Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*

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Abstract

Marine foundation organisms such as seagrasses, corals, and kelps facilitate the distribution of numerous organisms by creating refuges from environmental stressors and by providing food and substrate for settlement and growth. Barren soft-sediment systems often have faunal organisms that facilitate other species by habitat modification. We investigated how an abundant ($21 \, \mathrm{m}^{-2}$) tube cap forming polychaete, *Diopatra cuprea*, facilitates macroalgal distribution in Hog Island Bay, a turbid shallow tidal lagoon in Virginia (USA). Seventy percent of the number of mudflat macroalgae were found incorporated into protruding *D. cuprea* tube caps and field experiments showed that *D. cuprea* facilitates algal persistence by providing a stable substrate retaining algae against hydrodynamic forces such as tidal flushing and storm surge. If tube caps were removed, simulating storm-induced erosion, they were rebuilt within days and new drift algae incorporated. Also, *D. cuprea* facilitated the algal assemblage by fragmenting thalli in the attachment process, thereby ensuring a constant fragment supply for vegetative re-growth if storm-induced pruning occurs. On a species-specific level, *Gracilaria verrucosa* and *Ulva curvata* benefited more from tube cap construction compared to *Fucus vesiculosus*, *Agardhiella subulata* and the alien *Codium fragile* ssp. *tomentosoides*. This was partly because *G. verrucosa* and *U. curvata* were incorporated and fragmented more readily, and partly because they probably have physiological, morphological and biomechanical traits that enable them to better co-exist with *D. cuprea*. These results suggest that macroalgal distribution throughout Hog Island Bay to a large extent is linked to the distribution of *D. cuprea*. The processes of algal attachment, retainment, recovery, re-growth and fragmentation, can have important ecosystem implications because of the sheer abundance of the *Diopatra-Gracilaria/Ulva* association.

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1. Introduction

Coastal marine ecosystems are often defined according to a few key organisms, the most well-known examples being kelp forests, coral reefs, and seagrass meadows (Dayton, 1971; Heck and Wetstone, 1977; Dayton et al., 1984; Connell et al., 1997). These foundation taxa provide substrate for settlement and growth, shelter from predators, an abundant food supply, increase propagule settlement rate, and alter the abiotic environment into more benign conditions (Bruno and Bertness, 2001). Positive interactions between foundation and co-existing species are key processes that can drive productivity, food web structure and nutrient flow within these habitats.

In soft-sediment communities, negative interactions such as predation and competition have been studied in more detail than positive interactions (Lenihan and Micheli, 2001). Nevertheless, soft-bottom systems often have organisms that facilitate other species by

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habitat-modifications, for example mussels beds (Albrecht, 1998), oyster reefs (Galtsoff, 1964; Barh and Lanier, 1981), and unattached drift algal mats (Norkko and Bonsdorff, 1996; Norkko et al., 2000). Also, burrowing, tube building or surface sediment casting polychaetes may facilitate other organisms, by oxygenating sediments, providing predator refuges, increasing larval settlement and retaining aquatic plant fragments (Fager, 1964; Eckman et al., 1981; Reise, 1983; Eckman, 1985). It is well documented that onuphid polychate tube builders create such habitat modifications through their tube-forming activities (Pillsbury, 1950; Emerson, 1975; Bell and Coen, 1982; Bailey-Brock, 1984; Luckenbach, 1986; Harwell and Orth, 2001). The onuphid *Diopatra cuprea* (Bosc) is abundant in North American east coast lagoons from north of Cape Cod to the south of Florida (Mangum et al., 1968) where it modifies its habitat by incorporating macroalgal fragments and bivalve shells into tube caps to provide tube structure and strength (Myers, 1972; Brenchley, 1976), shelter from predators (Brenchley, 1976; Luckenbach, 1984), a direct food supply (eating the algae, Mangum et al., 1968), and/or an indirect food supply (eating algae-associated invertebrates, Bell and Coen, 1982). The incorporation of algal fragments clearly benefit the polychaete and to a large extent the associated invertebrates, but no studies have investigated if and how *D. cuprea* affect the incorporated macroalgae (Thomsen, 2004).

We hypothesize that *D. cuprea* acts as a soft-bottom macroalgal facilitator by means of tube cap incorporation, physically controlling and enhancing the distribution and abundance of macroalgae. This was investigated by testing how common *D. cuprea* is within a shallow U.S. east coast lagoon, how abundant and stable the algae-tube cap assemblage is, how fast the association recovers after different levels of disturbance, and if certain algal species are favored by being incorporated more often than others. In addition to the investigated physically based links between *D. cuprea* and macroalgal abundance, nitrogen excretion by *D. cuprea* may also facilitate the incorporated algae, by stimulating growth (Fong et al., 1997; Giannotti and McGlathery, 2001), although this physiologically based aspect was not considered in the present study.

2. Methods

2.1. Site description

We investigated if *D. cuprea* facilitates algal communities in Hog Island Bay, a protected shallow-water temperate soft-bottom lagoon in the Virginia Coast Reserve, and an ecosystem under scrutiny being part of the U.S. Long Term Ecological Research Network

(Franklin et al., 1990; Swanson and Sparks, 1990; Hayden et al., 2000). Hog Island bay is located in the Machipongo drainage basin on the Delmarva peninsula, and is approximately 100 km^2 (McGlathery et al., 2001), where 30% is intertidal marshes, 7% is intertidal mudflats, and 52% is shallow mudflats to 2 m depth (Oertel, 2001). There is little topographic complexity; most of the bay is covered with sand, silt or clay, but scattered oyster reefs, unconsolidated bivalve shells and *Spartina alterniflora* stems provide hard substrate for sessile organisms. The sediment nitrogen and organic contents are higher and the bulk density lower near the mainland compared to near-ocean sites (McGlathery et al., 2001). Rooted angiosperms have been absent from the lagoon since the wasting disease of the 1930s, and today unattached macroalgae are ubiquitous, with peak biomass up to 650 g DW m^{-2}, and being dominated by unattached mats of *Gracilaria verrucosa* (Hudson) Papenfuss and *Ulva curvata* (Kutzing) De Toni (Humm, 1979; McGlathery et al., 2001). Because no rooted macrophytes exist to bind sediments and dampen hydrodynamic forces, tidal currents and storms frequently re-suspend, erode and deposits sediments, increase turbidity, and entrain and redistribute unattached algal mats (Dolan, 1996; Flindt et al., 1997; Lawson, 2002).

