Macroalgal distribution patterns and ecological performances in a tidal coastal lagoon, with emphasis on the non-indigenous *Codium fragile* ssp. *tomentosoides*

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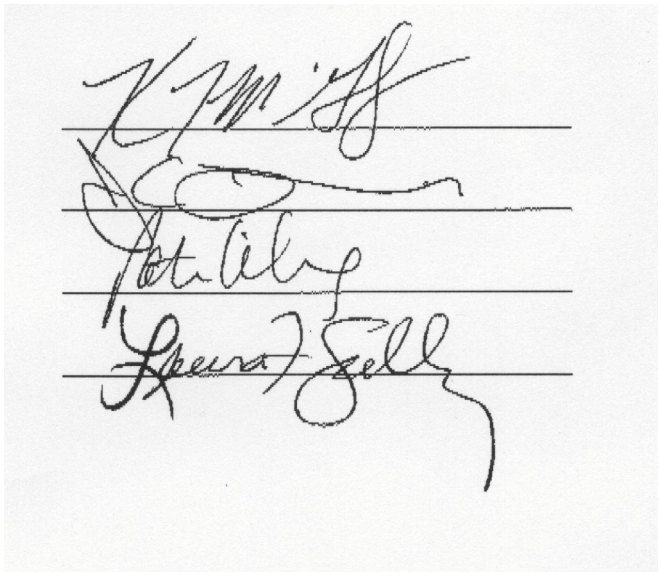

Abstract

Codium fragile ssp. *tomentosoides* is a North-West Pacific macroalgae that has invaded numerous lagoons. The success of *C. fragile* has been explained by its dispersal capacity, growth rate, nutrient uptake, salinity and temperature tolerances, and grazer resistance. I compared distribution, recruitment and growth of *Codium* to native algae in Hog Island Bay, a shallow water lagoon in Virginia. To determine the extent of invaded habitats algae were mapped from 1998-02. *Codium* was fourth most abundant, and hence considered successful compared to most species in terms of its biomass. *Codium* was found both unattached or attached to bivalve shells, while the majority of the dominant *Gracilaria verrucosa* and *Ulva curvata* were incorporated into tube caps of the polychaete *Diopatra cuprea*. Preference experiments showed that *Diopatra* incorporated *Ulva* and *Gracilaria* most, *Agardhiella subulata* intermediate, and *Codium* and *Fucus vesiculosus* least, and that the first 3 species were fragmented in the process. Thus, *Diopatra* facilitated *Ulva* and *Gracilaria,* by providing an abundant substrate, reducing flushing and maintaining a supply of fragments for regrowth. Tidal lagoons are characterized by sedimentation, desiccation, high turbidity, and high abundance of molluscan grazers. Short-term experiments showed that *Codium* was inferior under such conditions compared to *Gracilaria*, *Ulva, Hypnea musciformis*, and *Agardhiella*, decomposing faster when buried, being susceptible to desiccation, growing slower at high and low levels of nutrient and light, and being the only species grazed by *Ilyanasa obsolata*. To test if the success of *Codium fragile* could be related to its ability to colonize hard substrate, recruitment bricks were incubated in the shallow subtidal with

and without a cover of unattached algae or sediments. *Codium* recruited well onto control bricks, but not onto bricks covered by algae or sediments. After one year *Codium*, *Gracilaria*, *Crassostrea virginica* (oyster) and *Agardhiella* were space-dominants, having tolerated temperature regimes of 2-28ºC and desiccation at low spring tides. Thus *Codium* is only successful compared to native species by having moderate growth over a long season, and by being an effective colonizer of hard substrate in the shallow subtidal zone in the absence of high sedimentation or drift algae accumulations.

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Chapter 1. Introduction: Marine invasions and *Codium fragile* ssp. *tomentosoides* in Hog Island Bay

Marine invasions

Invasions of alien species are considered a major threat to local, regional, and global biodiversity because invaders often compete with, eat or infect native species (Carlton 1999, Meinesz 1999, Walker & Kendrick 1998). In addition invasions cause serious economic damage due to competition with and infections of financially important crops and livestocks (Carlton 1996b, Carlton 1999, McNeely 1999, Meinesz 1999, Ruiz et al. 1997). Alien species are also referred to as exotics, non-indigenous or non-native; all terms imply that the appearance of the species is related to human-mediated transportation (Minchin & Gollasch 2002, Wallentinus 2002). Today, it is difficult to estimate the 'original and natural' species assemblage given the long-term human perturbations of nature. Introductions of alien species have occurred at a steadily increasing pace in the last six centuries, due to growing human populations, increased international trade and transport, and decreased transportation time (Carlton 1996c, b, McNeely 1999). If alien species become spatially dominant in their new location and/or have major impacts on the ecosystem, they are referred to as invasive. In the marine environment, introductions are associated with transport of ballast water (e.g. *Mnemiopsis leidyi*, *Eriocheir sinensis*), of economically important species for aquacultural purposes (e.g. *Sargassum muticum*, *Styela clava* associated with transplanted oysters), by accidental releases/escapes (e.g. *Caulerpa taxifolia*, *Homarus americanus*), or on ship hulls and other floating manmade structures (e.g. *Codium fragile*, *Undaria pinnatifida*) (Meinesz 1999, Minchin & Gollasch 2002, Rueness 1989, Wallentinus 2002). Marine macroalgae are commonly introduced to new regions and have caused dramatic trans- and inter-oceanic invasions. Invasive species such as *C. taxifolia* (Vahl)

C. Agardh, *U. pinnatifida* (Harvey) Suringar, *S. muticum* (Yendo) Fensholt, and *C. fragile* (Sur.) Hariot ssp. *tomentosoides* (Van Goor) Silva are well known for clogging waterways, competing with native algae, altering the nursery habitat for fishes and invertebrates, reducing light penetration, changing biogeochemical cycling, and suffocating and/or drifting away with economically important shellfish (Chapman 1999, Den Hartog 1998, Meinesz 1999, Minchin & Gollasch 2002, Norton 1976, Rueness 1989, Stæhr et al. 2000, Trowbridge 1999, Walker & Kendrick 1998).

Codium fragile invasions

The invasive *C. fragile* is particular interesting, partly because the invasive organism is a sub-species that in many regions resembles native and/or less invasive populations and sub-species (Trowbridge 1998) and partly because it has invaded highly diverse habitats. Invasive *C. fragile* can be found in rocky and soft bottom habitats, low to medium levels of wave-energy, in both eurohaline and oligohaline systems, from intertidal rock-pools to 15 m depth, and in geographical regions ranging from high to low temperate latitudes (e.g. Garbary & Jess 2000, Malinowski & Ramus 1973, Mathieson et al. 2003, Scheibling & Anthony 2001, Searles et al. 1984). *C. fragile* invasions also highlight two important aspects of invasions. First, many introductions are cryptic because no baseline distribution data exist or because a similar looking organism is present (Carlton 1996a, b). For example, in New Zealand, Australia and the west coast of Northern America other *C. fragile* populations existed prior to invasions of ssp. *tomentosoides* and the invasions were difficult to detect (Trowbridge 1996b, 1998, 1999). In contrast, on the east coast of North America no *Codium* species were present and the dispersal and invasions were

more obvious (Fralick & Mathieson 1973, Garbary et al. 1997, Hillson 1976, Mathieson et al. 2003, Prince 1988, Searles et al. 1984). Second, introductions are caused by dispersal of populations or even a few individuals (Mack 1996, Trowbridge 1998), and not by the entire species. This means that the introduced organisms may have a different genetic fingerprint with slightly different traits, compared to the 'average homeland' population (Coleman 1996). *C. fragile* ssp. *tomentosoides* probably originated from the West Pacific (Trowbridge 1998) but is today present in the West Atlantic from Norway to northern Africa, the East Atlantic from southern Canada to North Carolina, the East Pacific in California and Chile, and at various sites in the Mediterranean sea, New Zealand, and southeast Australia (pers. com. Trowbridge, 2004, Chapman 1999, Mathieson et al. 2003, Trowbridge 1998). In the 1950's it appeared in New York harbor, probably introduced from fragments or propagules from individuals attached to ship hulls (Bouck & Morgan 1957). *C. fragile* arrived in Virginia in the 1970's (Hillson 1976) likely by drifting thalli, translocated bivalves (for the local oyster industry) and/or by ship hulls. No quantitative data exist from this region about the distribution pattern and performance abilities of *C. fragile* relative to native macroalgae.

Approaches to invasions: invader vs. invaded system

Models that are used to explain invasion patterns following introduction by human activities fall into two broad categories: those that focus on conditions related to the invader and those that emphasize conditions related to the invaded system (Mack & Antonio 1998, Rejmánek & Richardson 1996, Trowbridge 1998, 1999, Vermeij 1996, Williamson 1996). The first approach typically emphasizes organism-based 'super'-traits

such as fast growth (Campbell 1999, Vroom & Smith 2001, Wernberg et al. 2001), high dispersal (Ceccherelli & Piazzi 2001, Mathieson et al. 2003, Rueness 1989, Stæhr et al. 2000), strong recovery potential (Fletcher 1975, Meinesz 1999, Vroom & Smith 2001), high reproductive output (Arenas et al. 1995) and/or grazing and predation resistance (Begin & Scheibling 2003, Chapman 1999). The second approach emphasizes that a system is susceptible to invasions because (1) conditions are stressful (e.g eutrophication), (2) it is small and isolated and likely has impoverished functional diversity, (3) disturbances are frequent (e.g. following hurricanes or landslides), or (4) the system is young (e.g. following glacial retreats or volcanic island creations) (Carlton 1996c, Hengeveld 1985, MacArthur & Wilson 1967, Ruiz et al. 1997, Williamson 1996). A system that is susceptible to invasion would be characterized as 'open and unsaturated' with available space and niches (Myers & Bazely 2003). These two approaches merge when the species-specific traits are matched with the characteristics of the ecosystem, for example if an invader (e.g. *C. fragile*) has high nutrient uptake rates, is stress-tolerant and invades a eutrophied and stressed system (e.g. lagoons on the Delmarva Peninsula).

Traits of *Codium fragile*, the invader

C. fragile is classified in the order Caulerpales, a genus containing more than 100 species (Trowbridge 1998). *C. fragile* has a siphonious structure with intertwined multinucleated filaments and swollen utricles, no cell cross-walls, and has a large component of intra (vacuoles)- and inter (between filaments) cellular fluids which give the algae a soft spongy texture (Chapman 1999, Trowbridge 1998). From a form-functional perspective *C. fragile* is classified as a coarsely branched species with a low surface to volume ratios,

hereafter referred to as S:V (Littler 1980, Ramus & Venable 1987). Traits that have been suggested to cause success of *C. fragile* include the ability for rapid growth (Mathieson et al. 2003, Trowbridge 1999), high nutrient uptake efficiency at low concentrations and ability to utilize several nitrogen sources (Hanisak 1979a, b), low light requirements and high tolerance to high light levels (Ramus et al. 1976b, a, Trowbridge 1999), positive buoyancy and high drift capacity (Dromgoole 1982, Mathieson et al. 2003), low palatability for generalist grazers (Scheibling & Anthony 2001, Trowbridge 1998), and high temperature and salinity tolerances (Hanisak 1979a, Malinowski & Ramus 1973, Trowbridge 1998). To date, there have been few field based studies comparing ecological traits of *C. fragile* to an array of native species (Trowbridge 1998).

Lagoons, the invaded system

Numerous low energy soft bottom lagoons and estuaries have been invaded by *C. fragile* (Fralick & Mathieson 1973, Malinowski & Ramus 1973, Mathieson et al. 2003, Searles et al. 1984, Trowbridge 1999). Estuaries and lagoons are generally hot-spots for invasions in part because of high boat traffic and high human population densities, and in part because these systems are species-poor (with potentially open niches) and naturally and antropogenically ‘stressed’ (Moyle 1999, Ribera & Boudouresque 1995, Ruiz et al. 1997, Ruiz et al. 1999). Lagoons are characterized by shallow waters, low slopes, dominance of soft substrates, protection from coastal waves, and high sedimentation and re-suspension rates. In addition, tidal lagoons often have large intertidal mudflats, and typically have large spatio-temporal differences in salinity, temperature, light, and nutrients levels (Cromwell 1973, Flindt et al. 1997b, Hayden & Dolan 1979, McManus

1998, Reise 1985). Over the last many decades, numerious lagoons have changed dramatically due to anthropogenic forcing, including (in addition to transport of alien species) over-harvest of economically important species, increased sedimentation and nutrient loading, and various types of point-source pollution (Airoldi 2003, Morand & Briand 1996, Moyle 1999, Walker & Kendrick 1998). The main effects have been decreased light penetration, decreased abundance of perennial slow-growing rooted angiosperms, increased abundance of unattached macroalgal mats, epiphytes and phytoplankton and decreased sediment stability (Morand & Briand 1996, Raffaelli et al. 1998, Sand-Jensen & Borum 1991, Sfriso et al. 2001, Valiela et al. 1997).

Study site: Hog Island Bay

Distribution patterns and performance of *C. fragile* were compared to native species in Hog Island Bay on the Delmarva peninsula, on the eastern shore of Virginia (Fig. 1.1). Hog Island Bay is ca. 100 km^2 and is situated in the Virginia Coast Reserve which is part of the U.S. Long Term Ecological Research network (Swanson & Sparks 1990). It can be considered a model system representing the typical dynamic low slope tidal and turbid lagoons that dominate the eastern seaboard of the U. S. (Hayden et al. 2000). Hog Island Bay is characterized by soft substrates, high turbidity, high sedimentation/re-suspension rates (Lawson 2003), low water depth, and a tidal prism of ca. 1 m that creates large intertidal mudflats with high desiccation rates in summer month (Oertel 2001, Oertel et al. 2000). Nutrient loading to the lagoon is low relative to lagoons to the north along the Delmarva Peninsula (Boynton et al. 1986, Stanhope 2003), but standing stock nitrogen concentrations, primarily as DON, can be relatively high (McGlathery et al. 2001, Tyler

et al. 2001). Molluscan and amphipod grazers are prevalent and can control macroalgal biomass accumulation at low to moderate macroalgal densities (Chapter 2, Giannotti & McGlathery 2001, Rosinski 2004). There are numerous scattered unconsolidated bivalve shells and consolidated reef-structures that provide islands of hard substrate. Seagrasses have been extinct since the 1930's (Hayden et al. 2000), and unattached drift algae can occur in high abundances (Chapter 2, Giannotti & McGlathery 2001, McGlathery et al. 2001). A gradient in water residence time exist from near-mainland to near-ocean sites because of restricted tidal inputs via the Machipongo Inlet and relatively little freshwater input from the mainland (Lawson 2003). This gradient co-varies with sediment characteristics such as porosity, organic content and CN-ratios, and water quality parameters, such as nutrient levels and suspended solids (McGlathery et al. 2001).

The macroalgal species that are common and conspicuous in Hog Island Bay, and are found both attached to bivalve shells and in unattached mats, were compared to *C. fragile*, and include (Table 1.1): *Fucus vesiculosus*, *Ulva curvata*, *Agardhiella subulata*, and *Gracilaria verrucosa*. Also, in certain chapters *G. foliifera* (Chapter 3, 4, Appendix 1) and *Hypnea musciformis* (Wulfen) Lamouroux (Chapter 5, Appendix 1) were added. It is possible that *G. foliifera* and *G. verrucosa* are conspecific and should be referred to *G. tikvahiae* (Bird & Rice 1990, McLachlan 1979). In this thesis the two morphologies were treated as independent species and their old taxonomic nomenclature used (Humm 1979) because of significant differences in abundance patterns within Hog Island Bay. Each of the six native species have wide distribution patterns along the US east coast and co-exist with *C. fragile* in numerous regions (Goshorn et al. 2001, Harlin & Rines 1993, Humm

1979, Schneider & Searles 1991). *Gracilaria* and *Ulva* are cosmopolitan genera, and *Fucus* is cosmopolitan in the northern hemisphere (Lüning 1990). *H. musciformis* and *A. subulata* have been introduced to other regions but without being considered invasive (Perrone & Cecere 1994, Wallentinus 2002). The six species were chosen because they occupy relatively similar habitats to *C. fragile*, and hence were most likely to compete with *C. fragile* for substrate, light and nutrients. To evaluate the success of *C. fragile*, I compared fundamental performance variables to the native species including abundance and distribution patterns (Chapter 2, 3, 6, Appendix 1), likelihood of fragmentation/breakage by hydrodynamic forces (Chapter 3, 4, 6, Appendix 1), survival and growth (Chapter 5, 6, Appendix 1), and recruitment (Chapter 6, Appendix 1). Also, I briefly describe data from less well-defined performance variables, including tissue fragmentation rates, reattachment ability (Perrone & Cecere 1997, Santelices & Varela 1994), and electron transport capacity (Häder et al. 1999, Hader et al. 2000, Kühl et al. 2001) in Appendix 1.

Guidelines

This thesis has seven chapters. This first chapter outlines the conceptual background for the thesis and the working hypotheses. The last chapter synthesizes the findings of the five data chapters, and emphasizes aspects related to the performance of *C. fragile*.

A basic requirement for an alien population to be characterized as invasive is that it is abundant and has a wide distribution in the invaded system. However, virtually nothing is known about macroalgal distribution patterns in Virginia, particularly with regard to

invasive species. Hence the first task of this research was to describe the distribution patterns of macroalgae in Hog Island Bay (Chapter 2: 'Mapping'), and in particular to compare the abundance of *C. fragile* to native species with reference to spatial gradients and temporal cycles. Data presented are the first quantitative distribution data for macroalgae in Virginia. In addition to providing specific information on *C. fragile*, these data will also provide an important baseline for future studies, to assess changes in macroalgal populations with respect to new invasions, anthropogenic disturbances and recolonization of seagrass meadows. In Chapter 2, it is documented that some dominant algae are incorporated onto tube caps of *D. cuprea,* a ubiquitous polychaete. Despite the sympatric distributions of *D. cuprea* and macroalgae along North American coastlines, no study has quantified how this may affect the macroalgal distribution, including the relative success of *C. fragile*. Specific surveys and experiments were conducted to disentangle basic relationships between *D. cuprea* and algal stability, recovery from disturbances, and relative dominance (Chapter 3: '*Diopatra*'). In addition to algae being incorporated onto tube caps, most conspicuous algae are found attached to bivalve shells (Chapter 2, 3). In Chapter 4 I take a biomechanical approach to investigate how substrate type (bivalves vs. tube caps), species type (*C. fragile* vs. native macroalgae) and thallus size (large vs. small) interact to determine attachment strength. This information is used to develop simple allometric models that predict the likelihood of breakage during peak hydrodynamic events. Such thallus breakage feeds the drift algal assemblages, but also increases the likelihood of being transported to adverse habitats, such as high beaches, salt marshes, and the open ocean (Chapter 4: 'Biomechanics'). Only one study has published break forces of temperate lagoon algae, and the data collected for this chapter

fills a gap in the biomechanical literature. In Chapter 5 I take a direct and manipulative approach to test the '*C. fragile* -superiority' hypothesis, by conducting several multi-species and multi-factorial *in situ* tissue performance experiments (Chapter 5: 'Performance'). In particular, I manipulate lagoon characteristics (the invaded system) that have been suggested to influence performance of *C. fragile* (the invader), including light and nutrient levels, grazer densities, sedimentation levels, and positions at different elevations and distances from the mainland. These data indicated that long-term experiments with entire individuals, not fragments, could provide clues to the invasive success of *C. fragile*. I then conducted an experiment testing invasiveness, i.e. the recruitment of *C. fragile* compared to native species onto barren substrate around oyster reefs and under different levels of drift algae accumulations and sediments (Chapter 6: Recruitment). This experiment ran for one year and is one of very few studies to manipulate ecological processes on oyster-reef assemblages, in particular emphasizing the success of invasive macroalgae.

Hypothesis

Based on the background information the following working hypothesis was created: *C. fragile has high abundance and superior performance compared to native macroalgal species, particularly under conditions typical for shallow soft bottom turbid lagoons.*

This hypothesis was tested by comparing *C. fragile* to native species under similar conditions and exposing them to identical treatments. Each chapter treats a different ecological aspect of importance in determining the success of macroalgae in Hog Island

Bay. Note that this *C. fragile*-oriented approach is not necessarily as dominant in the chapters where the emphasis is on assemblage patterns or numerically dominant taxa. The following is a brief description of the questions and hypothesis addressed in each chapter.

