatial scales (Cafey, 1985; Glasby, 2000), the propagule supply in the water column would most likely have been similar between bricks due to tidal and wave-induced mixing (Lawson, 2003). The bricks also had identical rugosity, size, and structure. Thus, zonation patterns should primarily reflect differential post-settlement mortality and growth. *Crassostrea virginica* recruited at all positions and *Gracilaria vermiculophylla* mainly up to 55 cm below MSL, again suggesting broad environmental tolerances (Bartol et al., 1999; Rueness, 2005). In contrast, *Codium fragile*, *Agardhiella subulata* and *Amathia vidovici* had lower elevation thresholds and were completely absent above 70 cm below MSL, suggesting a high susceptibility to desiccation. This contradicts other studies that describe *C. fragile* as a common intertidal species (Trowbridge, 1998; Begin and Scheibling, 2003), but most of these studies actually refer to constantly submerged tide-pool populations. Opposite patterns were observed for *Ulva curvata*, *Enteromorpha* spp., *Scytosiphon lomentaria* and *Fucus vesiculosus* that were most abundant at higher elevations, probably limited downward by competition by *G. vermiculophylla*, *C. fragile* and *A. subulata* and/or grazing by abundant amphipods and gastropods (Duffy and Hay, 2000). Thus, in Hog Island Bay, only 10–30 cm in vertical elevation can make a large difference in recruitment success. Of the 14 most abundant recruiters we estimate that at least 9 of them (*C. fragile*, *G. vermiculophylla*, *U. curvata*, *Enteromorpha* spp., *F. vesiculosus*, *A. subulata*, *S. lomentaria*, *A. vidovici*, *Punctaria latifolia*, Fig. 6) at some time had a distinct upper or lower threshold even within the limited elevation levels sampled in this study. This reiterates that single elevation-recruitment data should be extrapolated to other elevation levels with caution. For example, we would expect different grazing effects below 70 cm (below MSL) where *G. vermiculophylla*, *C. fragile*, and *A. subulata* dominate compared to above 70 cm where the more palatable *Enteromorpha* spp. and *U. curvata* dominate.

It is well documented that in rocky intertidal systems, many species are limited upward by physiological desiccation stress and downward by biological interactions (Connell, 1961, 1970). We believe this is also important for hard-bottom reef assemblages, embedded in soft-bottom systems, where we often observed amphipod grazer scars on down-transplanted *Fucus vesiculosus* and *Enteromorpha* spp. (as in Duffy and Hay, 2000) and wilting and bleaching of up-transplanted algae. Nevertheless, light extinction, anoxia and sedimentation are likely stronger downward limiting factors in soft-bottom systems compared to rocky systems, because the former typically have more turbid water (Jerlov, 1970) and higher levels of organic matter, sedimentation and resuspension (Dyer, 1972; Airoldi, 2003). Our study only documents recruitment within the vertical range of existing Hog Island Bay reefs; however we have observed intense barnacle recruitment on structures positioned at higher elevation, suggesting that these key taxa would be more dominant if high-intertidal substratum was available. It is interesting to note that many reefs today are

vertically reduced compared to historical reefs due to human harvest, increased anoxia events, increased sedimentation and turbidity and rampant diseases (Haven and Whitcomb, 1983; Lenihan and Peterson, 1998; Coen and Luckenbach, 2000; Mann, 2000). Thus, if the vertical extent of present day reefs are reduced (even in the shallow non-stratified waters of Hog Island Bay), we suggest that, in concert with *Crassostrea virginica*, co-dependent high-elevation sessile taxa (barnacles, fucoids, opportunistic green algae) may have been “squeezed” downward and low-elevation taxa (*Codium fragile*, *Agardhiella subulata*, *Punctaria latifolia*, filter-feeding tunicates and bryozoans) upward, potentially causing a species-pauperization of entire sessile oyster reef assemblages. Finally, it should be noted that, similar to the location data, the elevation data were also unreplicated (between reefs) and suffered from co-variation between environmental variables (light, desiccation, grazing, sedimentation, anoxia, temperature fluctuations, etc). Again we call for multi-factorial manipulative experiments to disentangle interactions between elevation and causal factors, preferable to be repeated between reefs.

## 5. Conclusion

We conclude that recruitment of sessile algae and animals onto oyster reefs in soft-bottom systems is important and structured at both horizontal (km) and vertical (cm) scales. In particular, only 10–30 cm vertical difference can determine if recruits survive or die. We also document that the non-native algae, *Gracilaria vermiculophylla*, is an abundant and stress-tolerant invader of open space, making it a potential nuisance species in invaded regions on the United States east coast (Thomsen et al., 2006a), the U.S. west coast (Bellorin et al., 2004) and in many European countries (Rueness, 2005). The other non-native algae, *Codium fragile*, is also an abundant colonizer, but under more restricted conditions. Finally, if biodiversity is targeted as a conservation goal, reef managers should focus conservation and restoration projects on locations and elevations that support successful recruitment, survival and growth of many different species.

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