2.2. Ubiquity of tube caps

To test if *D. cuprea* has the potential to facilitate algae over a lagoon-wide scale we counted tube cap densities at 15 sites throughout the lagoon. Each site was allocated to one of two elevation levels (lower intertidal vs. shallow subtidal) and one of three adjacencies to the mainland (near-mainland, mid-lagoon, back-barrier island, cf. Tyler et al., 2001 for map of main sample locations). Each tube cap represents a live worm (Mangum et al., 1968), and there is generally little seasonal fluctuation in *D. cuprea* densities (Bell and Coen, 1982; Peckol and Baxter, 1986). All sites were sampled haphazardly in fall 2002, with a 0.15 m^2 sampling frame ($n = 6 - 9$ per site). Densities could not be transformed to variance homogeneity (Cochran's C: $P < 0.05$) and the P values from the two-way ANOVA, testing effects of elevation and distance from the mainland, should be interpreted with caution. This approach was preferred rather than using non-parametric tests, because the latter methods does not solve problems of variance heterogeneity (Anderson, 2001; Quinn and Keough, 2002).

2.3. Ubiquity of algae incorporated to tube caps

To test if the algae-tube cap associations were ubiquitous in Hog Island Bay, we conducted both qualitative and quantitative surveys. Qualitative observations were based on approximately 200 field days

from 1999 to 2002 covering all seasons, where tube caps were collected and examined for attached macroalgae ($n > 3000$). We also sampled 441 macroalgal individuals in the main growing season in 2002 (April to November) at 17 mudflat sites distributed along the previously described spatial gradients. Individuals were selected by randomly throwing an object and collecting the nearest algae. The species were identified, and attachment type recorded as loose-lying (=unattached), epiphytic, entangled, partly buried in sediment, attached to a tube cap, or attached to an unconsolidated bivalve shell. χ^2-tests were used to test if algae incorporated into tube caps were more common than algae with other types of attachments, and to test for associations between attachment type and elevation level, adjacency to mainland, and species type. Finally, to quantify incorporated species-specific algal abundance's 92 tube caps where randomly collected in summer 2002 from an intertidal mid-lagoon mudflat where algal richness and biomass generally are high (Shoal-site; Tyler et al., 2001). The tube caps were transported to the laboratory where the algae were removed, rinsed in fresh water, and wet weight (0.001 g accuracy) determined after blotting with a towel. Attachment type (associated with the tube cap or incorporated algae) and the presence of macroscopically visible reproductive tissue were also recorded.

2.4. Stability of algae incorporated to tube caps

To test if drift algae in Hog Island Bay move with the tides on low slope intertidal and shallow subtidal mudflats, strips of flagging tape were tossed on the substrate at low tide in 18 random plots on a mid-lagoon intertidal mudflat on 24 June, 2002 ($n = 6$ strips per plot, at 0.65 m below mean sea level, Shoal-site; McGlathery et al., 2001). Flagging tape was used as mimics of loose-lying algae because the slightly negatively buoyant and flat structure are similar to loose-lying *U. curvata* fragments, and because the strips were easily detected on the extensive mudflat often covered with patches of drift algae. None of the 108 strips were found the following day, despite an intense search-effort. To test if the algae-tube cap association was more stable than unattached algae, as exemplified by the instability of the loose-lying flagging strips, and test whatever stability differed between incorporated *G. verrucosa* and *U. curvata* (the two most abundant algae in Hog Island Bay; Thomsen, 2004), eight individuals and their host tube caps were double-tagged with flagging tape (tying a 7-cm flagging tape gently around the algal thalli and tube cap) on 24 June, 2002. Tag-survival was subsequently recorded nine times during a 46-day period. Two tags were tied to each algal thallus/tube cap to ensure that tag loss was caused by dislodgment of the algae or tube cap and not simply loss/breakage of the

tags themselves, i.e. a thallus observed with a single tag would indicate a poor tying procedure. However, tube caps were always observed either with incorporated thalli with both the tags intact (i.e. survival) or with no algae/tags at all (i.e. algal dislodgment). To test for the generality of the obtained results, the experiment was repeated on 4 October where survival was recorded six times over a 44-day period. It is unlikely that the tag influence algal survival because the tag provides minimal drag compared to the algal thallus (Thomsen, 2004). The percentage remaining tags, i.e. surviving algae, were calculated on each sampling date for each species and experiment. Finally, linear regression was used to calculate and compare the decay-slopes of percent tube cap incorporated algae remaining per day.