Chapter 2. Several fundamental spatio-temporal lagoonal characteristics cause biotic variability, including differences in distances from the mainland, vertical differences in elevation, seasonal variation, annual variation, and different types of substrates. How do these factors affect the abundance and distribution of *C. fragile* compared to native species? *H_1: C. fragile is more abundant and more widely distributed in space and time within Hog Island Bay compared to native species.*

Chapter 3. In many soft bottom lagoons, polychaetes act as active facilitators by maintaining algal gardens, potentially controlling the success of associated organisms. Along North American coastlines, *Diopatra* spp. can be very abundant. How does this worm affect the abundance of macroalgae, including *C. fragile*? *H_1: C. fragile is facilitated by Diopatra compared to native species, by being abundant on its tube caps and by being preferentially incorporated.*

Chapter 4. In soft bottom lagoons unconsolidated bivalve shells, consolidated reef-structures and polychate tube caps provide hard substrate islands for macroalgal attachment that reduce algal advection by tidal currents and storm waves. How does attachment type influence the stability, fragmentation and dislodgment of *C. fragile*

compared to native species? *H_1: C. fragile resists water forces better than native species, both when attached to tube caps and to bivalve shells.*

Chapter 5. Tidal soft bottom lagoons are characterized by high levels of sedimentation, intertidal desiccation, turbidity, molluscan abundance, and nutrient gradients. How do these factors affect short-term performance of *C. fragile* compared to native species, and do they interact with spatial location, which is characterized by predicable differences in nutrient and light levels? *H_1: Compared to native species C. fragile has higher growth rates, under low and high levels of mud snail densities, nutrient concentrations, light levels, desiccation levels, sedimentation, and at all sites along the distance-from-mainland gradient.*

Chapter 6. Oysters reefs facilitate high diversity and productivity in soft bottom lagoons by providing hard substrates for recruiting sessile organisms. However, increased burial by sediments or drift algal mats may threaten recruiting oysters and associated sessile organisms. Is *C. fragile* an efficient recruiter on oyster reefs, and do a cover of drift algae or sediments affect recruitment of *C. fragile* compared to native species? *H_1: C. fragile have higher recruitment than native species, including under algal mats and shallow sediments.*

Chapter 1. Tables

Table 1.1. Species of main interest, arranged from lowest SV ratio (*C. fragile*) to highest (*Ulva*).

Species	Order	Form group	Comment
Codium fragile (Sur) Harriot	Green	Coarsely branched	Invader
Fucus vesiculosus L.	Brown	Thick leathery	
Agardhiella subulata (C. Ag.) Kraft et Wynne	Red	Coarsely branched	Relatively unstudied
Gracilaria foliifera (Forsskal) Boergesen	Red	Coarsely branched	Potentially *G. tikvahiea*
Gracilaria verrucosa (Hudson) Papenfuss	Red	Coarsely branched	Potentially *G. tikvahiea*
Hypnea musciformis (Wulfen) Lamouroux	Red	Coarsely branched	Mainly epihytic/entangled
Ulva curvata (Kutzing) De Toni	Green	Sheet-like	Oppertunistic, ephemeral

Chapter 1. Figures

Fig. 1.1. Hog Island Bay (encircled) within the Virginia Coast Reserve on the Delmarva Peninsula. The 12 locations sampled in Aquatic Plant Monitoring Program is inserted (Chapter 2). Of these C1, S1 and H1 sites were revisited in Chapter 3, 5, and 6.

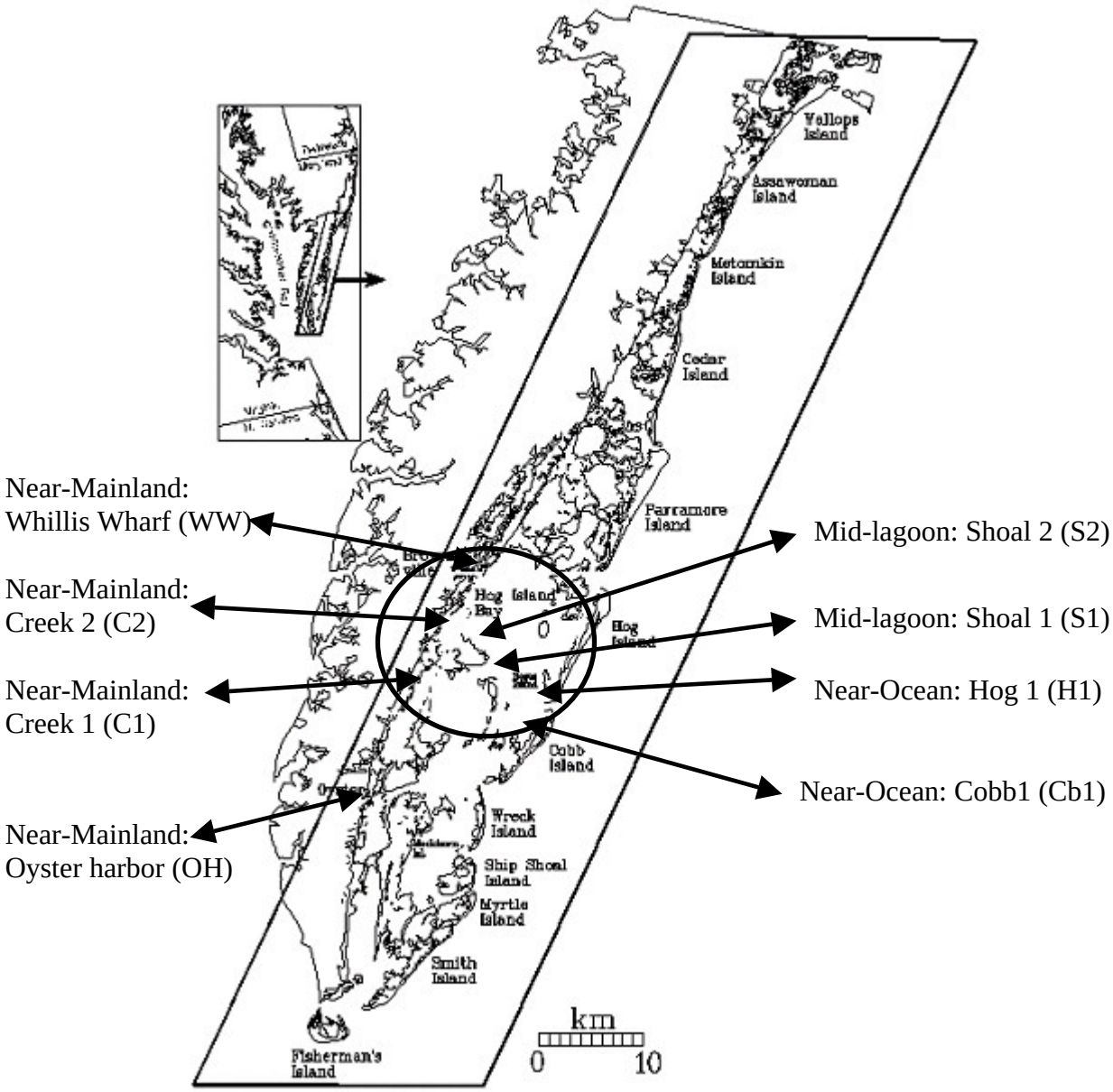
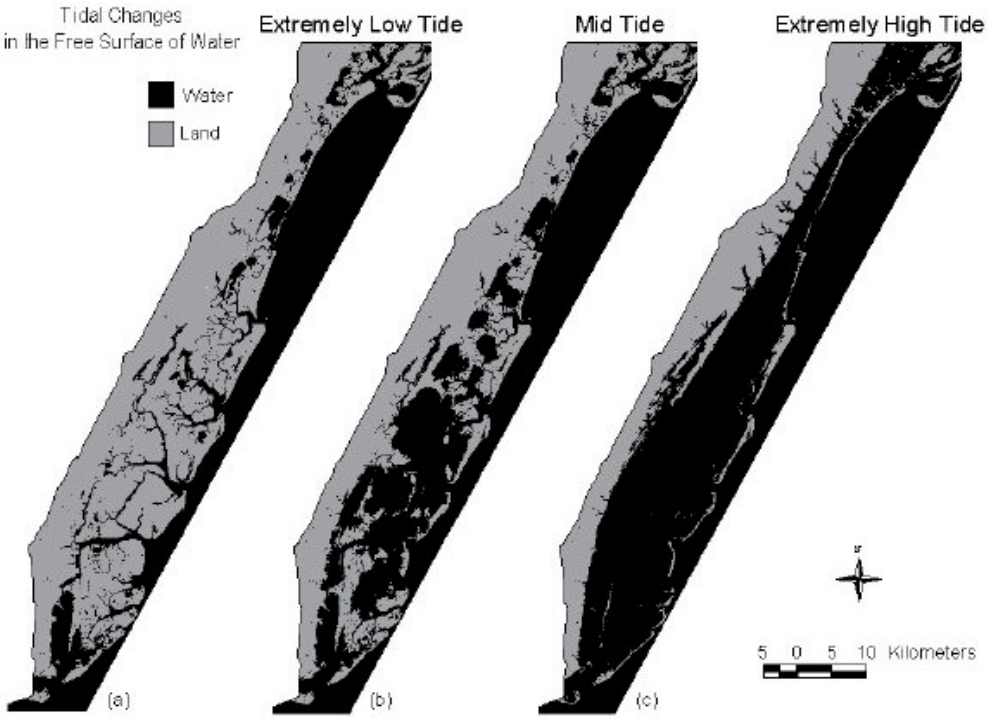


Fig. 1.2. Extreme water level differences in Eastern Shore barrier island lagoons. Maps from Hayden et al. (2000).



Chapter 2. Interaction of spatio-temporal gradients determines macroalgal distribution patterns in a shallow, soft-bottom lagoon

Abstract

Benthic algae and seagrasses typically dominate primary production in shallow coastal ecosystems. Despite their importance, we know relatively little about the temporal and spatial variability of macroalgae from soft-bottom habitats. The study area, Hog Island Bay, Virginia, was once a clear water seagrass and oyster-dominated lagoon, but as a result of storms and diseases it is currently dominated by benthic algae. From 1998 to 2002 we conducted 27 surveys of macroalgal biomass and species composition at 12 permanent sites. The red coarsely branched algae *Gracilaria verrucosa* was dominant, constituting 78% of the total biomass, and an additional 15% was accounted for by *Ulva curvata*, *Bryopsis plumosa*, and *Codium fragile* ssp. *tomentosoides*. *C. fragile* is an alien species that has been in Virginia for ca. 30 years. Taxonomic richness and total biomass were determined according to five test factors: attachment type, elevation relative to sea level (intertidal vs. subtidal), distance from the mainland, season, and annual variation. The biomass of attached and unattached algae was similar (17-19 gDW m^{-2}). However, taxonomic richness was higher for the attached algae, probably because attached algae are more stable, less often exported to stressful habitats, and can accumulate an epiphytic flora. Subtidal sites had higher richness and biomass than intertidal sites, presumably due to lower desiccation stress. Near-mainland and back-barrier island sites had low richness and biomass whereas mid-lagoon sites had high richness and biomass. Both richness and biomass peaked in the summer months when temperature and light availability were highest. In a separate, smaller survey we found that 70% of attached macroalgal thalli, particularly *G. verrucosa* and *U. curvata*, were incorporated into the tube caps of the polychaete *Diopatra cuprea*, suggesting that *D. cuprea* facilitates algal establishment. In

spite of low biomass and a patchy distribution, *C. fragile* was the fourth most abundant species in Hog Island Bay. *C. fragile* was not found attached to the *D. cuprea* tube caps, and the lack of this association may limit expansion of *C. fragile* within Hog Island Bay. In summary, the Hog Island Bay algal assemblage is taxonomically simple and dominated by a few stress tolerant and ephemeral algae. In addition, distribution patterns were to a large extent determined by a few, readily quantified, important spatio-temporal factors: distance from mainland, elevation, season and attachment type.

Introduction

Shallow lagoons are important land-margin ecosystems worldwide, constituting at least 14% of the world's coastline (Cromwell 1973). These shallow soft-bottom systems offer extensive euphotic areas for aquatic macrophytes such as seagrasses and macroalgae (Boynton et al. 1996, Hauxwell et al. 2001, Norton & Mathieson 1983, Sand-Jensen & Borum 1991), and differ from deep estuaries that typically have a restricted littoral zone. Many types of shallow littoral systems, such as seagrass beds and rocky macroalgal communities, have been well-described in relation to multiple spatial and temporal gradients and often show predictable zonational and successional patterns (Lewis 1964, Stephenson & Stephenson 1949). Multi-factorial approaches used to investigate rocky algal beds (Menge 1978, Underwood 1981a, Underwood & Jernakoff 1984) have less commonly been applied to distribution patterns of soft-bottom algal communities. These communities have typically been described with respect to one or two factors, e.g. seasonal variation (Cecere et al. 1992, Virnstein & Carbonara 1985), grazing (Rowcliffe et al. 2001), currents (Salomonsen et al. 1999, Salomonsen et al. 1997), waves and

nutrients (Pihl et al. 1996, Pihl et al. 1999), and nutrient levels or distance from a nutrient source (Castel et al. 1996, McComb & Humphries 1992, McGlathery 1992, Raffaelli et al. 1989, Taylor et al. 1995a, Taylor et al. 1995b). In the present study, our main objective was to describe the distribution of macroalgae in a soft-bottom system within a framework of multiple spatio-temporal factors (Keddy 1991). The factors we addressed included a horizontal distance-from-mainland gradient, a vertical elevation gradient, seasonal cycles, annual variation and different attachment types. This approach allowed us to generate hypotheses about what underlying biotic and abiotic factors are important in determining macroalgal distribution and abundance in soft-bottom lagoons.

Seagrasses and low density algal mats are important habitats for benthic fauna, providing nursery grounds for fish, substrate for attachment for invertebrates, shelter from predation, an abundant food supply, and amelioration of adverse stresses such as high current velocities and intertidal desiccation (Norkko 1998, Norkko et al. 2000). Along the Atlantic coast of North America, from Rhode Island to Texas, extensive barrier-island-lagoon complexes dominate the coastal environment. Drift algal mats have become increasingly abundant in these systems over the last 50 years, primarily in response to nutrient enrichment, and have had a negative impact on the productivity and distribution of seagrass meadows (Hauxwell et al. 2001, Lee & Olsen 1985, Taylor et al. 1995a, Taylor et al. 1995b). Because these two groups of aquatic plants have different environmental requirements, structural characteristics and ecosystem properties (Duarte 1992, 1995), it is important to know their relative distributions and dynamics. There have been several studies reporting changes in submerged aquatic plants in lagoons along the northern and southern U.S. Atlantic coast (e.g. Cowper 1978, Hauxwell et al. 2001,

Thorne-Miller et al. 1983, Virnstein & Carbonara 1985), yet little is known about mid-Atlantic systems. The only published data about algal distributions in Virginia lagoons are presence-absence or qualitative dominance studies (Connor 1980, Humm 1979, Rhodes 1970, Wulff & Webb 1969) or are reported in the non-refereed literature (Goshorn et al. 2001, Monti 1993). Thus, our secondary objectives were (1) to fill this gap by providing a quantitative description of macroalgal distribution patterns from Hog Island Bay, a part of the Virginia Coast Reserve and U.S. Long Term Ecological Research Network (VCR/LTER) (Franklin et al. 1990), and (2) to establish a baseline data set with which to track and evaluate future plant community changes. The VCR lagoons may be in transition from an algal-dominated system following the local extinction of seagrasses in the 1930's to a seagrass-dominated system. The return of seagrasses is the result of both natural recolonization and restoration efforts (R. Orth, personal communication), and is likely to result in dramatic changes in biogeochemical cycling and faunal communities.

In addition to eutrophication, overfishing, destruction of wetlands, and increased sediment load, many lagoons and estuaries have been invaded by alien species. These invasions have potentially large impacts on biodiversity and ecosystem functioning on local, regional and global scales (Ruiz et al. 1997, Ruiz et al. 1999). Our final objective was to screen the monitoring data for alien algal species and to provide a baseline for evaluation of future invasions. The alien macroalga *Codium fragile* ssp. *tomentosoides* (Chapman 1999, Trowbridge 1996b) has been present in Virginia for ca. 30 years (Hillson 1976), and special attention was paid to the distribution patterns of this species. Such analyses of species-specific distribution patterns can potentially provide insight into

invader traits, invasion effects and management and control (Rejmánek & Richardson 1996).

Methods

Study site and gradients

Hog Island Bay is located within the Machipongo drainage basin on the Delmarva Peninsula, and is ca. 100 km^2 in area. Intertidal *Spartina alterniflora* marshes border the bay on the mainland side and on the leeward side of the barrier islands. Most of the bay is soft-bottom sands and muds; unconsolidated bivalve shells, scattered relict oyster reefs, and *S. alterniflora* stems provide hard substrate for sessile organisms. There is little bathymetric complexity, except for a single deep channel. The average water depth is 1.5 m, 37% of the lagoonal surface area is intertidal and 81% is less than 3 m deep (Oertel 2001). The semidiurnal tidal range is ca. 1.5 m (Oertel 2001), although storm surges can add at least an extra meter of water (pers. obs.). Tidal currents reach 2 m s^{-1} in the inlets between the barrier islands (Oertel et al. 2000), but peak currents within the bay are generally 0.05-0.70 m s^{-1} (Lawson 2003). Light extinction in the water column is high ($k \approx 2$ m^{-1}) but varies across the lagoon, largely as a result of wind-driven sediment resuspension (Lawson 2003, McGlathery et al. 2001). There is a gradient of decreasing dissolved nutrients and total suspended solids with increasing distance from the mainland (Lawson 2003, McGlathery et al. 2001, Tyler et al. 2001). Air temperature varies seasonally from ca. –5 to 35°C and water temperature from ca. 2 to 27°C (VCR/LTER unpublished data). Salinity ranges from ca. 28 to 34 ppt. within the bay, but is relatively constant throughout the year (VCR/LTER unpublished data).

VCR/LTER Aquatic Plant Monitoring Program

Twelve permanent sites were established in Hog Island Bay in summer 1998. There were 6 near-mainland sites, 2 mid-lagoon sites, and 4 near-ocean back-barrier island sites. This distribution of sites represents the distance from mainland gradient (DIS). The sites were further separated as 8 subtidal and 4 intertidal sites, which are used to represent the elevation gradient (ELE). All sampling was conducted on low-slope muddy substrate. Twenty seven surveys were conducted from June 1998 to November 2002, with the lowest sampling frequency in winter and highest in summer. The 12 sites were reduced to three representative subtidal sites (C1, S1 and H1, Table 2.1) during the last 14 surveys. For each survey, macroalgae were collected in 6 random replicates per site using 0.15 m^2 cores and separated *in situ* into attached and unattached groups (= attachment type, ATT). Attached algae were classified as thalli that presented a resistance to a pull and/or were attached to a bivalve shell, although specific attachment types were not recorded. The samples were separated into different taxa in the lab, rinsed in deionized water, and the dry weight was determined after lyophilization. A few inconspicuous and rare taxa were only determined to genus or form-group. These groups were treated as separate taxonomic units in our analysis.