2.5. Recovery of algae incorporated to tube caps

To estimate the recovery ability of the algae-tube cap association, removal experiments where conducted simulating different degrees of disturbances. Randomly allocated 0.1 m^2 plots were manipulated using different combinations of disturbance intensities and frequencies, and the recovery of tube caps and algal biomass were compared to control plots. A low-intensity treatment was achieved by removing incorporated algae (simulating hydrodynamic induced dislodgment) and a high-intensity treatment by removing tube caps (simulating severe sediment erosion or deposition). In a summer experiment the two intensities were applied on the 24 and/or 28 June, 2002 (Expt. 1: 0.65 m below mean sea level, mid-lagoon site, $n = 4$). The following five treatment combinations were applied (arranged from high to low severity): (1) tube caps removed on 24 and 28; (2) algae removed on 24 and tube caps on 28; (3) tube caps removed on 28; (4) tube caps removed on 24; and (5) algae removed on 28 June. On 4 July, i.e. after 10 and/or 6 days of recovery, regenerated tube caps and incorporated algae were collected, brought to the laboratory, the number of tube caps counted, the algae identified, and wet weight determined after blotting with a towel. To investigate if the findings were robust a second removal experiment was conducted in November 2002 (Expt. 2, near the mainland, same elevation level). To increase the ability to detect disturbance effects (see result section) the number of replicates were doubled ($n = 8$), but the applied treatments reduced to only include: (1) tube caps removed on 7; (2) tube caps removed on 4; and (3) algae removed on 4 November. The treatments were compared to control plots on 12 November, i.e. after 8 and 5 days of recovery. Because the two experiments differed in number of replicates and treatments and were conducted at different sites and seasons, they were analyzed independently. To test for disturbance effects ANOVAs were conduced on densities of re-generated tube caps and biomass of

G. verrucosa, *U. curvata* and the total algal assemblage, followed by SNK-unplanned multiple comparisons to separate different treatments (Underwood, 1981). To overcome the problem of low test power (few replicates) in the summer experiment, an additional set of ANOVAs were conducted with the three high disturbance treatments pooled and tested against the two low treatments pooled together with the control plots ('High' vs. 'Low' disturbances, Expt. 1b, Fig. 3). Some response variables were Log-transformed to ensure variance homogeneity (Cochran's $C > 0.05$, Table 4). It should finally be noted that at the termination of the two experiments all plots were also searched for unattached algae, but none were found.

2.6. Preference of algae incorporated to tube caps

Finally, to test if some algae are preferred over others an in situ preference experiment was conducted. The six most conspicuous macroalgae to be found year round in Hog Island Bay were included (arranged after increasing S:V ratio, unpublished data): *Codium fragile* ssp. *tomentosoides* (Suringar) Hariot, *Fucus vesiculosus* Linnaeus, *Agardhiella subulata* (C. Agardh) Kraft et Wynne (*Solieria tenera* in Humm, 1979), *Gracilaria foliifera* (Forsskal) Børgensen, *G. verrucosa*, and *U. curvata*. A 30-cm round PVC cage was inserted vertically 20 cm into the sediment around a haphazardly selected tube cap at a near-mainland site. The tube cap-algae association was removed to force *D. cuprea* to build a new cap. Fresh algal fragments were added to cages in November 2002 either as single-species (three fragments per cage) or multiple-species treatment (one fragment per cage, cf. Fig. 4a for specific biomass), and cages were capped with 2 mm of screening mesh. After 2 days of incubation tube caps with incorporated algae and unattached algae were collected, and the total and attached number of fragments were counted to calculate 'percent attachment' and 'percent fragmentation'. Fragmentation was not measured in control plots (i.e. without *D. cuprea*) because pilot experiments had revealed that healthy tissue of the six species rarely fragmented in caged experiments with only two days of incubation (Thomsen, 2004). Because some cages were lost due to storms, vandalism and heavy sedimentation, the final sampling design was uneven ($n = 4 - 11$, cf. Fig. 4). These response variables were tested with a two-factorial ANOVA on species and addition type, followed by SNK-tests to indicate different groupings. It should be noted that because fragmentation could not be transformed to variance homogeneity, because species responses potentially are non-independent in the multi-species cages, and because *F. vesiculosus* and *G. foliifera* had fewer replicates that the other species, the *P*-values may be biased and should be interpreted with caution (Quinn and Keough, 2002).

3. Results

3.1. Ubiquity of tube caps

The overall mean tube cap density was 21 m^{-2} (± 27, $n = 105$), and there was a significant interaction between densities found along the mainland-ocean and elevation gradients (Table 1). Highest densities were found at intertidal mainland sites and at subtidal mid-lagoon sites with typical mean densities of 35–40 caps m^{-2} and with maximum densities up to 180 caps m^{-2} (Fig. 1).

3.2. Ubiquity of algae incorporated to tube caps

Of the >3000 tube caps that were examined qualitatively in the field more than 90% had algal fragments attached. The size range of fragments varied from pieces smaller than 1 cm, to 60 cm long *U. curvata* and 50 cm *G. verrucosa*. Algae were more often encountered on tube caps than any other attachment type. The species observed on the tube caps were *G. verrucosa*; *U. curvata* (ubiquitous), *A. subulata*, *F. vesiculosus*, *G. foliifera*, and *Enteromorpha linza* (up to 10 observations); and *C. fragile*, *Punctaria latifolia* Greville and *Grinnellia americana* (C. Agardh) Harvey (one observation each). Approximately 10 attached carposporophytic *G. verrucosa* were also observed. The quantitative observations showed that significantly more algae were found attached to tube caps (70%, $\chi^2_6 = 927.2$, d.f. = 5, $P < 0.001$, Table 2) than any other attachment type, that the proportions of tube cap-attached algae varied with distance from mainland (smallest proportion attached at mid-lagoon sites, $\chi^2_{6,3} = 46.4$, d.f. = 10, $P < 0.001$) but not with elevation ($\chi^2_{6,2} = 12.5$, d.f. = 5, $P = 0.028$) and that *G. verrucosa* were found in significantly higher proportions than *U. curvata* (64 vs. 34%, $\chi^2_{6,2} = 27.2$, d.f. = 1, $P < 0.001$). Other species found on tube caps (*A. subulata, G. foliifera* and *F. vesiculosus*) were found in less than 1% of the cases, and were omitted from tests. All of the 92 collected tube caps had incorporated algal fragments, with an average of 8.9 gWW and a species richness of 2.7 per tube cap (Table 3). *Gracilaria verrucosa* was found attached to 90 tube caps, three of them with cystocarps, accounting for 94% of the total biomass,

Table 1
ANOVA of tube cap densities

Source	SS	%	d.f.	F	P
Distance	3232	4	2	2.44	0.097
Elevation	69	0	1	0.10	0.748
Distance × Elevation	8608	11	2	6.49	**0.002**
Error	66280	85	100		

The '%' column corresponds to percent sum of squares calculated from the total sum of squares. Significant results ($P < 0.05$) are shown in bold.
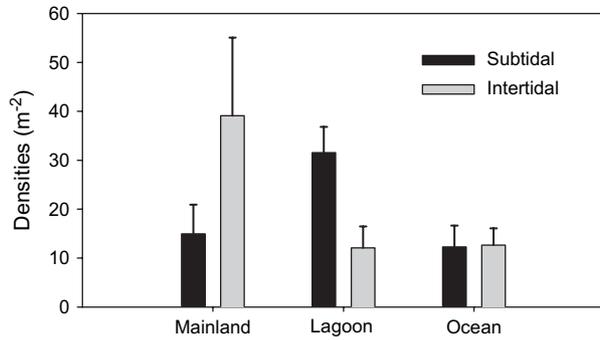
Fig. 1. Ubiquity of tube caps in Hog Island Bay: *Diopatra cuprea* densities along the mainland-ocean and elevations gradients ($\pm$SE, from left $n = 18, 18, 21, 16, 10, 23$).

and 33 had *U. curvata* incorporated, corresponding to 2.4% of the total biomass. Three tube caps had more than 50 gWW and 11 more than 20 gWW. Very few species were found incorporated, and some taxa (e.g. *Ceramium* sp., *Polysiphonia* sp., *Hypnea musciformis* (Wulfen) Lamouroux, *Champia parvula* (C. Agardh) Harvey), were only recorded as epiphytic or entangled/secondarily attached on *G. verrucosa* (Norton and Mathieson, 1983; Perrone and Cecere, 1997), thereby adding 1–2 taxa to the total tube cap richness.

3.3. Stability of algae incorporated to tube caps

All loose-lying flagging tape strings were lost from the mudflat in less than 24 h, i.e. in less than two complete tidal cycles. This corresponded well to our general observations, with unattached algae on open tidal flats typically being mobile and probably only accumulating under specific hydrodynamic, topographic, biological and meteorological conditions. In the tagging experiments some tube caps were apparently lost, but subsequently digging into the sediment revealed that the tags were buried under a few cm of sediments. Thus, no tube caps were lost in any of the experiments, markedly different for the incorporated algal fragments that were physically removed from tube caps within days to month (Fig. 2). In both tagging experiments,

incorporated *U. curvata* were removed faster than *G. verrucosa* (7.0% and 21.1% d^{-1} vs. 2.2% and 2.0% d^{-1}, $r^2 > 0.93$, $P < 0.05$, for all slope coefficients). Using the mean slope coefficients from the two experiments for each species, 50% survival periods were calculated to respectively four and 24 days. It was also observed that after tagged algae were lost from the tube caps, small fragments (1–2 cm) remained incorporated, suggesting that re-growth is possible.

3.4. Recovery of algae incorporated to tube caps

All response variables showed significant effects on abundance to different levels of disturbances (except one near-significant effect, Table 4). However, the un-planned multiple SNK-comparisons could only distinguish significant different subgroups for the 'weakest' disturbance treatment for *U. curvata* in Expt. 1 (Fig. 3c), and for the controls of *G. verrucosa* (Fig. 3b) and *U. curvata* in Expt. 2 (Fig. 3c). Thus, the relatively few replicates in the summer experiment made it difficult to statistically separate groups, although graphical inspection indicated a tendency for highest abundance's at the low disturbance plots, a pattern especially clear for total algal biomass (Fig. 3d). Domination reversal was observed in the 'algae removed on 24' treatment, that had less *G. verrucosa* incorporated compared to the other plots with low levels of disturbances (the 'control' and 'caps removed on 24' treatment, Fig. 3b). However, this deficiency was compensated for by incorporation of *U. curvata* (Fig. 3c), resulting in near-identical total biomass (Fig. 3d). The tendencies noted in Expt. 1 were verified statistically when the three lowest disturbance levels plots were pooled and compared to the three highest levels (Expt. 1b, Fig. 3 and Table 4e–h). Here the abundance's of tube caps, *G. verrucosa*, *U. curvata* and total incorporated algal biomass were significantly less in high-disturbance plots, suggesting general algal facilitation on the 0.1 m^2 plot-scale (most algal biomass in plots with highest tube cap densities).

In the second experiment, the SNK-tests did not detect significant subgroups for either tube cap densities (Fig. 3a) or total algal biomass (Fig. 3d), despite

Table 2
Relative abundance (in counts) of the different attachment types and species incorporated onto tube caps

Gradient	Attachment type						Species				
	Tub	Loo	Bur	Epi	Ent	She	Gra	Ulv	Aga	Fol	Fuc
Near-mainland	116	12	1	1	1	1	73	43	0	0	0
Mid-lagoon	127	29	14	8	3	39	89	36	1	0	1
Near-ocean	66	4	4	4	1	10	36	28	0	1	1
Intertidal	149	24	11	1	1	28	99	49	0	0	1
Subtidal	160	21	8	12	4	22	99	58	1	1	1
Total	309	45	19	13	5	50	198	107	1	1	2

Tub, tube cap; Loo, loose-lying; Bur, Buried; Epi, Epiphytic; Ent, Entangled; She, Shell; Gra, *Gracilaria verrucosa*; Ulv, *Ulva curvata*; Aga, *Agardhiella subulata*; Fol, *Gracilaria foliifera*; Fuc, *Fucus vesiculosus*.