Data analysis

In addition to the spatial patterns (DIS, ELE) and attachment type (ATT), the data were analyzed based on two scales of temporal variability, annual (ANN) and seasonal (SEA). Attached and unattached algae from the same core were treated as statistically independent samples because attached algae were separated vertically (closest to the

sediment surface) and decoupled temporally (not drifting with the tides) from unattached algae. ANOVA analyses were conducted on total algal dry weight, taxonomic richness and *C. fragile* dry weight using fixed-factor type III Sum of Squares (SPSS 8.0). The ANOVAs were performed both as full 5-factorial and as 5 single factor-ANOVAs, the former representing the most complex and the latter the simplest approach to evaluate factors of potential importance. All analyses were performed on Log(x+1) transformed data to reduce variance heterogeneity, and in particular to reduce the statistical influence of large outliers. Inspection of box-plots of raw data and with various transformation types showed that logarithm transformation most efficiently reduced variances, even though they remained heterogeneous ($p < 0.05$, Levines test) for all ANOVAs except for annual variability vs. Log(biomass). To arrange significant factors according to relative importance within an ANOVA, η^2 was calculated (Levine & Hullet 2002, Welden & Slauson 1986). Significant results should be interpreted conservatively because p-values could be biased due to uneven sampling design (except for the attachment factor), heterogeneous variances, and spatio-temporal autocorrelation effects (Underwood 1981b). Graphical analysis was used to suggest specific treatment effects following significant single-factor results. This approach was preferred over unplanned multiple statistical comparisons because the large sample size was likely to detect statistical differences, even if treatments would not be different in an ecological context. Also, to investigate if the dominant species had similar general distributions, a Pearson correlation matrix was calculated including total biomass, taxonomic richness and the biomass of each of the 12 most abundant species. Again, p-values should be interpreted with caution because of non-normal distributions.

Attachment survey

As a supplement to the monitoring program, we described the algal attachment types in more detail during April – November 2002, using the following categories: 1) loose, 2) partly buried, 3) incorporated into tube caps of the polychaete *Diopatra cuprea*, 4) attached to unconsolidated bivalve shells, 5) epiphytic on or 6) entangled around a basiphyte. We sampled 441 individuals from 17 soft-bottom sites, including the 12 sites from the main survey. Individual thalli were selected randomly at each site and the species and attachment type determined *in situ*. A X^2-contingency test was used to investigate if different algal species were attached to different categories in the same proportions. Species-substrate combinations observed less than five times were omitted to fulfill X^2-test assumptions.

Results

VCR-LTER Aquatic Plant Monitoring Program

The macroalgal assemblage in Hog Island Bay was species-poor and dominated by a few key taxa with relatively high biomass. The dominant species, *Gracilaria verrucosa*, was found in approximately one third of all samples and accounted for 78% of the total macroalgal biomass (Table 2.2). Together with *G. verrucosa, Ulva curvata, Bryopsis plumosa*, *C. fragile* and *Ectocarpus* spp. accounted for 95% of the total biomass. Eighteen other taxa were sampled in the 27 surveys, but most with few number of observations (Table 2.2).

Species richness

The 5-factorial ANOVA that tested effects on taxonomic richness produced 21 significant factor-combinations (Table 2.3). Because the 5-factorial and 2 of the 4-factorial combinations were significant, lower order interactions and single factor effects should be evaluated with caution. However, the significant factors and combinations that explained of the greatest proportion of the data-variability (>2% of the sum of squares) were of a lower order: DIS, ATT, DIS*ANN, SEA*ANN, and DIS*SEA*ANN. The temporal variations (SEA, ANN) were mainly important in interaction terms, but distance (DIS) was important both as a single factor and in interaction with the temporal factors. Thus, although numerous other factor combinations were significant, they were of relatively low importance. Elevation in particular explained a small proportion of the sum of squares. Species richness peaked at 4-6 taxa per sample in the summer months, particularly at mid-lagoon sites for both attached and unattached samples (Fig. 2.1). Temporal patterns were less clear for the low diversity back-barrier and near-mainland sites, which generally had 0-3 taxa per sample. All single factor ANOVAs were highly significant (Table 2.4) indicating that each test factor influenced species richness. The highest taxonomic richness was found in attached forms (ATT), in the subtidal zone (ELE), at mid-lagoon sites (DIS), during spring-summer (SEA) and during the last two sampling years (ANN) (Fig. 2.2).

Total biomass

Sixteen factor-combinations were significant for biomass, with the most important being DIS, SEA*ANN, and DIS*SEA*ANN which each explained 2-5% of the sum of squares (Table 2.3). Biomass, like species richness, was determined primarily by the distance

from the mainland and the temporal variations. Again, elevation and combinations including elevation were the least important factors. The greatest biomass was observed for unattached drift algae at mid-lagoon sites during summer months (2-300 gDW m^{-2}), although attached biomass also had a single pronounced peak at this site in summer 1999 (400 gDW m^{-2}; Fig. 2.3). Biomass was low at other sites and during the fall to spring months (0-30 gDW m^{-2}), except for two separate, but relatively small, summer blooms of unattached algae at the near-mainland sites (ca. 100 gDW m^{-2}). All single factor ANOVAs were highly significant (Table 2.4), indicating that each test factor influenced the accumulation of macroalgal biomass. Biomass was the highest in the subtidal zone (ELE), at mid-lagoon sites (DIS) and in summer months (SEA; Fig. 2.4). Although there were significantly more algae attached (19 gDW m^{-2}) than unattached (17 gDW m^{-2}) and more at year 2 (21 gDW m^{-2}) than year 1 (15 gDW m^{-2}) these small differences are probably of minor ecological importance (Fig. 2.4).

Biomass of *Codium fragile*

Although *C. fragile* was the fourth most abundant species (Fig. 2.5A, Table 2.2), it occurred as a few large and patchily distributed individuals. *C. fragile* accounted for ca. 4% of the total biomass and was only found in 27 samples. The 5-factorial ANOVA showed a single significant effect of season, which explained less than 1% of the data variability (Table 2.3). On the other hand, each of the single factor ANOVAs was highly significant, although they only explained a very small proportion of the data variability (Table 2.4). *C. fragile* was predominantly unattached (ATT), in the subtidal zone (ELE) and at mid-lagoon and back-barrier sites (DIS) (Fig. 2.4B-Q). In particular, *C. fragile* was

relatively important at back-barrier sites, being the most dominant species following *G. verrucosa* (Fig. 2.5O). *C. fragile* was not found in surveys near the mainland or on intertidal mudflats, but was occasionally observed in these habitats as ephemeral drift material (pers. obs.). *C. fragile* was most common in the summer months (SEA) and in years 3 and 4 (ANN). Even though *C. fragile* was not found during the winter surveys, it was, on rare occasions observed as reduced individuals (pers. obs.).

Species-specific correlation

Biomass and richness were significantly correlated with each other and with the 12 most important species in Hog Island Bay, although these only explained 1% of the sum of squares (r^2) for *Enteromorpha* spp. and *Hypnea musciformis* (Table 2.5). All of the 68 significant correlations (out of 90 combinations) were positive, suggesting similar responses to the ambient environmental conditions and that the likelihood of finding a species in a sample typically increased with the likelihood of finding any other species. *G. verrucosa* biomass was significantly correlated to most of the other species and explained 92% of the biomass data variability and 42% of the richness variability, emphasizing the key status of this species. *C. fragile* had significant correlations (arranged by highest r^2) with *Agardhiella subulata*, *U. curvata*, *G. verrucosa*, *B. plumosa*, *Ceramium* spp., *G. foliifera*, and *Polysiphonia* spp. These correlations, however, only explained from <1 – 6 % of the data variability. The species *B. plumosa*, *Ectocarpus* spp., *Polysiphonia* spp., *Ceramium* spp., *Champia parvula* and *H. musciformis* were only found unattached or epiphytic (primary attached, reattached or entangled) on *G. verrucosa*, *U. curvata*, *C. fragile* or *Fucus vesiculosus*.

Secondary species dominance

Even though *G. verrucosa* was dominant along all test-factors, there are interesting secondary dominance patterns across the test gradients (without *G. verrucosa*, Fig. 2.5). Among the different years of the study, we observed dominance by *U. curvata* and *B. plumosa* in year 1, even dominance among several species in year 2, *C. fragile* in year 3, *U. curvata* in year 4 and *B. plumosa* in year 5 (Fig. 2.5B-F). Seasonally, the secondary dominance patterns were as follows: (1) *Ectocarpus* spp. and *U. curvata* were particularly common in winter and spring months (Fig. 2.5J and G), (2) summer samples were dominated by *U. curvata*, *B. plumosa* and *C. fragile* (Fig. 2.5H), and (3) fall samples were dominated by *U. curvata* and *A. subulata* (Fig. 2.5I). Spatially, the secondary dominance patterns showed that the three most common taxa in the subtidal zone were *U. curvata*, *B. plumosa* and *C. fragile* whereas in the intertidal zone it was *U. curvata*, *B. plumosa* and *Ectocarpus* spp. (Fig. 2.5K, L). Near-mainland sites consisted mainly of *U. curvata* and *Ectocarpus* spp. (Fig. 2.5M), mid-lagoon sites had high abundance of *U. curvata* and *B. plumosa* (Fig. 2.5N), and back-barrier sites had high abundance of *C. fragile* and *B. plumosa* (Fig. 2.5O). Finally, attached assemblages were dominated by *U. curvata*, *B. plumosa*, *Ectocarpus* spp. and *A. subulata* (Fig. 2.5P), whereas unattached assemblages were dominated by *U. curvata*, *B. plumosa* and *C. fragile* (Fig. 2.5Q). It should be noted that the 'attached' *B. plumosa, Ectocarpus* spp., *Polysiphonia* spp., *Ceramium* spp., *C. parvula* and *H. musciformis* were found only as epiphytes on attached basiphytes.

Attachment survey

Algae were present on mudflats with different attachment types (i.e. algae and attachment types were not distributed in equal proportions, p = 0.000, n = 433, X^2 = 1014, Df = 45). *G. verrucosa* and *U. curvata* constituted ca. 85% of the species observations. *C. fragile* was overall the sixth most abundant species, following *G. verrucosa*, *U. curvata*, *Enteromorpha* spp., *F. vesiculosus*, and *A. subulata*. Seventy percent of all algae were attached to worm tubes, 10% were unattached, and 10% were attached to unconsolidated bivalve shells. Buried, epiphytic and entangled algae were rarely encountered in this survey. Of the 309 algae found attached to *D. cuprea* tube caps, *G. verrucosa* and *U. curvata* constituted 98%. *C. fragile* was observed unattached 4 times and attached to unconsolidated bivalve shells 5 times.

Discussion

Effects of macroalgal mats in lagoons

The quantification of the macroalgal assemblage in Hog Island Bay is ecologically and economically important. Dense macroalgal accumulations can have negative consequences by (1) creating anoxia when algal mats collapse and decompose, (2) altering the diversity and community composition of benthic infauna and epifauna, (3) out-competing seagrasses, (4) fouling trawl nets, (5) reducing performance of maricultured bivalve spat, (6) reducing waterway access and clogging boat motors (7) and creating foul smells and beach debris (Fletcher 1996, Hauxwell et al. 2001, Holmquist 1997, Nelson & Lee 2001, Norkko & Bonsdorff 1996b, Raffaelli et al. 1998). On the other hand, where algae are present in lower densities, they typically have a

positive influence, including: (1) acting as a temporary 'filter' for land derived nutrients, (2) creating habitats for invertebrates and fish, (3) providing protection from predators, (4) providing an abundant food supply for grazers, and (5) providing a mechanism for dispersal (Duffy & Hay 1991b, Holmquist 1994, McGlathery et al. 2001, Norkko et al. 2000, Raffaelli et al. 1998, Tyler 2002). Overall algal biomass in Hog Island Bay was patchy and primarily at low densities. However, the summer biomass peak, which is typical in temperate systems (Humm 1979, Lüning 1990), at the mid-lagoon sites, occasionally 'crashed' and were followed by areas of anoxia and the associated negative impacts listed previously (McGlathery et al. 2001, Tyler et al. 2001, 2003).

Species patterns

The patterns of macroalgal distribution that we describe are restricted to the shallow, soft-bottom portion of the lagoon; marsh areas, deep channels and oyster reefs may have different patterns of biomass and species richness, although the species pool is the same (pers. obs.). The species richness values of 20-30 species found in Hog Island Bay are typical of soft bottom lagoonal systems (Cecere et al. 1992, Cowper 1978, Fletcher 1996, Thorne-Miller et al. 1983). Likewise, the species assemblage, a mixture of filamentous and sheet-like opportunistic and coarsely branched and thick leathery perennial taxa, was similar to observations from other western mid-Atlantic systems (Connor 1980, Goshorn et al. 2001, Rhodes 1970, Wulff & Webb 1969, Wulff et al. 1968, Zaneweld & Barnes 1965). *G. verrucosa* was a key species explaining a large proportion of the richness data, typically carrying 1-3 epiphytic algal taxa. Thus, because of its wide distribution pattern, high biomass, high productivity (McLachlan & Bird 1986, Tyler 2002) and its consistent

epiphytic flora, *G. verrucosa* can be considered a foundation species within Hog Island Bay (sensu Dayton 1972). Species that were found year-round (*G. verrucosa*, *A. subulata*, *F. vesiculosus*, *C. fragile*, and *U. curvata*) have perennial life history strategies (Schneider & Searles 1991), with the exception of *U. curvata* which typically has an ephemeral and highly fluctuating appearance (Littler 1980, Sears 1975, Wallentinus 1984). *U. curvata* can, however, survive periods of low light, low temperature and sediment burial and this may facilitate its survival during adverse winter conditions in unattached forms (Vermaat & Sand-Jensen 1987). When attached to bivalve shells, *G. verrucosa*, *A. subulata*, and *C. fragile* were mainly found at reduced size during the winter months (pers. obs.), suggesting winter fragmentation and/or a pseudo-perennial life style (Fralick & Mathieson 1972, Sears 1975). *B. plumosa* and *Ectocarpus* spp. were clearly the most important filamentous taxa, with the latter being the dominant in spring and winter months, in the intertidal and at near-mainland sites. Although *Ectocarpus* spp. is a well-known bloom-forming algae, it is less common to observe *Bryopsis* blooms in temperate systems (Fletcher 1996, Morand & Briand 1996, Raffaelli et al. 1998).

Spatio-temporal gradients

In Hog Island Bay, the hydrodynamic regime provides a unifying framework for generating hypotheses about large-scale patterns of species distribution and abundance. First, the lunar cycle sets the stage for a vertical tidal wave with differences in inundation time and amount of overlying water. This will have an effect on light availability, sedimentation and grazing. Second, a horizontal tidal wave of nutrient-poor oceanic water from the inlet coupled with inputs of nutrient-enriched groundwater from the

mainland, results in a gradient in water residence times and nutrient availability. This will also be reflected in other water quality parameters (e.g., turbidity, light penetration, temperature, and sedimentation levels). Third, storm waves entrain unattached, buried and tube cap incorporated algae, and currents transport them in the lagoon, where they potentially can re-attach (Brenchley 1976, Santelices & Varela 1994). The interaction between tidal currents and attachment types can result in daily changes in the algal assemblages. Because nearly 50% of the algal community consisted of unattached forms, distribution patterns in Hog Island Bay can change dramatically within a tidal cycle and after storm events, as observed in other drift algae communities (Flindt et al. 1997a, Holmquist 1994, Salomonsen et al. 1999). Finally, storm-induced disturbances potentially create seasonal and annual differences in algal export rates (export areas include deep channels, high beaches, high marshes and the open ocean). Thus, if low-energy low-export years coincide with favorable growth conditions (e.g. high light and temperature), algal biomass is likely to accumulate in dense mats with increased risk of localized anoxia. This emphasizes that Hog Island Bay should be viewed as a dynamic algal system where currents and storms constantly relocate, import and export algal biomass.

Within the lagoon, we documented that 2 spatial gradients (DIS, ELE), 2 types of temporal variability (SEA, ANN) and attachment types (ATT) significantly affected the distribution and abundance of macroalgae, and that these factors interacted, particularly due to seasonal and annual variations. Elevation was considered relatively unimportant based on the 5-factorial ANOVAs but this could partly be caused by the lack of intertidal

mid-lagoon sites. Typical interpretations of the single factor effects would suggest that significant effects mainly were caused by differences in nutrients (along DIS, Castel et al. 1996, Flindt & Kamp-Nielsen 1997, McGlathery 1992, Tyler et al. 2001), desiccation (along ELE, Doty 1946, Dring & Brown 1982, Dromgoole 1980), hydrodynamic forces (along ATT, SEA and ANN, Lenihan 1999, Phillips et al. 1997, Pihl et al. 1999, Salomonsen et al. 1997) and light and temperature (along SEA and ANN, Connor 1980, Goshorn et al. 2001, Wolfe & Harlin 1988). However, because of covariation of these factors along the gradients, controlled manipulative experiments are clearly needed to demonstrate causation. For example, sedimentation and light co-vary with nutrient concentrations along the distance gradient (Airoldi 2003), sedimentation, grazing, light, and temperature co-vary with desiccation along the elevation-gradient (Lewis 1964), and abrasion and nutrient encounter rates co-vary with hydrodynamic forces along the attachment gradient (Hurd 2000).

The shallow portions of the lagoon can be divided into ‘low diversity-low biomass’ regions near the mainland and back-barrier islands and ‘high diversity-high biomass’ mid-lagoon regions. The three main environmental conditions that vary along this gradient include light availability (highest water visibility near back barrier island sites), nutrient availability (highest concentrations near mainland sites) and abrasion and burial by suspended solids (highest concentrations near mainland sites) (Lawson 2003, McGlathery et al. 2001). Most macroalgae could thus be limited by light and sediment abrasion/burial at near-mainland sites (Lawson 2003, McGlathery et al. 2001) and nutrients at near-ocean sites (McGlathery et al. 2001, Tyler et al. 2001), particularly in

summer months when the growth potential is highest (Tyler 2002). In comparison, mid-lagoon sites with intermediate levels of these limiting factors should have relatively benign growth conditions. *G. verrucosa* and *U. curvata* are frequently the dominant species in US east coast lagoons (Goshorn et al. 2001, Thorne-Miller et al. 1983). Because these two species were found most commonly incorporated into *D. cuprea* tube caps (this study, Mangum et al. 1968, Myers 1972), we suggest that this association is a neglected factor that potentially can structure benthic primary production and assemblage structure/stability in *D. cuprea*-algal dominated west-Atlantic lagoons (Bell & Coen 1982b, Luckenbach 1986, Woodin 1978).

Potential for seagrass recolonization

Species-poor soft-bottom drift algal associations are well known worldwide, and often are relatively similar to the Hog Island Bay assemblage in that they are dominated by a few red and green algae (e.g. Cecere et al. 1992, Cowper 1978, Fletcher 1996, Lowthion et al. 1985, Peckol & Rivers 1995, 1996, Pihl et al. 1996, Sfriso et al. 1992, Thorne-Miller et al. 1983, Virnstein & Carbonara 1985). In several of these studies, seagrasses were present in high quantities indicating that coexistence is possible as long as major anoxia and shading are avoided (Hauxwell et al. 2001). This is an important condition if *Zostera marina* should reestablish in Hog Island Bay (Goshorn et al. 2001, VCR/LTER unpublished data). We speculate that the large and consistent summer biomass accumulations at mid-lagoon sites could influence seagrass reestablishment in this region. If unattached and attached samples were pooled, as done in aforementioned lagoon studies, ca 10% of the samples would contain more than 100 gDW m^{-2}, with a maximum

of 1807 gDW m^{-2}. This indicates that Hog Island Bay does at certain times and sites have high macroalgal densities, primarily at mid-lagoon sites, but also occasionally as patchy and ephemeral drift accumulations at near-mainland and back-barrier sites. However, given that these blooms occur in localized patches in Hog Island Bay (McGlathery et al. 2001), we believe that the potential for seagrass recolonization is high provided that eutrophication does not accelerate appreciably in the region (Goshorn et al. 2001). Nutrient inputs to the lagoon via groundwater and atmospheric deposition are impacted by human activities such as agriculture and development (Stanhope 2003), however overall loading rates are low relative to northern lagoons on the Delmarva Peninsula (Boynton et al. 1996, Goshorn et al. 2001, Stanhope 2003). The rapid turnover of nutrients in the sediments and the low, but steady supply of water column nutrients provided by tidal currents are probably the mechanisms that currently support the localized macroalgal blooms (McGlathery et al. 2001).

Distribution of *Codium fragile*

C. fragile ssp. *tomentosoides* originates from the North West Pacific Ocean, but has in the last century dispersed to the East Pacific-, Southern-, East Atlantic-, and West Atlantic-Oceans, probably using ship-hulls and imported oysters as vectors (Trowbridge 1998). *C. fragile* appeared in the East Atlantic in the late 1950s (Bouck & Morgan 1957) and probably arrived in Virginia in the 1970s (Hillson 1976). Thirty years after it arrival, *C. fragile* could be considered a successful invader in Hog Island Bay based on its relative dominance, although absolute biomass remains low. It is interesting that *C. fragile* was less common in a large-scale macroalgal survey in adjacent lagoons north of

Hog Island Bay (Goshorn et al. 2001), although details in the sampling procedures and results of this study are unclear. All introduced species have some community and ecosystem impacts (Carlton 1996b, Carlton 1999). However, the low biomass of *C. fragile* in Hog Island Bay and the northern lagoons suggest relatively small effects on larger spatio-temporal scales, particularly compared to other invaded systems where *C. fragile* has formed dense monocultures and large canopies (Begin & Scheibling 2003, Fralick & Mathieson 1973, Mathieson et al. 2003). We suggest that *C. fragile* was most abundant in subtidal mid-lagoon and back-barrier sites because shell-substrates, a necessity for recruitment (Borden & Stein 1969, Fralick & Mathieson 1973, Malinowski & Ramus 1973), are relative abundant and that recruits probably experience less frequent sediment burial compared to near-mainland sites. The lack of *C. fragile* in the high intertidal zones and in winter months may be caused by low desiccation resistance and winter fragmentation (Fralick & Mathieson 1972). This should be tested by future work coupling the distribution patterns with manipulative growth experiments.

Conclusions

We have provided the first quantitative description of macroalgal distribution patterns from Virginia by using a framework of multiple spatio-temporal test factors. Each of these test factors was important in structuring the algal assemblages. Thus, if algal distribution patterns are to be compared within and between soft-bottom lagoonal systems, our data indicate that attachment types, horizontal and vertical position and seasonal and yearly sampling time at the least should be considered. Despite the large pool of 20-30 species and multiple interacting spatio-temporal gradients, Hog Island Bay

is a simple algal system because *G. verrucosa* constitute most of the biomass, followed by a few common, but sub-dominant taxa (*U. curvata*, *B. plumosa*, *C. fragile*, *Ectocarpus* spp). These patterns were relatively similar to other protected turbid soft-bottom shallow systems. Finally, the only non-indigenous species we found in the system, *C. fragile*, although the fourth most abundant species, was only present with relatively low biomass. Hence, it is unlikely that *C. fragile* has had major effects at the ecosystem level.

Chapter 2. Tables

Table 2.1. Characteristics of 12 study sites (mudflats). Subtidal (S) sites are from 0.7-1 m below mean sea level and intertidal (I) sites from 0.5-0.2 m. ELE = elevation level, DIS = Distance from mainland, NM = near-mainland, ML = mid-lagoon and BB = back barrier island.

Site name	ELE	DIS	Survey	Comments
Oyster Harbor (OH_s)	S	NM	13	In the harbor of the town Oyster, silt
Willis Wharf (WW_s)	S	NM	13	Near the town Whillis Wharf, creek side next to marsh, silt
Creek 1a ($C1_s$)	S	NM	27	Near Nassawadox, 10 m broad creek, next to marsh, silt
Creek 1b ($C1_i$)	I	NM	13	As $C1_s$
Creek 2a ($C2_s$)	S	NM	13	500 m south of C1, 15 m broad creek, next to marsh, silt
Creek 2b ($C2_i$)	I	NM	13	As $C2_s$
Shoal 1 ($S1_s$)	S	ML	27	Middle lagoon, south of Machipongo channel, open low slope area, oyster reefs within 100 m, sand
Shoal 2 ($S2_s$)	S	ML	13	As Shoal 1 but ca. 1 km closer to the mainland
Hog Island 1a ($H1_s$)	S	BB	27	East of Southern Hog Island, opposite Rogue Island, 100 m to marsh, sand
Hog Island 1b ($H1_i$)	I	BB	13	As $H1_s$, 50 m to marsh
Cobb Island 2a ($H2_s$)	S	BB	13	East of Northern Cobb island, open area, ca. 200 m to sand flats, sand
Cobb Island 2b ($H2_i$)	I	BB	13	As $H2_s$, sand

Sampling dates: June 2-98, July 6-98, August 4-98, October 8-98, January 11-99, March 23-99, May 11-99, June 9-99, July 6-99, August 3-99, October 7-99, February 1-00, March 17-00, May 1-00, June 1-00, July 2-00, August 14-00, October 23-00, February 6-01, April 17-01, June 28-01, July 26-01, August 20-01, October 1-01, February 22-02, June 6-02, November 4-02. The first 13 surveys included all 12 sites but the last 14 only $C1_s$, $S1_s$, and $H1_s$

Table 2.2. Macroalgal taxa recorded in survey. Taxonomic units (B = brown, G = green and R = red algae), abbreviations, mean, standard deviation and maximum biomass per sample (gDW m^{-2}), and number of recordings out of 2476 samples. Some additional taxa were observed a few times outside the sample cores (cf. footnote below).

A. Taxonomic unit	Abr.	Mean	Max	SD	% of Mean	# Obs.
Total biomass	TOT	18.225	1437.0	77.094	100.0	951
[2]*Gracilaria verrucosa* (R)	GRA	14.288	1303.8	65.176	78.4	848
[3]*Ulva curvata* (G)	ULV	1.311	296.5	10.456	7.2	394
Bryopsis plumosa (G)	BRY	0.970	344.3	10.333	5.3	323
[4]*Codium fragile* (G)	COD	0.500	743.5	15.604	2.8	27
Ectocarpus spp. (B)	ECT	0.338	60.2	2.518	1.8	215
[5]*Agardhiella subulata* (R)	AGA	0.297	138.4	3.921	1.6	132
[6]*Polysiphonia* spp. (R)	POL	0.187	33.6	1.685	1.1	167
[2]*Gracilaria foliifera* (R)	FOL	0.109	37.3	1.530	0.6	32
[7]*Ceramium* spp. (R)	CER	0.074	37.4	1.117	0.4	77
Hypnea musciformis (R)	HYP	0.059	129.0	2.647	0.3	29
[8]*Enteromorpha* spp. (G)	ENT	0.037	28.3	0.787	0.2	64
Fucus vesiculosus (B)	FUC	0.017	11.4	0.355	0.1	10
Champia parvula (R)	CHA	0.016	6.0	0.223	0.1	46
Leathesia difformis (B)	LEA	0.007	5.7	0.155	0.0	21
[9]Red filaments (R)	RED	0.004	8.5	0.175	0.0	12
[10]*Punctaria latifolia* (B)	PUN	0.003	3.0	0.073	0.0	16
Gelidium pusillum (R)	GEL	0.003	6.6	0.134	0.0	1
Scytosiphon lomentaria (B)	SCY	0.002	3.3	0.071	0.0	4
Grinnellia americana (R)	GRI	0.001	1.2	0.031	0.0	10
Lomentaria baileyana (R)	LOM	0.000	0.2	0.005	0.0	3
[11]*Cladophora* spp. (G)	CLA	0.000	0.0	0.000	0.0	2
Rhizoclonium spp. (G)	RHI	0.000	0.0	0.000	0.0	1
Dasya baillouviana (D)	DAS	0.000	0.0	0.000	0.0	1

[1]The following taxa were observed, but not sampled, in the surveys: *Ralfsia verrucosa* (inconspicuous, but common on consolidated oyster reefs), *Sargassum natans* (a drift population in summer 1999), *Porphyra* sp. (Mainly *P. umbicalis*, common on high intertidal hard substrate), *Spyridia filamentosa* (a single observation at S1), *Chondria baileyana* (a few observations at back barrier island sites in 2000), *Melobesia membranacea* (on a drift *Zostera marina*), and *Caloglossa leprideurii* (epiphytic on *Spartina alterniflora* stems). [2]The terete *Gracilaria* form is referred to as *G. verrucosa* (Humm 1979, Schneider & Searles 1991) and the flat as *G. foliifera*, although they may be conspecific and potentially should be referred to as *G. tikvahiea* (Bird & Rice 1990, McLachlan 1979). [3]Potentially with a minor component of *U. rotunda* and *Monostroma* sp. [4]ssp. *tomentosoides*. [5]West Atlantic *A. subulata* have been described as *Neoagardhiella baileyi* (Orris 1980), *A. tenera* (Zaneweld & Barnes 1965) and *Solieria tenera* (Humm 1979). But in Schneider and Searles (1991) *S. tenera* is synonym with *S. filiformis* but different from *A. subulata*. Although *S. filiformis* and *A. subulata* cannot be separated based on morphological differences, and have sympatric distributions in Mediterranean lagoons (Perrone & Cecere 1994), *A. subulata* is probably the only species present in Virginia (Searles, personal communication). [6]Mainly *P. denudata* and *P. nigrescens*. [7]Mainly *C. rubrum* and *C. strictum*. [8]Mainly *E. prolifera* and *E. intestinalis*. [9]Mainly *Calithamnium* spp. [10]With a few *Petalonia fascia* inter-mixed. [11]Probably *C. vagabunda*.

Table 2.3. Five-factorial ANOVAs of Log(x+1) transformed taxonomic richness and total and *C. fragile* biomass. Significant results ($p < 0.05$) are in bold. Only one source of variability was significant for *C. fragile* (SEA: $p = 0.02$, $\eta^2 = 0.4\%$, SS = 0.04, F = 3.19) and the ANOVA table for *C. fragile* biomass data therefor omitted.

		Richness				Total Biomass			
Source	**Df**	**SS**	**η^2(%)**	**F**	**p**	**SS**	**η^2(%)**	**F**	**p**
ATT (Attachment type)	1	4.72	3.0	98.00	**0.00**	4.98	1.5	45.54	**0.00**
ELE (Elevation level)	1	0.46	0.3	9.57	**0.00**	0.19	0.1	1.70	0.19
DIS (Distance from mainland)	2	11.57	7.5	120.03	**0.00**	11.20	3.5	51.27	**0.00**
SEA (Seasonal changes)	3	0.46	0.3	3.18	**0.02**	3.04	0.9	9.29	**0.00**
ANN (Annual changes)	4	0.62	0.4	3.22	**0.01**	0.41	0.1	0.95	0.44
ATT*ELE	1	1.56	1.0	32.39	**0.00**	2.05	0.6	18.80	**0.00**
ATT*DIS	2	0.21	0.1	2.16	0.12	0.43	0.1	1.97	0.14
ATT*SEA	3	1.50	1.0	10.38	**0.00**	2.02	0.6	6.15	**0.00**
DIS*SEA	6	2.16	1.4	7.48	**0.00**	5.65	1.7	8.62	**0.00**
ELE*DIS	1	0.50	0.3	10.29	**0.00**	0.42	0.1	3.85	0.05
ELE*SEA	3	0.48	0.3	3.33	**0.02**	1.14	0.4	3.49	**0.02**
ATT*ANN	4	1.68	1.1	8.72	**0.00**	1.60	0.5	3.67	**0.01**
ELE*ANN	1	0.10	0.1	2.01	0.16	0.03	0.0	0.29	0.59
DIS*ANN	8	4.37	2.8	11.34	**0.00**	4.73	1.5	5.41	**0.00**
SEA*ANN	9	3.50	2.3	8.06	**0.00**	7.88	2.4	8.02	**0.00**
ATT*ELE*SEA	3	0.09	0.1	0.63	0.60	0.66	0.2	2.02	0.11
ATT*ELE*DIS	1	0.03	0.0	0.72	0.40	0.61	0.2	5.57	**0.02**
ATT*DIS*SEA	6	0.63	0.4	2.18	**0.04**	1.11	0.3	1.70	0.12
ELE*DIS*SEA	3	0.39	0.3	2.69	0.05	0.42	0.1	1.28	0.28
ATT*ELE*ANN	1	0.00	0.0	0.00	0.95	0.04	0.0	0.39	0.53
ATT*DIS*ANN	8	1.86	1.2	4.81	**0.00**	2.81	0.9	3.21	**0.00**
ELE*DIS*ANN	1	0.07	0.0	1.51	0.22	0.00	0.0	0.02	0.90
ATT*SEA*ANN	9	1.51	1.0	3.49	**0.00**	4.26	1.3	4.33	**0.00**
ELE*SEA*ANN	3	0.02	0.0	0.16	0.93	0.12	0.0	0.37	0.77
DIS*SEA*ANN	18	4.23	2.7	4.88	**0.00**	15.59	4.8	7.93	**0.00**
ATT*ELE*SEA*ANN	3	0.06	0.0	0.40	0.75	0.03	0.0	0.08	0.97
ATT*ELE*DIS*SEA	3	0.03	0.0	0.20	0.90	0.14	0.0	0.43	0.73
ATT*DIS*SEA*ANN	18	2.30	1.5	2.65	**0.00**	5.58	1.7	2.84	**0.00**
ATT*ELE*DIS*ANN	1	0.08	0.1	1.71	0.19	0.08	0.0	0.71	0.40
ELE*DIS*SEA*ANN	3	0.50	0.3	3.46	**0.02**	0.65	0.2	2.00	0.11
ATT*DIS*ELE*ANN*SEA	3	1.01	0.7	6.95	**0.00**	0.58	0.2	1.78	0.15
Error	2242	108.10	69.8			244.90	75.7		

Table 2.4. Single factor ANOVAs of biomass, taxonomic richness and *C. fragile* biomass (Log(x+1)-transformed). Significant factors ($p < 0.05$) are in bold. ATT = attachment type, ELE = elevation level, DIS = distance from mainland, SEA = season, ANN = annual groups.

		Richness				**Total Biomass**				***C. fragile***			
Source	**Df**	**SS**	**η^2(%)**	**F**	**p**	**SS**	**η^2(%)**	**F**	**p**	**SS**	**η^2(%)**	**F**	**p**
ATT	2	99.5	36	680.0	**0.00**	103.2	22	326.25	**0.00**	0.06	1	6.62	**0.00**
Error	2374	173.7	64			375.5	78			11.12	99		
ELE	2	104.5	38	735.8	**0.00**	111.3	23	359.79	**0.00**	0.07	1	7.88	**0.00**
Error	2374	168.6	662			367.4	77			11.11	99		
DIS	3	126.7	46	684.5	**0.00**	151.9	32	367.62	**0.00**	0.16	1	11.22	**0.00**
Error	2373	146.4	54			326.8	68			11.03	99		
SEA	4	98.3	36	333.6	**0.00**	106.3	22	169.22	**0.00**	0.10	1	5.11	**0.00**
Error	2372	174.8	64			372.5	78			11.09	99		
ANN	5	98.7	36	268.2	**0.00**	101.5	21	127.56	**0.00**	0.12	1	5.06	**0.00**
Error	2371	174.5	64			377.3	79			11.07	99		

Total number of replicates per single factor treatment level: ATT: Attached = Unattached = 1188, ELE: Intertidal = 624, Subtidal = 1752, DIS: Back Barrier sites = 792, Mid Lagoon sites = 480, Near Mainland sties = 1104, SEA: Fall = 396, Spring = 504, Summer = 1116, Winter = 360, ANN: year 1 = 1008, year 2 = 900, year 3 = 216, year 4 = 180, year 5 = 72.

Table 2.5. Correlation matrix for taxonomic richness, total biomass, and biomass of the 12 most abundant species. Significant factors ($p < 0.05$, bottom values) are in bold. The corresponding $r^2_{Pearson}$ (top value) was multiplied by 100. None of the significant correlations had negative $r_{Pearson}$. n = 2476. Cf. Table 2.2 for species-abbreviations.

	Bio	**AGA**	**BRY**	**CER**	**CHA**	**COD**	**ECT**	**ENT**	**FOL**	**GRA**	**HYP**	**POL**	**ULV**
Rich	53	6	13	4	3	2	7	1	5	42	1	6	14
p	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
	Bio	12	18	6	3	6	4	1	7	92	1	7	26
	p	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
		AGA	4	2	1	4	0	0	4	10	0	1	4
		p	**0.00**	**0.00**	**0.00**	**0.00**	0.78	0.73	**0.00**	**0.00**	0.12	**0.00**	**0.00**
			BRY	24	16	3	0	0	13	10	0	19	6
			p	**0.00**	**0.00**	**0.00**	0.96	0.84	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
				CER	8	1	0	0	8	3	3	8	1
				p	**0.00**	**0.00**	0.13	0.81	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
					CHA	0	0	0	3	2	0	9	0
					p	0.60	0.94	0.84	**0.00**	**0.00**	0.77	**0.00**	**0.00**
						COD	0	0	1	3	0	0	4
						p	0.91	0.84	**0.00**	**0.00**	0.92	**0.01**	**0.00**
							ECT	1	0	1	0	0	0
							p	**0.00**	0.71	**0.00**	0.81	0.48	0.94
								ENT	0	1	0	0	1
								p	0.82	**0.00**	0.93	0.71	**0.00**
									FOL	7	1	1	4
									p	**0.00**	**0.00**	**0.00**	**0.00**
										GRA	0	4	17
										p	**0.01**	**0.00**	**0.00**
											HYP	0	3
											p	0.65	**0.00**
												POL	1
												p	**0.00**

Chapter 2. Figures

Fig. 2.1. Temporal variability in taxonomic richness of attached (A) and unattached (B) algae along the distance from mainland gradient (elevation factor pooled) with standard errors (n for first 13 surveys = 24 (Back-Barrier sites), 12 (Mid-Lagoon sites) and 36 (Near-Mainland sites) and n for last 14 surveys = 6 for each location).

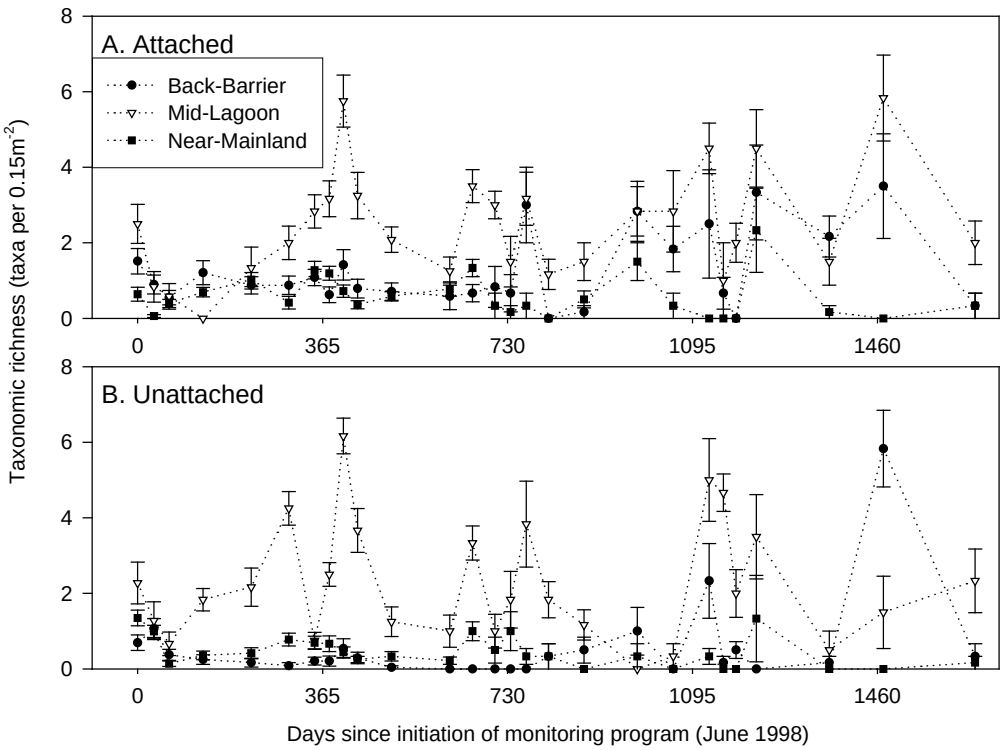


Fig. 2.2. Single factor effects of attachment (ATT), elevation (ELE), distance from mainland (DIS), season (SEA) and annual changes (ANN) on taxonomic richness. With standard errors, cf. Table 2.4 for number of replicates and corresponding single factor ANOVA results (each factor was significant).