Table 3
Biomass per tube cap (gWW), relative abundance (%), frequency of occurrence (Counts) and attachment types of algae incorporated into tube caps ($n = 92$)

Taxa	gWW	Variance	%	Counts	Attachment
Richness[a]	2.674	1.849		92	
Biomass	8.911	137.720		92	
Gracilaria verrucosa	8.384	125.275	94.08	90	Tub
Ulva lactura	0.215	0.909	2.42	33	Tub
Ceramium rubrum	0.109	0.217	1.23	23	Epi
Hypnea musciformis	0.089	0.113	1.00	15	Epi
Bulgula turrita[b]	0.050	0.115	0.56	18	Epi
Champia parvula	0.019	0.016	0.21	10	Epi
Agardhiella subulata	0.016	0.012	0.18	2	Tub
Polysiphonia sp.	0.011	0.011	0.13	3	Epi
G. verrucosa carp.[c]	0.008	0.003	0.09	3	Tub
Ceramium strictum	0.002	0.000	0.02	2	Epi
Fucus vesiculosus	0.001	0.000	0.01	1	Tub
Enteromorpha linza	0.001	0.000	0.01	3	Epi

Tub, tube cap; Epi, Epiphytic (entangled; hooked, primary attached, re-attached).

[a] In number of taxa per tube cap.
[b] A bryozoa.
[c] Caroposporophytic life stage, potentially with viable propagules.

significant ANOVAs (Table 4i, l), indicating a full recovery in less than 5 days. However, splicing the total algal assemblage data into species-specific abundances clearly demonstrated significant SNK-group effects on both *U. curvata* and *G. verrucosa* (Table 4 and Fig. 3b,c), and a marked shift was observed from *G. verrucosa* to *U. curvata* domination after all of the three disturbance treatments. The control plots were characterized by high *G. verrucosa* (ca. 130 gWW m^{-2}) and low *U. curvata* (ca. 20 gWW m^{-2}) biomass relatively similar to the controls from Expt.1. However, in the fall experiment, the disturbed plots changed into high *U. curvata* (ca. 150 gWW m^{-2}) and low *G. verrucosa* associations (ca. 20 gWW m^{-2}) similar to the aforementioned 'algae removed on 24' treatment.
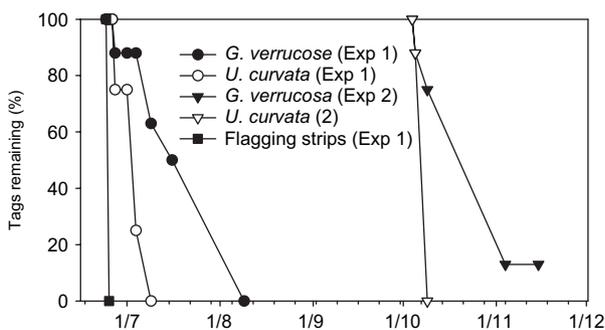

Fig. 2. Stability experiments: 'Survival' of algae incorporated into tube caps ($n = 8$ per algal species and experiment) and of unattached flagging strips ($n = 108$) on an intertidal mudflat.

Table 4
ANOVAs from recovery experiments

Test and source	SS	d.f.	F	P
a: Expt. 1 *Diopatra*	223.0	6	22.30	**<0.0005**
Error	30.0	18		
b: Expt. 1 *Gracilaria*	16685.2	6	6.36	**0.001**
Error	7869.0	18		
c: Expt. 1 Log *Ulva*	3.9	6	5.40	**0.002**
Error	2.2	18		
d: Expt. 1 Log Biomass	42.7	6	66.03	**<0.0005**
Error	1.9	18		
e: Expt. 1b *Diopatra*	215.0	2	62.32	**<0.0005**
Error	38.0	22		
f: Expt. 1b Log *Gracilaria*	36.4	2	134.18	**<0.0005**
Error	3.0	22		
g: Expt. 1b *Ulva*	212.4	2	2.94	0.074
Error	795.4	22		
h: Expt. 1b Log Biomass	42.7	2	240.94	**<0.0005**
Error	1.9	22		
i: Expt. 2 *Diopatra*	2895.3	4	37.20	**<0.0005**
Error	544.8	28		
j: Expt. 2 *Gracilaria*	4598.1	4	8.15	**<0.0005**
Error	3949.6	28		
k: Expt. 2 Log *Ulva*	32.0	4	91.70	**<0.0005**
Error	2.4	28		
l: Expt. 2 Biomass	14758.1	4	15.62	**<0.0005**
Error	6613.8	28		

Expt. 1 was initialized in June and Expt. 2 in November 2002. Expt. 1b corresponds to treatments from Expt. 1 pooled into 'low' vs. 'high' disturbance levels (cf. Fig. 3). Significant results ($P < 0.05$) are shown in bold. Log, Logarithm transformed.