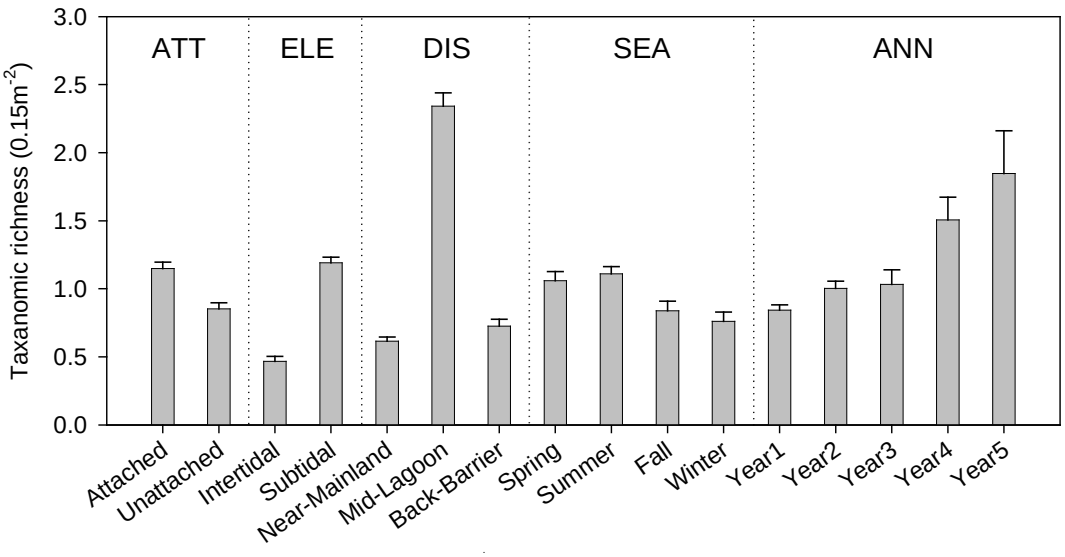


Fig. 2.3. Temporal variability in total assemblage biomass of attached (A) and unattached (B) algae along the distance from mainland gradient (elevation factor pooled) with standard errors (Cf. Fig. 2.1 for number of replicates)

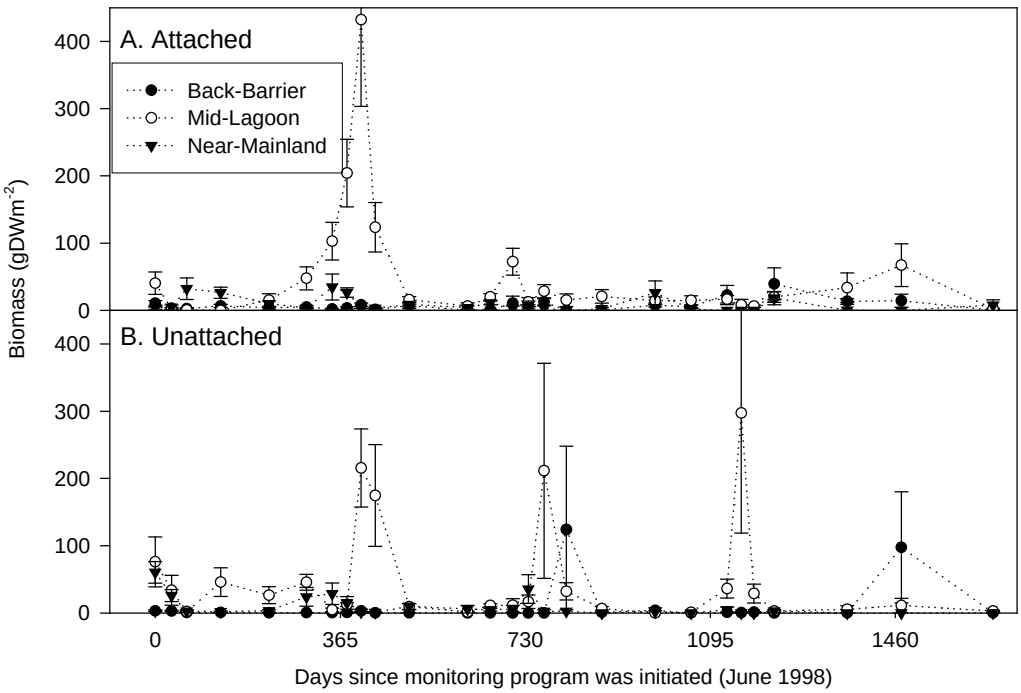


Fig. 2.4. Single factor effects of attachment (ATT), elevation (ELE), distance from mainland (DIS), season (SEA) and annual changes (ANN) on biomass of the total algal assemblage, *G. verrucosa* and *C. fragile*. With standard errors, cf. Table 2.4 for number of replicates and corresponding single factor ANOVA results for biomass and *C. fragile* (each factor was significant for both variables).

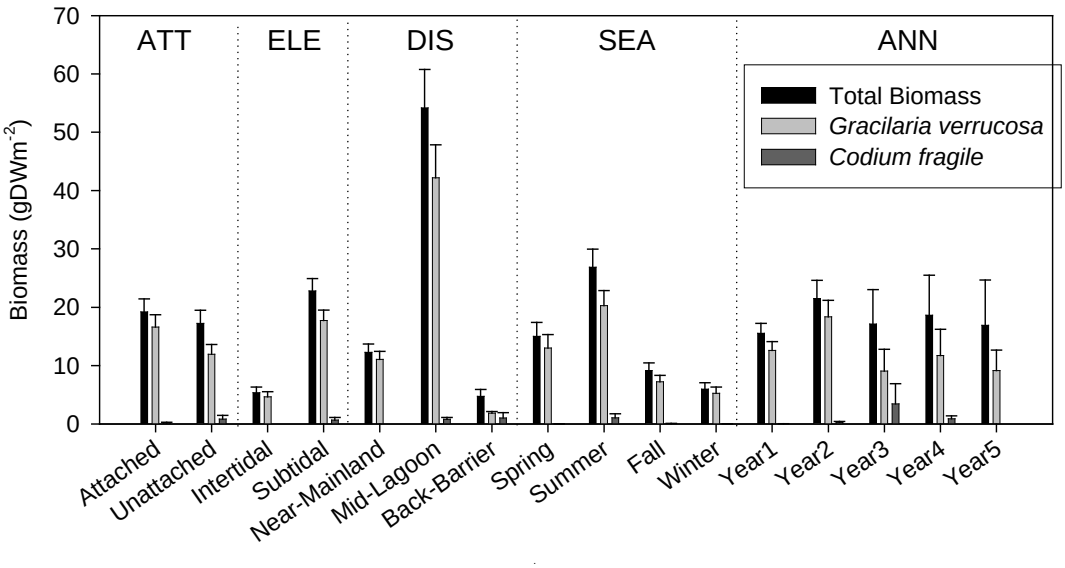
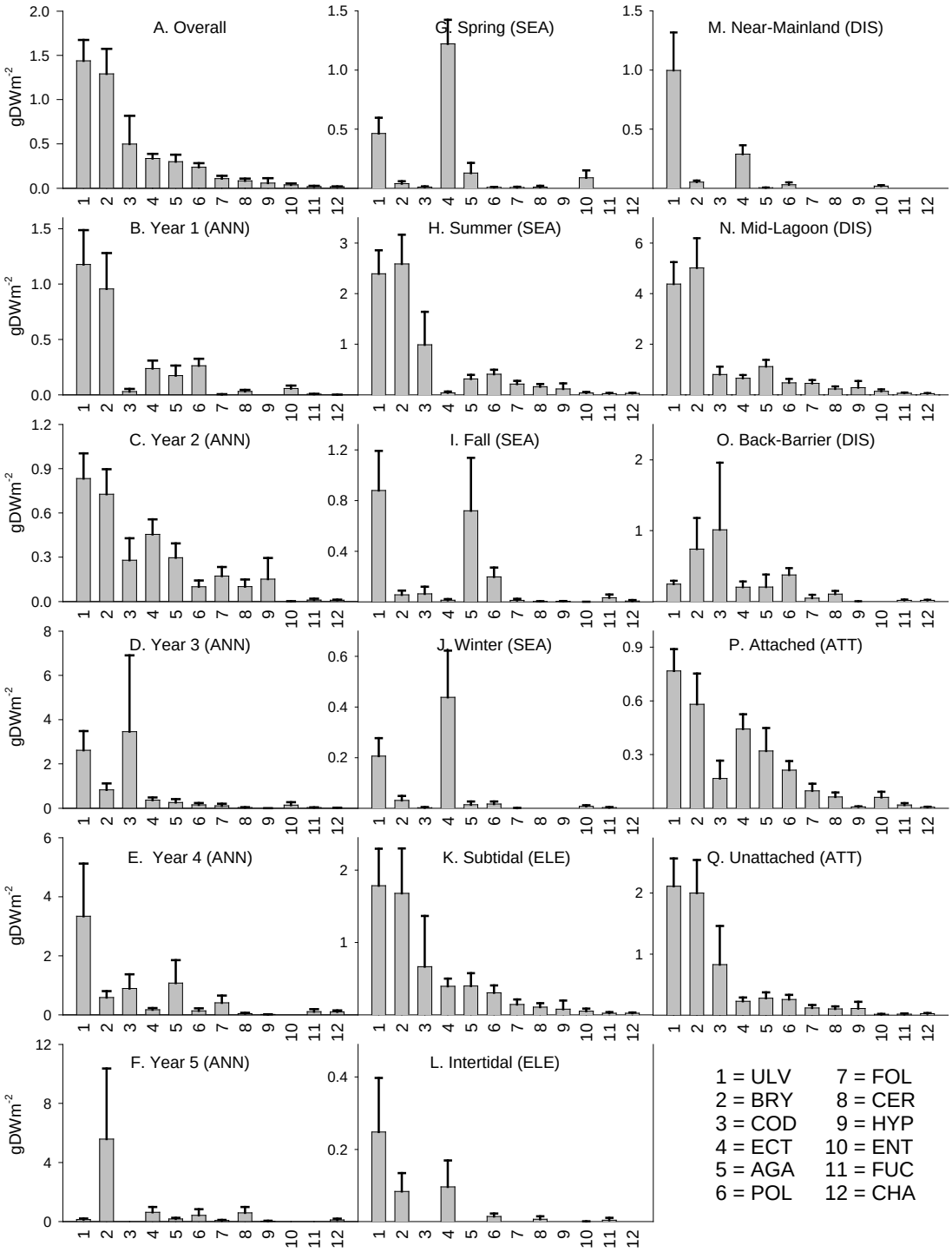


Fig. 2.5. Single factor effects of attachment (ATT), elevation (ELE), distance from mainland (DIS), season (SEA) and annual changes (ANN) on biomass of the most common species following the dominant *G. verrucosa* (cf. Fig. 2.3B). With standard errors, cf. Table 2.2 for species abbreviations and Table 2.4 for number of replicates.



Chapter 3. Facilitation of Macroalgae by the Sedimentary Tube Forming Polychaete *Diopatra cuprea*

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 m^{-2}) tube cap forming polychaete, *Diopatra cuprea*, facilitates macroalgal distribution in Hog Island Bay, a turbid shallow tidal lagoon, Virginia, USA. 70% of the number of mudflat macroalgae were found incorporated into protruding *D. cupreas* tube caps and field experiments showed that *D. cuprea* facilitates algal persistence by providing a stable substrate that retains 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.

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 (Connell et al. 1997, Dayton 1971, Dayton et al. 1984, Heck & Wetstone 1977). These foundation taxa provide substrate for settlement and growth, shelter from predators, an abundant food supply, enhance propagule settlement rate, and alter the abiotic environment into more benign conditions (Bruno & 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 & Micheli 2001). Nevertheless, soft-bottom systems often have organisms that facilitate other species by habitat-modifications, for example mussels beds (Albrecht 1998), oyster reefs (Barh & Lanier 1981), and unattached drift algal mats (Norkko & Bonsdorff 1996c, 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 (Eckman et al. 1981, Fager 1964, Reise 1983). It is well documented that onuphid polychate tube builders create such habitat modifications through their tube-forming activities (Bailey-Brock

1984, Bell & Coen 1982a, Luckenbach 1986, Pillsbury 1950). The onuphid *Diopatra cuprea* (Bosc) is abundant in North American east coast lagoons from north of Cape Cod to 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 (Brenchley 1976, Myers 1972), 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 & Coen 1982a). 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.

We hypothesize that *D. cuprea* acts as a soft-bottom macroalgal facilitator by means of tube cap incorporation, thereby physically controlling and enhancing the distribution and abundance of macroalgae. This was investigated by testing how common *D. cuprea* is within a shallow US east coast lagoon, how abundant and stable the algal-tube cap assemblage is, how fast the association recovers after different levels of disturbance, and if certain algal species are incorporated into tube caps 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 & McGlathery 2001), although this physiologically based aspect was not considered in the present study.

Methods

Site description

We investigated if *Diopatra 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 (Hayden et al. 2000, Swanson & Sparks 1990). 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 1930ties, 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. 1997a, Lawson 2003).

Ubiquity of tube caps

To test if *Diopatra 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 & Coen 1982a, Peckol & 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 2-way ANOVA, testing effects of elevation and distance from the mainland, should be interpreted with caution.

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 1999-2002 covering all seasons, where random tube caps were collected haphazardly and examined for attached macroalgae (n > 3000). Quantitative observations were based on 441 macroalgal individuals sampled 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. X^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) 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.

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 allocated to 18 random plots on a mid-lagoon intertidal mudflat on 24 June 2002 (n = 6 strips per plot, at 0.65 m below MSL, Shoal-site) (McGlathery et al. 2001). Flagging tape was used partly because the slightly negatively buoyant and flat structure mimic small *Ulva curvata* fragment, partly 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 stability of the flagging strips) and whatever stability differed between the two most common algae eight *Gracilaria verrucosa* and *U. curvata*, and their host tube caps were double-tagged on 24 June 2002 and tag-survival recorded nine times during a 46 day period. Double tags were used to ensure that tag loss was caused by algal or tube cap removal and not loss of tags. To test for the generality of

the results, the experiment was repeated on 4 October where survival was recorded 6 times over a 44 day period. It is unlikely that the tags (5 cm flagging tape) influence algal survival because the tag provides minimal drag compared to the algal thallus. The percentage remaining tags were calculated on each sampling date for each species and experiment, and linear regression was used to calculate and compare decay-slopes (percent algae remaining per day).

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 disturbance. Randomly allocated 0.1 m^2 squared 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 the summer experiment the two intensities were applied on the 24 and/or 28 of June 2002 (Exp. 1: 0.65 m below MSL, 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. On 4 July, *i.e.* after 10 and/or 6 days of recovery, re-generated tube caps and incorporated algae were collected, brought to the laboratory, the number of tube caps counted, the algae identified, and wet weight (0.001 g) determined after blotting with a towel. To investigate if the findings were robust a

second removal experiment was conducted in November 2002 (Exp. 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. The treatments were compared to control plots on November 12, *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 *Gracilaria verrucosa, Ulva curvata* and the total algal assemblage, followed by SNK-post hoc test to separate different treatments (Underwood 1981b). To reduce 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, corresponding to a test of 'High' vs. 'Low' disturbancve levels (= Exp. 1b, Fig. 3.3). Some response variables were Log-transformed to ensure variance homogeneity (Cochran's C > 0.05, Table 3.4). 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.

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, Chapter 4): *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 *Ulva 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 *Diopatra cuprea* to build a new cap. Fresh algal fragments were added to cages in November 2002 either as single-species (3 fragments per cage) or multiple-species treatment (1 fragment per cage, cf. Fig. 3.4a for specific biomass'), and cages were capped with 2 mm screening mesh. After two 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'. Autogenic fragmentation (i.e. without *D. cuprea* influence) was not measured because pilot experiments had revealed that healthy tissue of the six species rarely fragmented in caged experiments with only two days of incubation. Because some cages were lost due to storms, vandalism and heavy sedimentation, the final sampling design was uneven (n = 4-11, cf. Fig. 3.4). These response variables were tested with a 2-factorial ANOVA (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.

Results

Ubiquity of tube caps

The overall tube cap density was 21 m^{-2}, and there was a significant interaction between densities found along the mainland-ocean and elevation gradients (Table 3.1). 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. 3.1).

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 *Ulva curvata* and 50 cm *Gracilaria verrucosa*. Algae were more often encountered on tube caps than any other attachment type. The species observed on the tube caps were *G. verrucosa*, and *U. curvata* (ubiquitous), *Agardhiella subulata*, *Fucus vesiculosus*, *G. foliifera*, and *Enteromorpha linza* (up to 10 observations), and *Codium fragile*, *Punctaria latifolia* Greville and *Grinnellia americana* (C. Agardh) Harvey (1 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%, $X^2_6 = 927.2$, Df = 5, $p < 0.001$, Table 3.2) than any other attachment type. Also, the proportions of tube cap-attached algae varied with distance from the mainland (smallest proportion attached at mid-lagoon sites, $X^2_{6,3} = 46.4$, Df = 10, $p < 0.001$) but not with elevation ($X^2_{6,2} = 12.5$, Df = 5, $p = 0.028$), and *G. verrucosa* were found in significantly higher proportions than *U. curvata* (64 vs. 34%, $X^2_{6,2} = 27.2$, Df = 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 taxonomic richness of 2.7 per tube cap (Table 3.3). *G. verrucosa* was found attached to 90 tube caps, three of them with cystocarps, accounting for 94% of the total biomass, 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 & Mathieson 1983, Perrone & Cecere 1997), thereby adding 1-2 taxa to the total tube cap richness.

Stability of algae incorporated to tube caps

All loose-lying flagging tape strings were lost from the mudflat in less than 24 hours, i.e. in less than two complete tidal cycles. This correspond 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 was physically removed from tube caps within days to month (Fig. 3.2). In both tagging experiments, incorporated *Ulva curvata* were removed faster than *Gracilaria 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 4 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.

Recovery of algae incorporated to tube caps

All response variables (tube cap densities and biomass of *Gracilaria verrucosa* and *Ulva curvata*) showed significant effects to different levels of disturbances (except one near-significant effect, Table 3.4). However, the unplanned multiple SNK-comparisons could only distinguish significant different subgroups for the 'weakest' disturbance treatment for *U. curva* in Exp. 1 (Fig. 3.3C), and for the controls of *G. verrucosa* (Fig. 3.3B) and *U. curvata* in Exp. 2 (Fig. 3.3C). 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. 3.3D). 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. 3.3B). However, this deficiency was compensated for by incorporation of *U. curvata* (Fig. 3.3C), resulting in near-identical total biomass (Fig. 3.3D). The tendencies noted in Exp. 1 were verified statistically when the three lowest disturbance levels plots were pooled and compared to the three highest levels (Exp. 1b, Fig. 3.3, Table 3.4E-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. 3.3A) or total algal biomass (Fig. 3.3D), despite significant ANOVAs (Table 3.4I, L), indicating a full recovery in less than 5 days. However, splicing the total algal assemblage data into species-specific abundance's demonstrated significant SNK-group effects on both *U. curvata* and *G. verrucosa* (Table 3.4, Fig. 3.3B, 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 Exp.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.

Preference of algae incorporated to tube caps

In the test of effects on algal incorporation rates (= attachment), there was a significant interaction between species and addition type, and a highly significant species effect (Table 3.5, Fig. 3.4B). 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 (*Codium fragile* = 17%, *Fucus vesiculosus* = 18%, *Agardhiella subulata* = 28%) compared to the species with highest S:V ratio (*Gracilaria foliifera* =

68%, *G. verrucosa* = 54%, *Ulva curvata* = 75%). There were no significant interaction term for fragmentation, but two significant single factor effects (Table 3.5, Fig. 3.4C). Again the species factor explained far more of the data variability compared to the addition type factor and the latter could be ignored for practical purposes. The SNK-test again grouped the three species with 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.