3.5. Preference of algae incorporated to tube caps

In the test of effects on algal incorporation rates, there was a significant interaction between species and addition type, and a highly significant species effect (Table 5, Fig. 4b). However, because the interaction effect only explained 7% of the sum of squares compared to 49% for the species factor, the latter clearly was most important. The SNK-test grouped the three species with lowest S:V ratios into a distinct 'low-incorporation' group (*C. fragile* = 17%, *F. vesiculosus* = 18%, *A. subulata* = 28%) compared to the species with highest S:V ratio (*G. foliifera* = 68%, *G. verrucosa* = 54%, *U. curvata* = 75%). There were no significant interaction terms for fragmentation, but two significant single factor effects (Table 5, Fig. 4c). Again the species factor explained far more of the data variability compared to the addition type factor and the latter
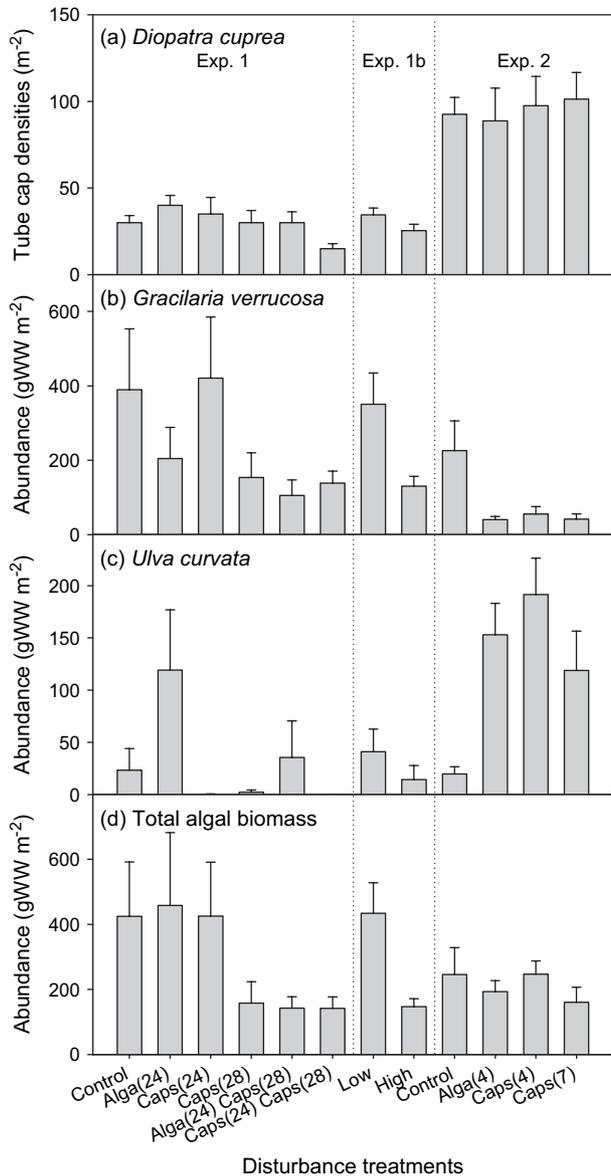
Fig. 3. Recovery experiments: Effects of various levels of disturbances on the abundance of *Diopatra cuprea* tube caps (a) and tube cap incorporated *Gracilaria verrucosa* (b), *Ulva curvata* (c), and total algal biomass (d) ($\pm$SE). The first six bars correspond to Expt. 1 treatments (terminated 4 July, $n = 4$), the next two to Expt. 1 pooled into low vs. high disturbance intensities ($n = 12$), and the last four to Expt. 2 treatments (terminated 11 November, $n = 8$). Treatment labels: Alga, algae removed; Caps, tube caps removed. The number in brackets corresponds to date of removal.

could be ignored for practical purposes. The SNK-test again grouped the three species with lowest S:V ratios into a distinct 'low-fragmentation' group (*C. fragile* = 0%, *F. vesiculosus* = 0%, *A. subulata* = 14%), but the species with highest S:V ratio were here spliced into two 'high-effect' groups (*U. curvata* = 50% and *G. foliifera* = 56% vs. *G. verrucosa* = 109%). Note that fragmentation could exceed 100% if a tissue was fragmented more than once.

4. Discussion

Habitat modifiers typically facilitate other species by providing shelter from predation, by reducing physical and physiological stress, by enhancing propagule supply and retention, and by increasing food supply (Bruno and Bertness, 2001). We argue that *D. cuprea* specifically facilitates macroalgal assemblages in North American soft-bottom shallow lagoons by (a) creating and maintaining attachment sites via incorporation of fragments into tube caps, (b) increasing algal residence time on mudflats compared to unattached algae and (c) enhancing and retaining a supply of small vegetative fragments. These mechanisms are particularly important in soft-substrate environment, were substrate for algal attachment is scarce, where hydrodynamic forces often transport unattached algae up high on the beach or deep into the aphotic zone, and where sexual reproduction in the drift algae population may be non-existing (Norton and Mathieson, 1983; Cecere et al., 1992). These specific facilitation mechanisms were not described for polychaete worms in the review by Bruno and Bertness (2001). It is further likely that summer growth and productivity also is enhanced by *D. cuprea*, by excretion of nitrogenous rich waste products (Fong et al., 1997; Giannotti and McGlathery, 2001), although this hypothesis were not tested in the present study.

The more abundant and ubiquitous a habitat modifier is the more likely it is that facilitation is important on a large scale. Our first survey demonstrated that *D. cuprea* exists in both subtidal and intertidal environments and from mainland to near-ocean sites in Hog Island Bay, and occasionally with very high densities, suggesting that *D. cuprea* has the potential to facilitate macroalgae throughout the lagoon. The mean of 21 *D. cuprea* m^{-2}, is similar to high density plots in Massachusetts lagoons, and our high density areas (up to 180 *D. cuprea* m^{-2}) were similar to previously recorded maximum values from Delmarva peninsula back-barrier island lagoons (50–300 tube caps m^{-2}; Mangum et al., 1968; Peckol and Baxter, 1986). The distance from the mainland and the elevation gradients represent predictable co-varying differences in water clarity, salinity, suspended solids, nutrient concentrations, sediment organic content, and sediment texture (the distance gradient, McGlathery et al., 2001) and desiccation, light, temperature fluctuations, sedimentation, and predation pressure (the elevation gradient). The widespread distribution suggests that *D. cuprea* is a stress-tolerant species with broad habitat requirements, clearly important if facilitation is to have a large-scale impact. Kim (1992) found a significant spatial interaction for subtidal *D. ornata* populations in California between exposure levels and small-scale spatial patterns, and Mangum et al. (1968) suggested that *D. cuprea* densities were positively correlated to

Table 5
ANOVAs from preference experiment

Source	Attachment					Fragmentation			
	d.f.	SS	%	F	P	SS	%	F	P
Species	5	176299	49	20.26	**<0.0005**	161091	42	15.16	**<0.0005**
Addition	1	4592	1	2.64	0.108	11372	3	5.35	**0.023**
Species×Addition	5	23346	7	2.68	**0.026**	20004	5	1.88	0.105
Error	89	154901	43			189156	50		

Percent attachment and percent fragmentation. The '%' column corresponds to percent sum of squares calculated from the total sum of squares. 'Addition' corresponds to the addition type, with fragments being added as single or multiple species to caged *Diopatra cuprea*. Significant results ($P < 0.05$) are shown in bold.

current velocities and latitude, but not with substrate particle size. It is today still unknown what factors control site-specific distribution patterns of *D. cuprea*, probably because the aforementioned co-variation
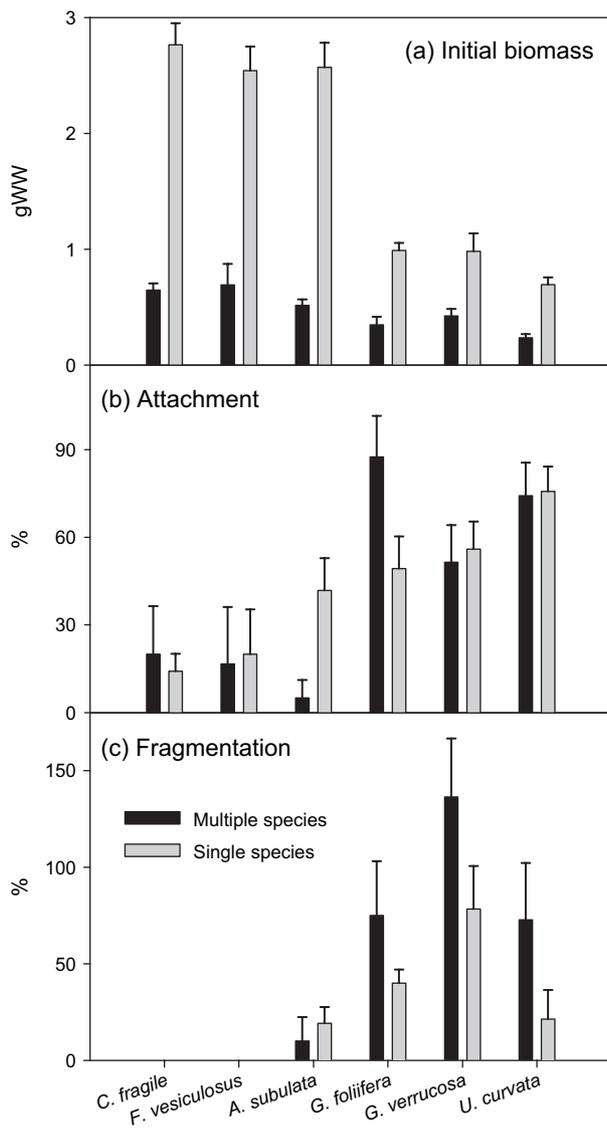

Fig. 4. Preference experiment: (a) Algal biomass added to *Diopatra cuprea* cages, (b) percent fragments incorporated into tube caps, and (c) percent fragmentation, based on single and multiple species additions. Species are arranged from low to high S:V ratios (±SE, from left n = 11, 9, 11, 10, 4, 5, 10, 5, 10, 10, 6, 5, 10, 10).

between ecological factors and spatial gradients makes it extremely difficult to relate single causes to distribution patterns. Algae incorporated into tube caps where much more common than algae being loose-lying or attached to bivalve shells. We are not aware of any study that have rigorously quantified the relative distribution of algal attachment types within soft bottom systems, but suspect such associations to be common on large scales (Reise, 1983). Also, the proportion of incorporated algae varied with distance from the mainland, probably because of differences in hydrodynamic regime and sedimentation levels (Lawson, 2002), and because large areas in the center of Hog Island Bay have nearby relict oyster reefs providing an abundant supply of shells for attachment (Thomsen, 2004). Thus, shell-substrate is most rare at near-ocean sites probably due to sand burial and water-induced removal, and at near-mainland sites where burial in silt is common (Thomsen, 2004).

It is well documented that macroalgae have created new habitats in numerous otherwise barren soft sediment systems, with specific associated species, food web structure, diversity and altered biogeochemical cycling (Everett, 1994; Holmquist, 1994; Escartin and Aubrey, 1995; Norkko and Bonsdorff, 1996; Raffaelli et al., 1998; Norkko et al., 2000). In this context, the incorporated algae are proximate habitat modifiers whereas *D. cuprea* is the ultimate modifier, and the algae may have an important ecosystem influence in the presence of *D. cuprea*. However, different species may have different effects on local environmental conditions, and hence it is of interest to know if certain species are more commonly incorporated than others. Our results clearly show that out of a taxonomic pool of ca. 20–40 species (Rhodes, 1970; Connor, 1980) only *G. verrucosa* or *U. lactuca* were found incorporated in abundance, and only a few other taxa were found very rarely. It was generally difficult to find tube caps in Hog Island Bay that did not contain fragments of either *G. verrucosa* or *U. lactuca*, an observation that was supported by each of the three surveys and the recovery experiment. Although the potential importance of algae attached to *D. cuprea* has been acknowledged several times (Pillsbury, 1950; Brenchley, 1976; Bell and Coen, 1982) only Mangum et al. (1968) provided a species list, describing 16 taxa

pooled from several sites in Virginia. Most of these taxa were also found in the present study (*Ulva, Gracilaria, Agardhiella, Enteromorpha, Ceramium, Polysiphonia, Bryopsis*). However, based on our data we suspect that especially the latter filamentous genera mainly were found as epiphytes on *Gracilaria*. It is interesting that older *D. cuprea*-studies from mid-Atlantic barrier island localities (Mangum et al., 1968; Brenchley, 1976; Woodin, 1978; Woodin, 1981) either did not describe incorporated algae, or only described attached species qualitatively, indicating much lower algal abundance in the 1960s–1970s. Due to the absence of published rigorous quantitative macroalgal surveys from this region we can only speculate on such temporal differences, but it is likely that the region has experienced intense coastal eutrophication in the last 30 years, similar to lagoonal systems worldwide (Fletcher, 1996; Raffaelli et al., 1998; Goshorn et al., 2001), resulting in high algal biomass increases and today supporting the abundant algal assemblages in conjunction with *D. cuprea*.