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 & Bertness 2001). We argue that *Diopatra cuprea* specifically facilitates macroalgal assemblages in North American soft-bottom shallow lagoons by a) creating and maintaining attachment sites, 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 important in soft-substrate environment, where 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 (Cecere et al. 1992, Norton & Mathieson 1983). These specific facilitation mechanisms were not described for polychaete worms in the review by Bruno & Bertness (Bruno & Bertness

2001). It is likely that summer growth and productivity also is enhanced by *D. cuprea*, by excretion of nitrogenous rich waste products (Fong et al. 1997, Giannotti & McGlathery 2001), although this hypothesis were not tested in our 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 & 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 (McGlathery et al. 2001) and desiccation, light, temperature fluctuations, sedimentation, and predation pressure. The widespread distribution suggests that *D. cuprea* is 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. (Mangum et al. 1968) suggested that *D. cuprea* densities were positively correlated to current velocities and latitude, but not with substrate particle size. It is today unknown what factors control site-specific distribution patterns of *D.*

cuprea, probably because co-variation between ecological factors and spatial gradients makes it difficult to relate single causes to distribution patterns.

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, Norkko & Bonsdorff 1996a, Norkko et al. 2000, Raffaelli et al. 1998). In this context, the incorporated algae are proximate habitat modifiers whereas *D. cuprea* is the ultimate modifier, and the algae 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 (Connor 1980, Rhodes 1970) only two 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 (Bell & Coen 1982a, Brenchley 1976, Pillsbury 1950) 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 the filamentous genera mainly were found as epiphytes on *Gracilaria*. It is interesting that older *D. cuprea*-studies from mid-Atlantic barrier island

localities (Brenchley 1976, Mangum et al. 1968, Woodin 1978, 1981) either did not describe incorporated algae, or only described attached species qualitatively, indicating much lower algal abundance in the 1960-70s. 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, Goshorn et al. 2001, Raffaelli et al. 1998), 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 *Gracilaria verrucosa* is slightly favored over *Ulva 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 (pers. obs.). 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, Duggins et al. 2001, Padilla 1993). 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 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 Meyers (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 (Petraitis & Latham 1999, Sousa 1984) 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 *Agardhiella subulata, Codium fragile* and *Fucus 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 caps, because larger thalli were only stable on the day-month time-scale. The low drag on the fragmented small thalli have a low risk of dislodgment compared to larger incorporated thalli (Gaylord et al. 1994) and the small fragments provides a biomass supply for regrowth if hydrodynamic forces removes larger thalli. *D. 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 (Chapman 1999, Hillson 1976, Trowbridge 1998), is today the fourth most common species in Hog Island Bay (Chapter 2) and is potentially still expanding its distribution. Because *C. fragile* does not fulfill the listed properties (unpublished data) 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 2003), 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.

Chapter 3. Tables

Table 3.1. ANOVA of tube cap densities. Significant results ($p < 0.05$) are shown in bold. 15 sites were sampled (n = 6-9 sample frames/site). Each site classified into 1 of 3 distances (near-mainland, mid-lagoon, near-ocean) and 1 of 2 elevation levels (shallow subtidal, intertidal). Densities could not be transformed to variance homogeneity (Levines test, $p > 0.05$).

Source	**Df**	**SS**	**η^2(%)**	**F**	**p**
Distance	2	3232	4	2.44	0.097
Elevation	1	69	0	0.10	0.748
Distance * Elevation	2	8608	11	6.49	**0.002**
Error	100	66280	85		

Table 3.2. Abundance (in counts) of different A: attachment types and B: species incorporated onto tube caps.

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

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

Table 3.3. Mean biomass and variance per tube cap (gWW), relative abundance (%), frequency of occurrence (counts) and attachment types of algae incorporated into tube caps (n = 92).

Taxa	**Mean**	**Variance**	**%**	**Counts**	**Attachment**
[a]Richness	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
[b]*Bulgula turrita*	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
[c]*G. verrucosa* carp.	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

[a]In number of taxa per tube cap. [b]A bryozoa. [c]Caroposporophytic life stage, potentially with viable propagules. Tub = tube cap; Epi = Epiphytic (entangled; hooked, primary attached, re-attached).

Table 3.4. ANOVAs from recovery experiments. Exp. 1 was initialized in June and Exp. 2 in November 2002. Exp. 1b correspond to treatments from Exp. 1 pooled into 'low' vs. 'high' disturbance levels (cf. Fig. 3.3). Significant results ($p < 0.05$) are shown in bold. Log = Logarithm transformed.

Test and source	**Df**	**SS**	**F**	**p**
A: Exp. 1 *Diopatra*	6	223.0	22.30	**0.000**
Error	18	30.0		
B: Exp. 1 *Gracilaria*	6	16685.2	6.36	**0.001**
Error	18	7869.0		
C: Exp. 1 Log *Ulva*	6	3.9	5.40	**0.002**
Error	18	2.2		
D: Exp. 1 Log Biomass	6	42.7	66.03	**0.000**
Error	18	1.9		
E: Exp. 1b *Diopatra*	2	215.0	62.32	**0.000**
Error	22	38.0		
F: Exp. 1b Log *Gracilaria*	2	36.4	134.18	**0.000**
Error	22	3.0		
G: Exp. 1b *Ulva*	2	212.4	2.94	0.074
Error	22	795.4		
H: Exp. 1b Log *Biomass*	2	42.7	240.94	**0.000**
Error	22	1.9		
I: Exp. 2 *Diopatra*	4	2895.3	37.20	**0.000**
Error	28	544.8		
J: Exp. 2 *Gracilaria*	4	4598.1	8.15	**0.000**
Error	28	3949.6		
K: Exp. 2 Log *Ulva*	4	32.0	91.70	**0.000**
Error	28	2.4		
L: Exp. 2 Biomass	4	14758.1	15.62	**0.000**
Error	28	6613.8		

Table 3.5. ANOVAs from preference experiment: Percent attachment and percent fragmentation. 'Addition' correspond 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. The fragmentation data could not be transformed to variance homogeneity (Levines test, $p > 0.05$).

		Attachment				Fragmentation			
Source	**Df**	**SS**	**η^2(%)**	**F**	**p**	**SS**	**η^2(%)**	**F**	**p**
Species	5	176299	49	20.26	**0.000**	161091	42	15.16	**0.000**
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		

Chapter 3. Figures

Fig. 3.1. Ubiquity of tube caps in Hog Island Bay: *Diopatra cuprea* densities along the mainland-ocean and elevations gradients. With SE, n from left = 18, 18, 21, 16, 10, 23.

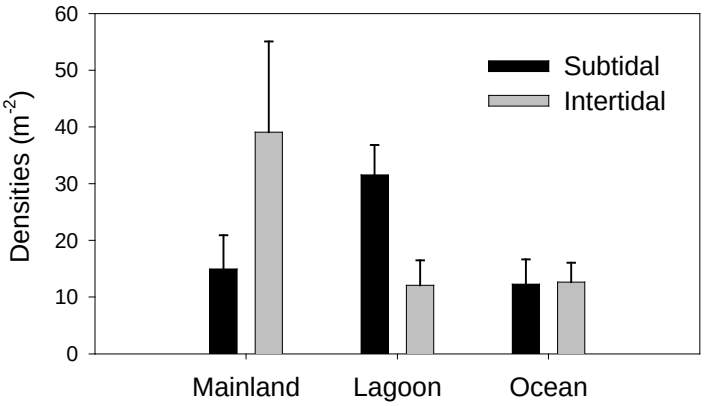


Fig. 3.2. Stability experiments: ‘Survival’ of algae incorporated into tube caps (n = 8 per algal species and experiment) and of unattached flagging strips (n = 108) on an intertidal mudflat.

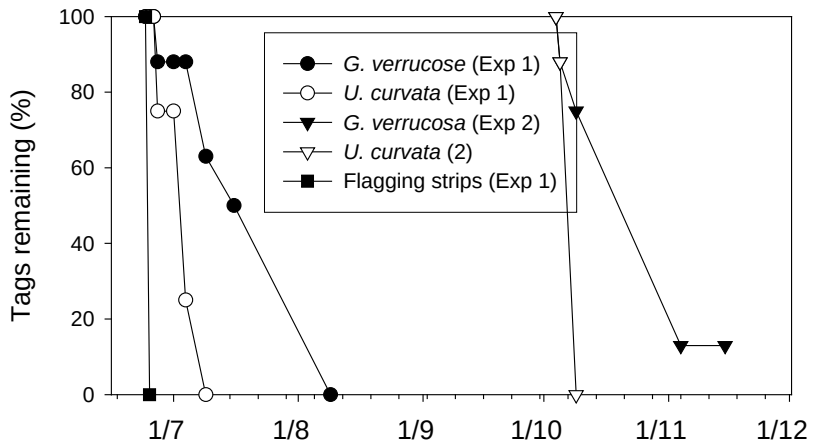


Fig. 3.3. Recovery experiment: Effects of disturbance on the abundance of *Diopatra* tube caps (a) and tube cap incorporated *Gracilaria* (b), *Ulva* (c), and total algal biomass (d) (± SE). The first 6 bars correspond to experiment 1 (terminated July 4, n = 4), the next 2 to experiment 1 pooled into low vs. high disturbance intensities (n = 12), and the last 4 to experiment 2 (terminated 11 November, n = 8). Treatment labels: Alga = algae removed, Caps = tube caps removed. The number in bracket correspond to date of removal.

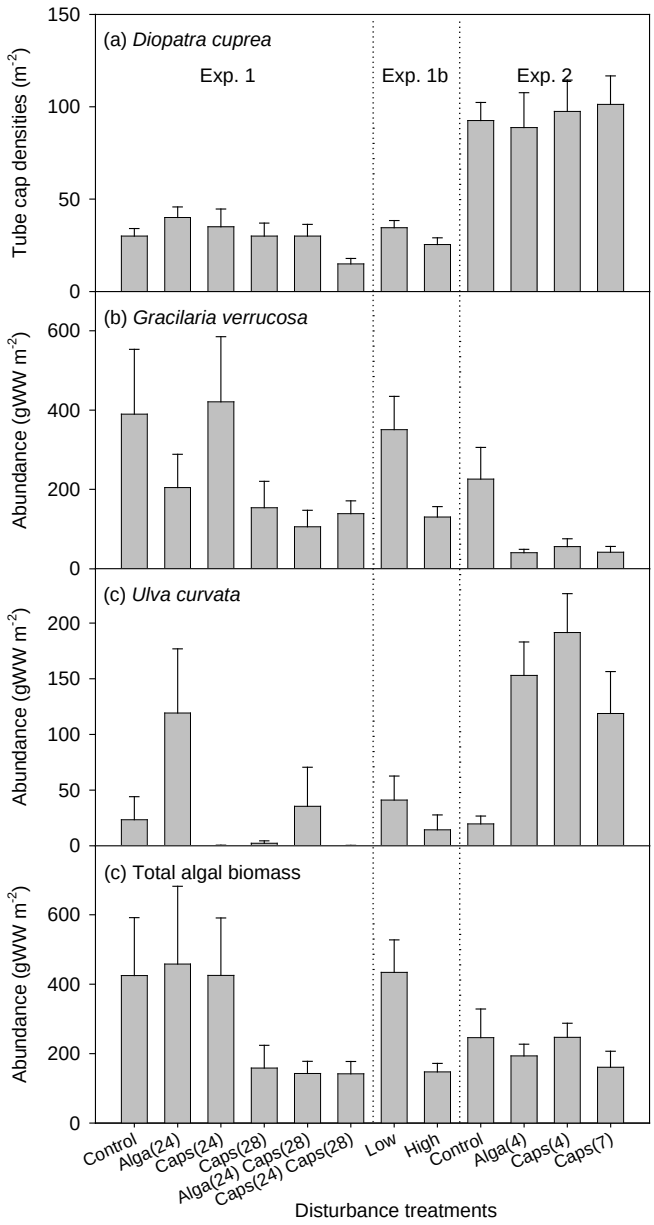
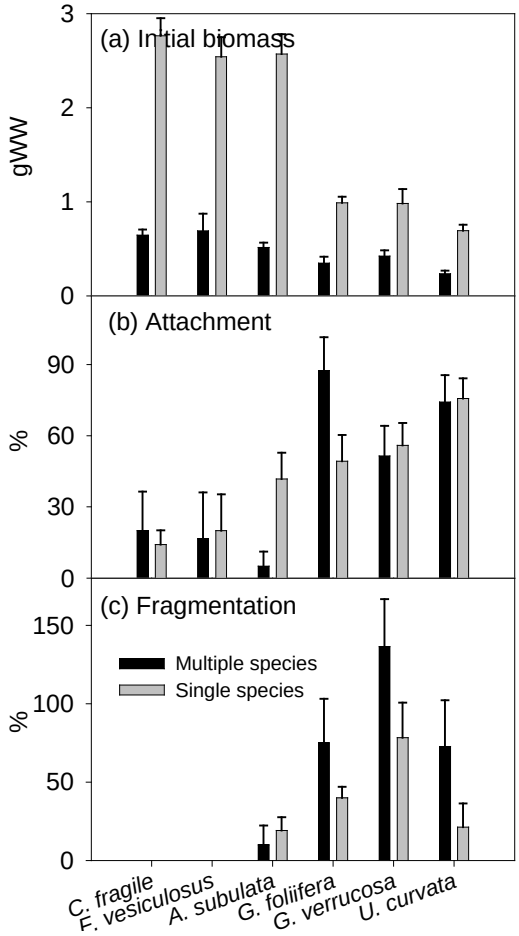


Fig. 3.4. Preference experiment: (a) Algal biomass added to *Diopatra cuprea* cages, (b) percent fragments incorporated into tube caps, and (c) percent fragmentation, based on single and multiple species additions. Species are arranged from low to high S:V ratios (± SE, n from left = 10, 10, 6, 5, 10, 10, 4, 5, 11, 10, 11, 9).



Chapter 4. Species type, thallus size and substrate condition determine macroalgal break forces, break velocities and break places in a western mid-Atlantic low energy soft bottom lagoon

Abstract

Wave-induced dislodgment of attached sessile marine macroalgae is an important structuring force influencing population and community dynamics in high energy habitats. However, little is known about whether hydrodynamic forces limit algal size and distribution patterns in low energy soft bottom systems. Biomechanical pull-tests were used to determine relationships between break force, break velocity and break place for 6 algal species collected from a shallow temperate lagoon (Hog Island Bay, Virginia), attached to 2 types of substrates, and divided into 2 size classes. *Ulva curvata*, *Agardhiella subulata, Gracilaria verrucosa*, small thalli and algae attached to polychatae tube caps (*Diopatra cuprea*) had break forces between 0.3 and 6 N, whereas large *Fucus vesiculosus*, *Codium fragile* ssp. *tomentosoides*, and *G. foliifera* attached to bivalve shells had break forces between 6 and 12 N. From break forces and thallus sizes, break velocities were calculated to range from 1-2 ms^{-1} for relatively large thalli on tube caps and 6-10 ms^{-1} for small thalli on shells. Because velocities often reach 1 ms^{-1} during hydrodynamic peak events in tidal soft bottom systems, thallus breakage is probably common, limiting algal size, particularly for *U. curvata* and for algae incorporated into tube-caps. It is suggested that entanglement by drift algal clumps, and entrainment of algae attached to unconsolidated shells should be incorporated into future biomechanical studies, to better understand algal breakage and mobility in shallow low energy soft bottom habitats.

Introduction

Survival of sessile marine organism against hydrodynamic forces

Survival is a fundamental process which marine macroalgae must accomplish before resources can be directed to growth, reproduction and dispersal. It is thus an important task for ecologists to understand survival mechanisms, especially under extreme environmental conditions where fatalities can be high. In marine open rocky coastal habitats 5-10 meter high storm waves can create external forces on sessile macroalgae that are higher than for any other habitats, with water velocities exceeding 15 ms^{-1} and accelerations of more than 400 ms^{-2} (Gaines & Denny 1993, Koehl 1984, 1986, Norton 1991). Exposure to such forces is a major cause of mortality (Colman 1933, Denny 1995, Denny 1987, Jones & Demetropoulus 1968, Lewis 1964, Norton 1991). In contrast, soft bottom shallow lagoons are only exposed to small waves because terrestrial structures and shallow depths reduce wave development. In these systems, tidal currents are often the dominant hydrodynamic force, imposing skin and form drag on sessile organisms. Hence acceleration forces can be neglected, and velocities rarely exceeds 1 ms^{-1} (Albrecht 1998, Hawes & Smith 1995, Lawson 2003, Oertel 2001).

Biomechanical models

Biomechanical models have been proposed as tools to understand and predict survival from a hydrodynamic perspective (1995, Denny 1999, Denny et al. 1989, Gaylord et al. 1994, Gaylord & Denny 1997). Here, the break force of sessile organisms is measured using pull tests (Dudgeon & Johnson 1992, Hawes & Smith 1995), and compared to the ambient hydrodynamic forces and the forces experienced by the organism. This break force is an important component of the drag equation and is used to calculate a corresponding break velocity (Bell 1999, Denny 1995, Shaughnessy et al. 1996). Break

velocities are then interpreted as measures of gap-creation and susceptibility to mortality (Bell 1999, Blanchette 1997, Denny 1995, Gaylord et al. 1994). Break forces are mainly known for macroalgal species within the Fucales (Blanchette 1997, Haring et al. 2002, Norton 1986), Gigartinales (Bell 1999, Carrington 1990, Shaughnessy et al. 1996) and Laminarales (Blanchette et al. 2002, Milligan & DeWreede 2000, Utter & Denny 1996), and are practically unknown for species from other taxonomic orders (Thomsen & Wernberg submitted). Two of the most important factors that determine macroalgal break forces are substrate type (Barnes & Topinka 1969, Milligan & DeWreede 2000, van Tamelen & Stekoll 1996) and algal size (Gaylord et al. 1994, Shaughnessy et al. 1996), where large individuals attached to hard substrates usually have higher break forces than small individuals on soft substrates (Thomsen & Wernberg submitted). These biomechanical finding are based on studies from high energy rocky coastlines; little is known about if algal species, thallus size or substrate condition influence break forces and break velocities in low energy soft bottom habitats, typically dominated by macroalgae, being unattached or attached to bivalve shells (Anderson & Underwood 1997, Connor 1980, Cowper 1978, Havens et al. 2001, Hawes & Smith 1995, Norton & Mathieson 1983). However, Hawes and Smith (1995), in the only macroalgal biomechanical study from a temperate soft bottom lagoon, calculated that tidal forces can set an upper limit to the size of the opportunistic green algae *Ulva lactuca*. Because of the paucity of biomechanical studies from soft bottom tidal lagoons, the primary objective was to test if species, substrate type or algal thallus size affects break forces. Furthermore, to explore if breakage is a likely process, a second objective was to estimate break velocities and compare these to typical lagoon velocities. Finally, because algae do

not always break at the holdfast-substrate junction under peak hydrodynamic events (complete biomass removal = dislodgment), but sometimes break above the holdfast-substrate junction (partial biomass removal = pruning) and thereby increase the chance of recovery (Blanchette 1997, Dudgeon et al. 1999, Scrosati 1998, Shaughnessy et al. 1996), the last objective was to investigate if the break place was on the substrate, holdfast, stipe or frond.

Methods

Species and substrate types

Descriptions of the study site (Hog Island Bay), macroalgal species assemblages, distribution patterns, taxonomic considerations and typical growth conditions are reported in previous papers (Chapter 2, 5, McGlathery et al. 2001, Tyler et al. 2001). The six conspicuous macroalgal species that are common year-round attached to bivalve shells were included in the study for comparison: *Codium fragile* ssp. *tomentosoides* (van Goor) Silva, *Agardhiella subulata* (C. Ag.) Kraft et Wynne, *Fucus vesiculosus* L., *Ulva curvata* (Kutzing) De Toni, *Gracilaria verrucosa* (Hudson) Papenfuss, and *G. foliifera* (Forsskal) Boergesen (Humm 1979). In addition to algae attached to bivalve shells, *U. curvata* and *G. verrucosa* are commonly found incorporated into tube caps of the ubiquitous polychaete *Diopatra cuprea* (Bosc) (Chapter 3). These algae likely provide tube-cap strength (Brenchley 1976, Harwell & Orth 2001, Myers 1972), shelter from predators (Brenchley 1976, Harwell & Orth 2001, Luckenbach 1984), and/or a direct or indirect food supply (Bell & Coen 1982b, Mangum et al. 1968).

Measurements of break force, size and break place

Algal individuals attached to bivalve shells and *D. cuprea* tube caps were sampled haphazardly from several shallow subtidal mid-lagoon sites in summer 2001 and 2002. To determine break force, a piece of nylon webbing was tied around the mid-thallus and pulled steadily and horizontal to the substrate with a 5 kg Imrad spring scale (0.001 kg) for 2 - 5 seconds until breakage. The algae were then brought to the laboratory for wet weight determination after blotting with a towel. Break place was classified into one of nine categories, ordered from the substrate to the webbing: 1) substrate (shell or tube cap), 2) subtrate-holdfast junction, 3) holdfast with minute fractions remaining attached, 4) holdfast with major parts remaining, 5) holdfast-stipe junction, 6) stipe, 7) stipe-thallus junction, 8) the lower thallus below the webbing, and 9) the lower thallus near the webbing. The measurement was discarded if the break location was near the webbing (class 9) because the webbing itself can induce breakage and result in an underestimate of F_{break}. Categories 1-3 correspond to dislodgment, whereas categories 4 - 8 correspond to progressively decreasing levels of pruning intensity with increasing survival and recovery probabilities. At least 30 individuals were sampled for each of the six species attached to shells and of *U. curvata* and *G. verrucosa* attached to tube caps. *Agardhiella*, *C. fragile*, *F. vesiculosus* and *G. foliifera* were extremely rare on tube caps (Chapter 2, 3). To obtain estimates of break forces for these four species, algal fragments were added in fall 2002 to cages inserted into the sediment around live polychaetes at a mid-lagoon and a near-mainland site (McGlathery et al. 2001). Tube caps within cages were removed in order to force the polychaetes to build new caps and incorporate the added algae in the process (Brenchley 1976). The cages were closed with 1 mm mesh to ensure no other algal

species were incorporated. Regenerated tube caps with attached algae were collected two days later for biomechanical pull tests. Fifteen replicates were sampled using this method for each of the four species.

Calculation of break velocities

Break velocities were calculated from the drag equation (Denny 1995, Denny 1988):

$$U_{break} = [(2 * F_{break}) / (C_{drag} * A_{plan} * \rho)]^{0.5}$$

where U_{break} is the water velocity (ms^{-1}) required to break a seaweed with planform area A_{plan} (m^2), F_{break} is the break force (Newton = $kgms^{-2}$), C_{drag} is the drag coefficient (dimensionless) and ρ is the density of seawater (set to 1026 kgm^{-3} for seawater at 10°C). Because there is consensus that drag is the main hydrodynamic force on macroalgae (Bell 1999, Denny 1999, Gaylord 2000) lift, buoyancy, wave impact and acceleration forces were ignored. C_{drag} reflects an alga's ability to streamline and re-configure in the flow, and although C_{drag} can vary with size, morphology, species, and velocity (Denny, 1995; Koehl, 2000) a constant of 0.1 was assumed, partly to keep the models as simple as possible, partly because 0.1 is a typical drag coefficient for algae exposed to steady flows of 0.1-1 ms^{-1} (Collado-Vides et al. 1998, Hawes & Smith 1995, Johnson & Koehl 1994, Kawamata 2001, Koehl 2000). To convert wet weight to planform area A_{plan}:WW, values of 6 (*C. fragile*), 12.5 (*F. vesiculosus*), 14 (*A. subulata*), 15 (*G. foliifera*), 16 (*G. verrucosa*), and 105 (*U. curvata*) cm^2g^{-1} were applied. The ratios were obtained from area-analysis in Scion Image of digital photos of algal fragments (n = 8 per species)

spread out on a white background, and by measuring the corresponding weight wet of the fragments.

Data analysis

To test for allometric relationships between thallus area and break force, Model II linear regressions were performed on Log-transformed data on the six species and two substrate types. The relationship between thallus area and break velocity was also modeled by linear regression on Log-transformed data. Because U_{break} is calculated from thallus area, i.e. the two variables are not independent, no inferential statistical tests were performed on the models, but Pearson correlation coefficients were listed as simple estimates of the model's explanatory power. The effects of species, substrate type and size were further tested with fixed factorial ANOVA on Log-transformed data. This transformation ensured variance homogeneity for most variables (cf. Table 4.2). The effect on break place was tested with logistic regressions for each species and substrate group vs. thallus size, and with χ^2-tests on different combinations of species, substrate and size classes. However, to fulfill χ^2-tests assumptions (maximum 20% of groups can have expected frequencies < 5, Quinn & Keough 2002), the original categories were reduced to two groups: Class 1-3 = complete biomass removal (dislodgment), and Class 4-8 = partial biomass removal (pruning). Alpha < 0.05 and < 0.1 were used to indicate significant and near-significant effects, and all statistical tests were conducted in SPSS 8.0.

Ambient hydrodynamic forces

To compare algal break forces with the ambient hydrodynamic forces, current velocities were measured where algal biomass is highest in Hog Island Bay (Chapter 2, McGlathery

et al. 2001). Currents were measured with a Marsh-McBirney electromagnetic current meter 13 times in summer 2001 in front, between and behind oyster reefs at a mid-lagoon site (Chapter 6) at 0.6 to 0.8 m below mean sea level, when the water depth was 15-40 cm. These three sub-sites were sampled because oyster reefs potentially differentiated hydro-dynamic regimes (Chapter 6, Lenihan 1999). The effects of sample day and reef location on velocities were tested with ANOVA. Temporal velocity changes over several tidal cycles were described using an Acoustic Doppler Profiler (ADP) during a two month sample period (Lawson 2003). The ADP was located behind Rouge Island at ca. 2 m depth during a winter period (November 17 2002 to 23 January 23 2003) when winter-storms potentially enhance tidal currents (Lawson 2003). The ADP measured currents at 20 cm vertical intervals starting at Z_0 = 74 cm above the seabed, and with a 30 min sampling interval. Finally, to compare large-scale horizontal differences within Hog Island Bay, a map of maximum surface currents was presented based on a 2d Bellamy Kinematic hydrodynamic model (Fugate & Friedrichs, Submitted) forced with a SWASS wind-model using wind data from November 2002 (the current map was produced by S. Lawson, UVa, Lawson 2003).

Flume dislodgment

To test if the calculated break velocity and measured break place results in dislodgment, 50 oyster shells (10 with each of 5 species attached; *U. curvata* was not found attached to shells at the time of collection) and 16 tub caps with *G. verrucosa* and *U. curvata.* incorporated were collected in November 2002 for flume tests (Hawes & Smith 1995). At the time of collection, the five algal species on shells were mainly found attached as

relatively small individuals (approximately corresponding to size class 1, cf. Fig. 4.1A). The flume dimensions were 0.3 m x 0.5 m x 3 m and could produce a maximum velocity of 0.45 ms^{-1}. Each oyster and tube cap were fixed in the mid-section of the flume, and attached algae encountered water velocities of 0.10, 0.30 and 0.45 ms^{-1}. No dislodgment occurred at any flow velocity for algae attached to the oyster shells. However, some algae broke on tube caps and the algae were collected downstream. The wet weight per species and per tube cap was measured after blotting with a towel (removed and non-removed algae pooled). After each flume run, the tube cap algae were divided into two size-classes and the proportion of dislodged algae (pooled for the three flume velocities) was calculated and tested with an ANOVA for effects of species type and size-class on Log-transformed data.

Drift algae collections

Entanglement of drifting algal 'clumps' (Holmquist 1994) can potentially increase the total drag of attached algae without any increase in attachment strength. To quantify the likelihood of clump encounter and to measure typical clump sizes, drifting algae were collected 4 times in July 2002 on incoming tides at a mid-lagoon site between two small oyster reefs. Two PVC poles were inserted into the oyster reef approximately 2 m apart. All drifting clumps passing through the poles were collected at 2-3 min time intervals. The water height and velocity was measured and the collected clumps were brought to the laboratory, where wet weight was determined for each species after blotting with a towel. Reproductive features were recorded if present and attachment types were recorded as either unattached, attached to tube caps or attached to unconsolidated shells.

Results

Thallus size and break force, velocity and place

C. fragile, *F. vesiculosus*, *G. verrucosa*, and *G. foliifera* had significant positive relationships between thallus area and break force (Table 4.1). In contrast, no species attached to *D. cuprea* tube caps had significant relationships. All species had negative relationships between thallus size and break velocity, with highest r^2 when attached to shells (except *U. curvata*). No logistic regressions were significant (Table 4.3), suggesting that break place is independent of algal size.

All single factors and interactions were significant in the ANOVA on thallus area vs. species, substrate and size-class (Table 4.2). *A. subulata* was largest, *C. fragile* and *F. vesiculosus* intermediate, and *G. foliifera*, *G. verrucosa* and *U. curvata* smallest for size-class 2 individuals attached to shells (Fig. 4.1A). All species attached to tube caps, except *U. curvata*, had comparatively small planform areas for both size class 1 and 2. However, *U. curvata* had large thallus areas for size class two individuals incorporated into tube caps. The size-factor explained most data variability (28%) followed by the species * substrate interaction (15%) and the species factor (6%).

Break force was significant for all single factors and the substrate * size and species * size interactions (Table 4.2). For all species, except *U. curvata*, break forces were (1) clearly larger for size-class 2 compared to size-class 1 when attached to shells, (2) were clearly larger on shells compared to on tube caps, and (3) there was a tendency for algae

on shells with low A_{plan}:WW ratio to have high break forces (Fig. 4.2B). For algae attached to tube caps, the break force was low and constant for all species and both size groups (0.3-0.5 N). Substrate explained most of the data-variability (57%) followed by species * substrate (10%) and the species factor (5%).

All single factors and interactions were significant or near-significant on break velocity vs. species, substrate and size-class (Table 4.2). Size-class 2 individuals had smaller break velocities than size-class 1, and algae on tube caps had smaller break velocities than on shells (Fig. 4.1C). In addition the break velocities of size-class 2 were as follows: *F. vesiculosus* and *G. verrucosa* > *G. foliifera* and *C. fragile* > *A. subulata* > *U. curvata*. Substrate explained 39% of the data variability, followed by species (13%) and size (8%), and with higher order interactions explaining less than 1%.

For break place there were significant main effects of species and substrate, but not size (Table 4.3, Fig. 4.1D). This means that dislodgment to pruning ratios differed between species and substrates, but not between size-classes. Out of the 6 species-specific tests of size effects, only *U. curvata* had a significant effect with larger individuals experiencing a higher degree of pruning compared to small individuals. On the other hand, all the 6 species-specific tests of substrate effects were significant or near-significant. Thus, *C. fragile*, *F. vesiculosus*, *G. verrucosa*, *G. foliifera* and *A. subulata* had higher dislodgment on tube caps, whereas *U. curvata* had highest dislodgment on shells.

Ambient hydrodynamic regime

Benthic velocities at the mid-lagoon shoal site (Fig. 4.2) were generally between 0.02 and 0.15 ms^{-1}, and only rarely exceeded 0.3 ms^{-1} between oyster reefs. There were no significant single factor effects, however, there was a significant interaction between reef location and sample day (SS = 2.67, F = 3.25, Df = 26, p = 0.003, Fig. 4.2). This interaction was significant because tidal currents between the oyster reefs vary more than current velocities in front and behind reefs, which were always low. Thus, algae at mid-lagoon sites are exposed to relatively low currents, and with algae between reefs experiencing highest drag forces. The ADP profiles (Fig. 4.3) showed a maximum surface current of 0.82 ms^{-1} during the two-month sample period. However, the ADP data also showed that tidal peak surface currents of 0.75-0.80 ms^{-1} were encountered regularly during each month. Near-bottom peak currents, i.e. corresponding to the flow conditions sessile algae are exposed to, had a tendency to be slightly lower than surface currents, typically between 0.55-0.65 ms^{-1}. Currents at this near-ocean site were somewhat higher than at the mid-lagoon site (although not measured at the same time). The map of surface currents (Fig. 4.4) showed that velocities were low on the shallow mudflats but higher near the inlet and in the main channel (> 0.3 ms^{-1}). This map predicts that algal drag would be highest at near-ocean sites.

Flume dislodgment

Algae attached to shells had no breakage at any velocities in the flume trials. This is in agreement with the calculated break velocities (Fig. 4.1) which predict breakage at velocities a factor ten higher than could be obtained in the flume (0.45 ms^{-1}). However, *U. curvata* and *G. verrucosa* attached to tube caps experienced breakage at the velocities

obtained in the flume, which is also in agreement with the calculated break velocities. *U. curvata* tended to break at lower velocities than *G. verrucosa*. The ANOVA showed no effect of species or species * size but a significant effect of size ($F = 4.59$, $p = 0.04$), with most breakage occurring for large individuals. The break place in the flume trials was in agreement with the *in situ* pull tests, with a relatively high degree of breakage at the frond for *U. curvata* (7 out of 10) and high breakage at the substrate for *G. verrucosa* (5 out of 7). However, because the actual number of breakage observations was low, a χ^2 test did not lend statistical support to any association between species and break place ($\chi^2 = 0.93$, $Df = 3$, $p = 0.81$). Only a small proportion of the total algal biomass was removed during the flume runs (2-6%). Nevertheless, as predicted from the drag equation, breakage occurred within the velocity ranges encountered in Hog Island Bay: *U. curvata* dislodged at lower velocities than *G. verrucosa*, and large thalli were significantly more severely affected than small thalli.

Drift of algal clumps

Sixty-nine drifting algal clumps were captured during 1080 sec of sampling at the mid-lagoon site (pooled from four consecutive summer sample days, Table 4.5). The mean clump size was 80 gWW, corresponding to *ca*. 0.23 m^2 of algal area, and had a recurrence interval of 10 sec along 1 m of coastline (with a mean current velocity of 0.17 ms^{-1}). An algal clump typically contained 3-4 entangled species with highest biomass of *G. verrucosa* and *C. fragile*, and highest frequency of *Bryopsis plumosa*. Larger multi-species clumps were generally observed tumbling (Holmquist 1994), whereas smaller single species clumps, particularly of the positively buoyant *C. fragile* and *F. vesiculosus*,

typically were in the middle or upper regions of the water column. One *G. verrucosa* and one *G. foliifera* were observed with tetrasporangia. All algae caught in the drifting clumps were observed unattached, i.e. without any shells attached.

Discussion

This study is the first to present macroalgal break forces, break velocities and break places for algae incorporated into tube caps of the polychaete *D. cuprea*, and only one study have conducted pull tests of algae attached to bivalve shells (Hawes & Smith 1995). Considering that algae typically are abundant on these substrates (Bell & Coen 1982a, Brenchley 1976, Chapter 2, 3, Connor 1980, Mangum et al. 1968, Mathieson et al. 2003), and that the type of substrate have been documented to influence algal survival (Barnes & Topinka 1969, Malm et al. 2003, Milligan & DeWreede 2000, van Tamelen & Stekoll 1996) these data fill a gap in the biomechanical literature. Here it is documented that substrate type and thallus size determine break forces, break velocities and break places for 6 algal species in a low energy soft bottom lagoon.

Unattached survival

In soft bottom semi-enclosed systems breakage is not necessarily adverse but can under some conditions and for certain species have beneficial effects on growth, dispersal and re-colonization. Hence, whereas it is assumed that breakage equals mortality in biomechanical studies from high energy rocky open habitats (Bell 1999, Blanchette 1997, Denny 1995, Friedland & Denny 1995, Gaylord et al. 1994), in shallow semi-enclosed systems survival will also depends on topography, residence time, and bordering habitats

(Flindt et al. 1997a, Rowcliffe et al. 2001, Salomonsen et al. 1999), the likelihood for drifting fragments to remain within the wet photic zone (Cecere et al. 1992), and on buoyancy structures, *e.g*. vesicles in *F. vesiculosus* and trapped gasses in *C. fragile* (Dromgoole 1982, Kingsford 1995, Lapointe 1995). Also, the likelihood of survival depends on the break place, where the probability of survival generally increases with breaking distance from the substrate, as well as the ability to recover from the breakage (Carrington 1990, Shaughnessy et al. 1996). Hence, whereas simpler algae can recover from holdfast and stipe tissue alone (Dudgeon et al. 1999, Scrosati 1998), more complex types with meristems above the break point (e.g. Fucales and Laminarales) would fail (Kennelly 1987, Lüning 1990, Printz & Baardseth 1956). It is likely that the species tested in this study, with the possible exception of *F. vesiculosus* can recover from remaining holdfast (Dudgeon et al. 1999, Fralick & Mathieson 1972). While it is rare for a seaweed to become reproductive after dislodgment (Bird & McLachlan 1977, Norton 1977, Norton & Mathieson 1983), it is relatively common to find drifting reproductive fragments due to dislodgment from nearby attached beds. In Hog Island Bay, drifting reproductive fragments have been observed for all the tested species (pers. obs.), although propagule viability were not evaluated. Drifting fragments provide an opportunity for long range dispersal, compared to propagules in the water column (Kendrick & Walker 1991, Lüning 1990, Norton 1992, Santelices 1990). Some algae also have the ability to produce secondary rhizoids and re-attach to the substrate (Macchiavello et al. 2003, Perrone & Cecere 1997, Santelices & Varela 1994), although it is unlikely that the tested species are capable of this, except *C. fragile* under very rare

circumstances (Appendix 1, Fralick & Mathieson 1972, Mathieson et al. 2003, Yotsui & Migita 1989).

Allometric models of break force and break velocity

In Hog Island Bay the four least opportunistic species (*C. fragile, G. foliifera, F. vesiculosus, G. verrucosa* (Chapter 5, Appendix 1, Littler 1980, Nielsen & Sand-Jensen 1990) had significant increases of break forces versus thallus area when attached to bivalve shells probably because large individuals have large holdfasts and thick stipes (Friedland & Denny 1995, Gaylord et al. 1994, Kawamata 2001, Malm et al. 2003). However, the two most opportunistic species (*U. curvata, A. subulata*) did not (Hawes & Smith 1995). Also, the study documented that the F_{break}-A_{plan} relationship breaks down when organisms are attached to weak substrates like *D. cuprea* tube caps. Even though some species increased attachment force with size, it did not match the drag increase, and hence all species on both substrate types showed an increasing likelihood of breakage with size. This supports the hypothesis that the upper size of marine organisms can be limited by hydrodynamic forces (Denny et al. 1985, Gaylord et al. 1994). The allometric models support a mechanistic based model of the absence of *C. fragile, A. subulata* and *F. vesiculosus* from tube caps (Chapter 3). These species typically grow into large individuals, but because of low break velocities would dislodge at tidal peak currents. Other possible explanations of the absence of these species on tube caps include low encounter rates (Chapter 2, this Chapter), low desiccation and/or low burial tolerance (Chapter 5, 6, Appendix 1), and low worm-preference (Chapter 3).

Effects of species, substrate and size on break force and velocity

Algal individuals in Hog Island Bay were small compared to dominant algae from open temperate coasts, where kelps and large fucoids often have fronds 5-100 times larger than observed in Hog Island Bay (Thomsen & Wernberg submitted)). It should be noted that because size was presented as thallus area 'light' species, e.g. *U. curvata*, were comparable in size to 'heavy' seaweeds like *C. fragile* and *F. vesiculosus*. Substrate was the most important of the three test-factor both for break forces and break velocities similar to other studies which have documented strong relationship between substrate hardness and likelihood of biomass loss (Barnes & Topinka 1969, Malm et al. 2003, Milligan & DeWreede 2000). *U. curvata* differed from the 5 other species by having a low difference in break forces and velocities between the two substrate types. Thus, soft substrates (tube caps) may potentially be beneficial for small and opportunistic algae with weak attachment strengths, by providing space free of large competitors. The morphological similar *G. verrucosa*, *A. subulata* and *G. foliifera* had relatively similar break forces, being smaller than the larger *C. fragile* and *F. vesiculosus*, and larger than the opportunistic *U. curvata* (based on WW). This is consistent with other studies that found similar break forces between species of relatively similar morphologies and sizes (Pratt & Johnson 2002, Shaughnessy et al. 1996).