The tagging experiment demonstrated that algal residence time on the mudflats, was enhanced by association with *D. cuprea*, and that *G. verrucosa* is slightly favored over *U. curvata* because of lower decay slope coefficients. We suggest that *G. verrucosa* and *U. curvata* biomass loss was caused by peak tidal currents or storm-induced waves forces (Bell, 1999). Grazing is an alternative loss process, but is unlikely to be important because Hog Island Bay have few grazers capable of consuming entire thalli (personal observation). However, it is likely that the interaction between mesograzer wounding and hydrodynamic forces increase the likelihood of biomass removal, especially for *U. curvata*, that rarely were observed with intact thalli (Denny et al., 1989; Padilla, 1993; Duggins et al., 2001). The calculated 50% survival time periods are constrained by site- and time-specific effects of the lunar cycle, wind patterns, bathymetry, and fetch (Thomas, 1986), and we suspect that the incorporated algae have higher meta-population stability on large scales (Hanski, 1998) especially if dislodged biomass is re-captured and re-attached downstream of the disturbed site. It should be noted that the reported removal rates only reflected main thallus loss, and that small fragments remained on tube caps, making re-growth possible independently on the supply of drift algae.

The third aspect of algal facilitation is the rapid regeneration of the algae-tube cap association, within a few days to weeks of disturbance. This is consistent with the observation by Myers (1972) that tube caps can be rebuilt within 48 hours. We observed that repeated removal of tube caps did affect the abundance of macroalgae within the time scale of 5–10 days, and that disturbances can trigger species-specific dominance reversal (from *G. verrucosa* to *U. curvata*). Thus, because

a high local supply of drift *U. curvata* was observed at the time of the manipulations at the fall recovery experiment, this species became the all-dominant taxa after disturbances. This suggests that *D. cuprea* uses the available drift algae, and emphasize that the timing of disturbance (Sousa, 1984; Petraitis and Latham, 1999) combined with the drift algal supply can change the composition of the macroalgal assemblages overnight. It is likely that these effects would be less prominent if the disturbances occur in late winter partly because less algae are present and partly because the ability of *D. cuprea* to maintain its tube cap ceases below 2 °C (Myers, 1972). Also, the observation from the summer experiment that significantly less algae were found in the highly disturbed plots (with fewer tube-caps), lend strong support to our general hypothesis that *D. cuprea* facilitate algal distribution and abundance, at least on the small spatial scale manipulated in the present study. However, future studies should repeat these experiments on larger spatio-temporal scales to enable stronger inferences about lagoon wide facilitation effects.

The preference experiment specifically tested for control mechanisms on the algal assemblage structure. Even when added in less biomass, *G. verrucosa, G. foliifera* and *U. curvata* were still preferred as building material over *A. subulata, C. fragile* and *F. vesiculosus*. This is different to findings by Brenchley (1976) who reported that *D. cuprea* did not select, but used *Ulva* and bivalve shells according to abundance. The pattern suggests that the S:V ratio is an important property for successful incorporation, although it is likely that other species-specific properties (e.g. morphology, chemistry, structure, biomechanics) also influence the attachment process. Fragmentation was also positively related to the S:V ratio. Fragmentation is probably an important process in maintaining algae on tube cap, because larger thalli were only stable on the day-month time scale. The low drag on the fragmented cm-small thalli have a low risk of dislodgment compared to the larger incorporated thalli (Gaylord et al., 1994) and the fragments provides a small but constant biomass supply for re-growth if hydrodynamic forces removes larger thalli. *Diopatra cuprea* is therefore not fully dependent on locating new drift algae to replace what currents and waves remove, although re-growth of small fragments primarily should be important at sites and seasons with low and unpredictable drift algae supply.

In conclusion, our data suggest that *D. cuprea* affect the distribution, abundance and stability of macroalgae in shallow soft-bottom systems along the North American east coast, although studies from more localities are needed to verify this. Because of high attachment, fragmentation, stability, and recovery rates the incorporated algae are abundant in areas where they would otherwise be flushed. We also suggest that *G. verrucosa* and *U. curvata* dominate tube caps in

Hog Island Bay because (1) they are selectively incorporated, (2) they are already present as building material in large quantities, (3) they have structure, size, morphology and buoyancy properties that allows *D. cuprea* to encounter, capture, fragment and incorporate them into a relatively strong attachment, (4) they have high intrinsic growth rates, and (5) they are stress-tolerant species that can survive sediment burial, fragmentation and desiccation. On the other hand, the few other conspicuous perennial algae in Hog Island Bay are not dominants probably because they lack above properties. For example, the alien invasive *C. fragile* spread to in Virginia in the 1970s (Hillson, 1976; Trowbridge, 1998; Chapman, 1999), is today the fourth most common species in Hog Island Bay (Thomsen and McGlathery, 2003) and is potentially still expanding its distribution. Because *C. fragile* does not fulfill the listed properties (unpublished data, work in progress) we predict that it will not become a lagoon-wide dominant species under the current ambient conditions. However, if eelgrass re-colonize Hog Island Bay, a process observed in several nearby bays, a state change may occur with reduced water turbidity and increased sediment stability (Hayden et al., 2000; Lawson, 2002), potentially altering *D. cuprea* recruitment, feeding success and survival, and thereby ultimately also affecting the relative competitiveness of *G. verrucosa*, *U. curvata*, *C. fragile* and other macroalgae.

Acknowledgments

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