Effect of species, substrate and size on break place

Algal break place can determine the likelihood of survival and hence the stability of communities (Blanchette 1997, Dudgeon et al. 1999, Shaughnessy & DeWreede 2001). In Hog Island Bay, all six algal species had between 30-60% pruning on bivalve shells, suggesting that re-growth from holdfast and stipes likely are important recovery

mechanisms, potentially ensuring long term algal survival on oyster reefs (Chapter 6). On the other hand most species attached to tube caps dislodged with no chance of thallus recovery, except for *U. curvata* that had a high degree of pruning. Thus, the high degree of pruning and recovery mechanisms can to some extent explain the ubiquity of the *U. curvata - D. cuprea* association (Chapter 3). The ubiquity of the *G. verrucosa- D. cuprea* association could instead be caused by polychaete preference, polychaete-induced fragmentation, high algal stress tolerance and high algal-polychaete encounter rates (Chapter 3, 5, Stokke 1956).

Break place can also have implications for succession trajectories. If dislodgment occurs under hydrodynamic stress, new substrate becomes available and primary succession will follow. However, if pruning occurs biogenic material will remain on the substrate and secondary succession will follow (Connell and Slatyer, 1977). In this case re-colonization will depend on recovery abilities, in addition to propagule settlement and growth, and encroachment from neighbors. In Hog Island Bay primary succession should be relatively important on shells (50-70% of disturbance events) but highly important on tube caps (90-100% of disturbance events), although this pattern would be reversed if *U. curvata* is the substrate occupier. Field experiments should test if small scale succession differ between tube caps and shells with and without minute algal fragments.

Comparing break velocities to hydrodynamic regime

Hydrodynamic forces within Hog Island Bay are likely to induce size-limitations for all species and substrate-types, but more so for algae on tube caps (Fig. 4.5A) compared to

bivalve shells (Fig. 4.5B), and in the following order of severity: *U. curvata* > *A. subulata* > *G. foliifera* = *G. verrucosa* > *F. vesiculosus* = *C. fragile* (on shells, Fig 4.5B). Based on the allometric break velocity models it is further predicted that velocities typical of Hog island Bay and other soft bottom tidal systems (0.1-1 ms^{-1})(Albrecht 1998, Hawes & Smith 1995) would dislodge individuals in the size range of 0.01-0.1 m^2 for algae attached to tube caps, and for individuals in the size range of 0.1-1 m^2 for algae attached to shells. Such size limitations and thallus breakage would be most likely at near-ocean sites and/or between physical structures were flow is elevated. It should be noted that these estimates are based on a constant C_{drag}, species-specific, not individual based, A_{plan}:WW ratios and ignoring lift or acceleration forces. Whereas the two first assumptions can under- or overestimate the true break velocity depending on whatever the drag coefficient and thallus area are higher or lower than estimated here, the addition of more hydrodynamic forces will always result in an lowering of U_{break} (Friedland & Denny 1995, Shaughnessy et al. 1996, Utter & Denny 1996). Ignoring acceleration and impact forces seems appropriate in low energy lagoons where waves are small. Lift could be of importance for the positively buoyant *F. vesiculosus* and *C. fragile*, but Dromgoole (1982a) showed that for *C. fragile* lift was small compared to drag and Friedland & Denny (1995) also documented low lift for the vesiculated kelp *Egregia menzeii*. In spite of the simplicity of the models, flume runs supported the predicted break velocities and Hawes and Smith (1995) also found a similar correspondence for *Ulva lactuca*. Water velocities have been interpreted as being generated from tidal currents. However, Lawson (2003) calculated that during storms shallow water high frequency benthic wave stresses may be similar in magnitude to tidal current stresses within Hog Island Bay, especially on

the extensive mudflats. Thus, future biomechanical models should incorporate added velocity components from storm waves.

Entrainment and entanglement

Two additional processes can affect the likelihood of thallus breakage: entrainment and entanglement. In the present study, it has been assumed (as in Hawes & Smith 1995) that algae attached to shells either break or stay in place. This is mainly valid for algae attached to consolidated oyster reefs because healthy oysters typically have stronger adhesives than the algae-shell binding (but diseases, a small oyster attachment surface and erosion by boring sponges may increase the likelihood of oyster breakage)(Barh & Lanier 1981). A large proportion of the individuals found in this study were attached to unconsolidated shells and hence 'entrainment' of the algae-shell complex could be an alternative to dislodgment or pruning. A typical oyster shell of 0.05 kg (WW) corresponds to a weight of 0.25 N in water (specific limestone gravity of ca. 2 gcm^{-3}). This weight is an order of magnitudes lower than most measured break forces, and entrainment should therefore be of main importance for algae attached to unconsolidated shells (Ben Avraham 1971, Dromgoole 1982, Smith & Bayliss-Smith 1998), even though sediment-shell resistance was ignored. Thus, size-limitations are less likely on single shells, partly explaining why these algae can be found as larger thalli in Hog Island Bay compared to algae attached to consolidated substrates (pers. obs.). The second process, 'entanglement', can add drag proportional to the biomass of the tumbling clump (Holmquist 1994, Holmquist 1997, Norton & Mathieson 1983) to attached algae instantaneously but without increasing the attachment strength (Friedland & Denny 1995,

Koehl & Wainwright 1977, Utter & Denny 1996). Here, encounter rates were documented to be high, indicating that entanglement can be an important drag-increasing process in Hog Island Bay. However, in addition to the encounter rate, the actual entanglement also depends on properties of both attached and drift algae and flow rates. For example, *C. fragile* was often entangled by filamentous genera like *Ectocarpus* spp. and *Bryopsis* spp., which would break before their host. Also whereas *G.* and *U. curvata* tumble along the bottom, *F. vesiculosus* and *C. fragile* drift in the water column making it unlikely for the latter taxa to entangle benthic algae.

Other factors of importance

Many factors other than species, size and substrate types influence algal break forces and break velocities, e.g. season, exposure level, and wounding (Duggins et al. 2001, Pratt & Johnson 2002, Thomsen & Wernberg submitted). It is likely that storm and spring-tide currents remove weakly attached large individuals on predictable temporal scales (fall and winter in Hog Island Bay, Dolan 1996, Lucy et al. 1986). Such temporal cycles can create substantial variability in break forces depending on whatever sampling was conducted before or after the storm (Bell 1999, Blanchette 1997, Milligan & DeWreede 2000, Pratt & Johnson 2002). Similarly, grazer scars may reduce break forces (DeWreede et al. 1992, Duggins et al. 2001, Padilla 1993), and it was observed that *U. curvata* generally had a 'Swiss-cheese' morphology, probably due to amphipod grazing. Because Hawes and Smith (1995) observed *U. curvata* breaking at the stipe, the high degree of *U. curvata* breaking at the thallus in the present study could be caused by grazer scars. Finally, sediment burial and anoxia can also lower break forces, and algae attached to

buried shells typically had black and necrotic holdfasts with lower break forces than individuals sampled in the present survey (preliminary trials). Future biomechanical studies from low energy soft bottom habitats should include entrainment and entanglement process as well as more test factors into a multi-factorial biomechanical framework, to improve on the proposed dislodgment models, and ultimately be able to predict break events.

In conclusion, species and substrate type determine where an algae break, and species, substrate type and thallus size further determine algal break forces and break velocities in a low energy soft bottom lagoon. Dislodgment and pruning are probably common processes at peak hydrodynamic stresses, particularly for opportunistic species, and for large individuals attached to soft substrates like polychaete tube caps, although field testing are needed to verify these prediction.

Chapter 4. Tables

Table 4.1. Linear models of Log A_{plan} (m^2) vs. Log F_{break} (Newton) and Log U_{break} (ms^{-1}). Significant results are in bold ($p < 0.05$). Note that p-values were not provided for U_{break} because interdependency between A_{plan} and U_{break} invalidates statistical testing.

			F_{break}				U_{break}		
Species	**Substrate**	**n**	**Slope**	**Intercept**	**r^2**	**p**	**Slope**	**Intercept**	**r^2**
C. fragile	Tube cap	15	-0.27	-1.21	0.01	0.73	-0.63	-1.90	0.18
F. vesiculosus	Tube cap	15	-0.26	-0.77	0.02	0.60	-0.63	-1.62	0.34
A. subulata	Tube cap	15	-0.74	-0.87	0.06	0.39	-0.87	-2.35	0.25
G. foliifera	Tube cap	15	0.12	-0.79	0.01	0.80	-0.44	-1.08	0.20
G. verrucosa	Tube cap	32	0.18	-0.58	0.03	0.85	-0.41	-0.89	0.36
U. curvata	Tube cap	30	0.13	-0.77	0.03	0.86	-0.44	-1.11	0.58
C. fragile	Shell	64	0.37	0.35	0.17	**0.00**	-0.31	-0.12	0.39
F. vesiculosus	Shell	83	0.39	0.39	0.43	**0.00**	-0.30	-0.02	0.64
A. subulata	Shell	29	0.11	0.41	0.07	0.17	-0.45	-0.50	0.84
G. foliifera	Shell	31	0.35	0.52	0.38	**0.00**	-0.32	-0.10	0.67
G. verrucosa	Shell	50	0.35	0.41	0.29	**0.00**	-0.32	-0.16	0.58
U. curvata	Shell	55	0.16	0.21	0.03	0.19	-0.42	-0.81	0.49

Table 4.2. ANOVA on thallus area (A_{plan}), break force (F_{break}) and break velocity (U_{break}) for 6 species, 2 substrate types and 2 size-classes. Significant results ($p < 0.05$) are in bold. Cf. Table 4.1 for number of replicates (divide into large vs. small sizes). Variances were homogeneous (all variables Log-transformed), except for A_{plan} vs. substrate, F_{break} vs. species and U_{break} vs. species.

			A_{plan}		
Source	**Df**	**SS**	**η^2(%)**	**F**	**p**
Species (SPE)	5	7.43	6	11.25	**0.00**
Substrate (SUB)	1	2.86	2	21.66	**0.00**
Size-class (SIZ)	1	36.85	28	278.88	**0.00**
SPE * SUB	5	19.47	15	29.47	**0.00**
SPE * SIZ	5	4.20	3	6.36	**0.00**
SUB * SIZ	1	4.20	3	31.81	**0.00**
SPE * SUB * SIZ	5	2.32	2	3.52	**0.00**
Error	413	54.57	41		
			F_{break}		
Source	**Df**	**SS**	**η^2(%)**	**F**	**p**
Species (SPE)	5	12.00	5	14.40	**0.00**
Substrate (SUB)	1	143.28	57	859.67	**0.00**
Size-class (SIZ)	1	1.86	1	11.16	**0.00**
SPE * SUB	5	24.00	10	28.81	**0.00**
SPE * SIZ	5	0.46	0	0.55	0.74
SUB * SIZ	1	1.07	0	6.43	**0.01**
SPE * SUB * SIZ	5	0.48	0	0.58	0.72
Error	413	68.83	27		
			U_{break}		
Source	**SS**	**η^2(%)**	**F**	**p**	
Species (SPE)	5	9.12	13	31.22	**0.00**
Substrate (SUB)	1	26.41	39	452.11	**0.00**
Size-class (SIZ)	1	5.54	8	94.79	**0.00**
SPE * SUB	5	1.48	2	5.06	**0.00**
SPE * SIZ	5	0.81	1	2.77	**0.02**
SUB * SIZ	1	0.26	0	4.41	**0.04**
SPE * SUB * SIZ	5	0.54	1	1.85	0.09
Error	413	24.13	35		

Table 4.3. χ^2-tests results on break place. Results from the species-specific logistic regressions of P_{break} vs. A_{plan} were not included in the table, but all p-values were non-significant (p = 0.22-0.94). Significant results are in bold (p < 0.05).

Test	χ^2	Df	p	n
Main effects				
Species (SPE)	29.0	5	**0.00**	419
Substrate (SUB)	4.76	1	**0.03**	419
Size-class (SIZ)	0.48	1	0.48	419
Size class for each species				
C. fragile	0.51	1	0.48	74
F. vesiculosus	0.00	1	0.95	93
A. subulata	0.03	1	0.87	42
G. foliifera	0.19	1	0.66	43
G. verrucosa	0.21	1	0.65	82
U. curvata	2.75	1	0.10	85
Substrate for each species				
C. fragile	7.5	1	**0.01**	74
F. vesiculosus	4.34	1	**0.04**	93
A. subulata	2.77	1	0.10	42
G. foliifera	4.75	1	**0.03**	43
G. verrucosa	9.93	1	**0.00**	82
U. curvata	7.84	1	**0.01**	85

Table 4.4. Flume dislodgment of small vs. large *G. verrucosa* and *U. curvata* incorporated into *D. cuprea* tube caps at 3 velocities (n = 8 per species and size class, with standard errors). The first rows correspond to the initial biomass of per tube cap before flume induced breakage.

Velocity	Species	Size 1	SD	Size 2	SD
Initial biomass per tube cap (gWW)	*G. verrucosa*	0.86	0.78	9.19	3.46
	U. curvata	0.40	0.26	1.85	0.88
% dislodgment of initial biomass at 10 cm s^{-1}	*G. verrucosa*	0.00	0.00	0.03	0.08
	U. curvata	0.00	0.00	0.37	1.06
% dislodgment of initial biomass at 30 cm s^{-1}	*G. verrucosa*	0.28	0.80	0.14	0.40
	U. curvata	0.33	0.92	8.72	24.67
% dislodgment of initial biomass at 45 cm s^{-1}	*G. verrucosa*	2.02	4.84	9.64	26.55
	U. curvata	0.00	0.00	3.66	3.95
% dislodgment of initial biomass - Total	*G. verrucosa*	2.30	5.62	9.81	26.48
	U. curvata	0.33	0.92	12.75	25.90

Table 4.5. Species and sizes of drift algal clumps. Results from four summer surveys were pooled (mean sample condition per survey were: 2.18 m between poles, 0.28 m water height, 0.17 ms^{-1} current velocity, 270 sec sampling time). The average reoccurrence interval (number of clumps encountered for a sessile benthic algae) was 8.9 $secm^{-1}$ coastline. The median clump wet weight was 10 g and the maximum 1060 g. SE = Standard errors.

Taxa	**gWW**	**SE**	**m^2**	**#**
Richness	3.19	0.25		69
Total	80.34	21.14	0.2306	69
G. verrucosa	36.41	10.76	0.0583	41
C. fragile	15.80	8.49	0.0079	8
B. plumosa	11.52	4.17	0.1152	50
G. foliifera	8.74	3.15	0.0131	17
A. subulata	3.22	1.61	0.0045	11
C. parvula	1.44	0.45	0.0036	31
Polysiphonia spp.	1.30	0.62	0.0130	23
U. curvata	1.03	0.61	0.0103	11
Ceramium spp.	0.44	0.25	0.0044	11
F. vesiculosus	0.19	0.18	0.0002	2
L. bayileyana	0.04	0.04	0.0001	2

Chapter 4. Figures

Fig. 4.1. Thallus planform area (A), break force (B), break velocity (C) and break place (D) for 6 species, 2 substrate types and 2 size classes. Species are arranged from low (left) to high S_{plan}:WW ratios (± SE, cf. Table 4.1 for number of replicates).

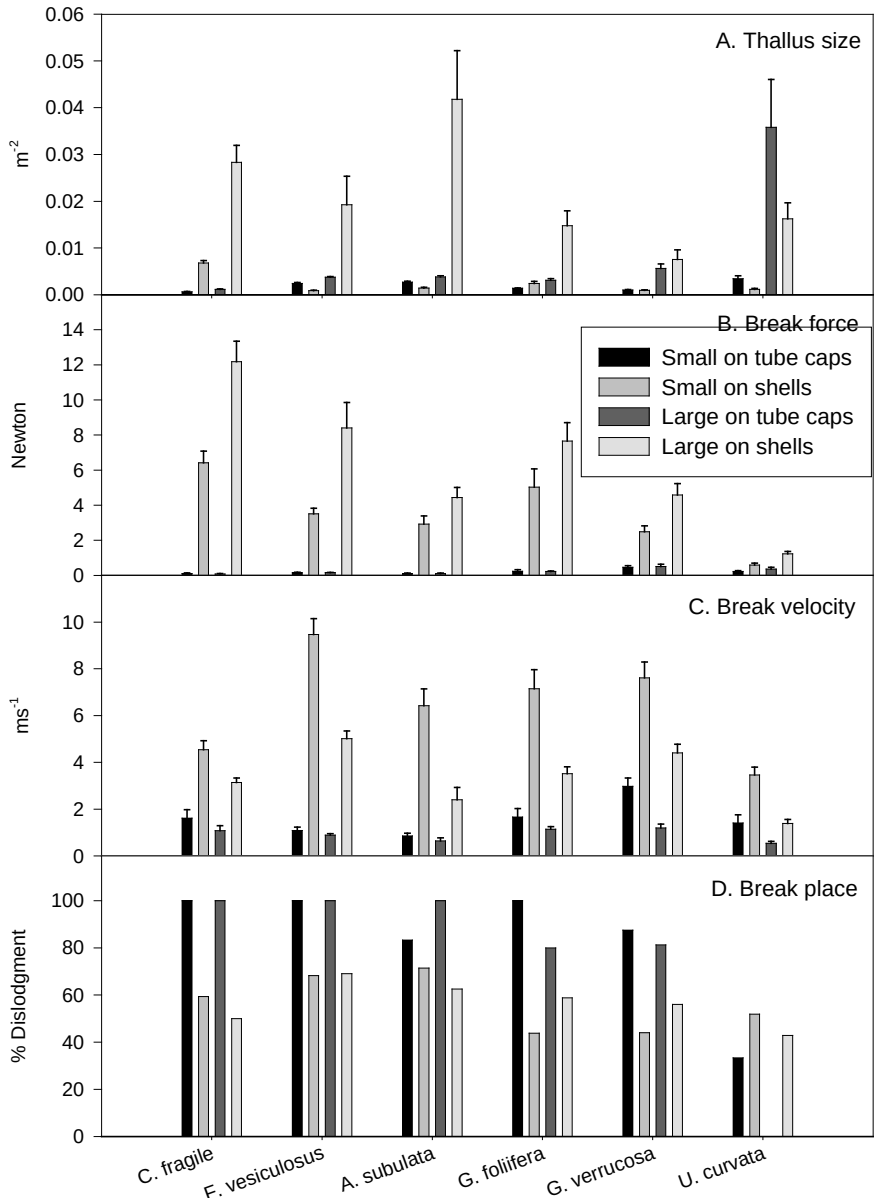


Fig. 4.2. Current velocities in front, between and behind oyster bars in a mid-lagoon site (S1) with high algal biomass. Currents were measured with a Marsh-McBirney electromagnetic current meter at 15-40 cm water level. Error bars are 95% CL (n = 4).

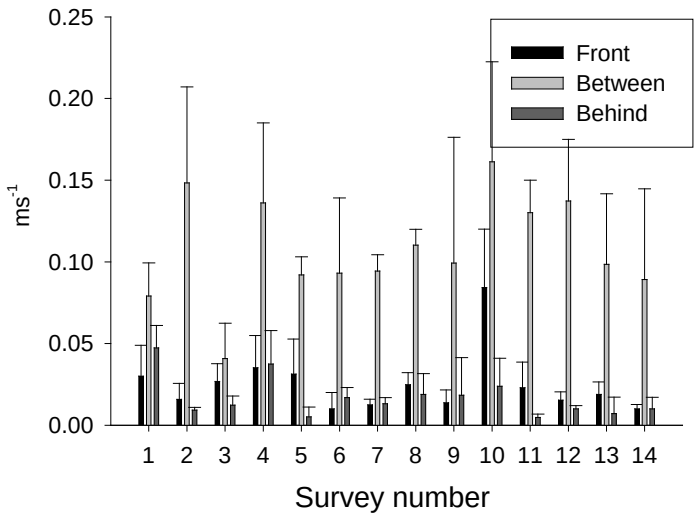


Fig. 4.3. Current velocities at 3 distances from the bottom measured with an Acoustic Doppler Profiler. The ADP was put out on January 17 2002 and currents were measured every 30 minutes for several months. Only a small subset of the total data set is shown, to document typical tidal changes and to show the maximum currents measured (0.82 ms^{-1}) (data from P. Wiberg and S. Lawson, University of Virginia).

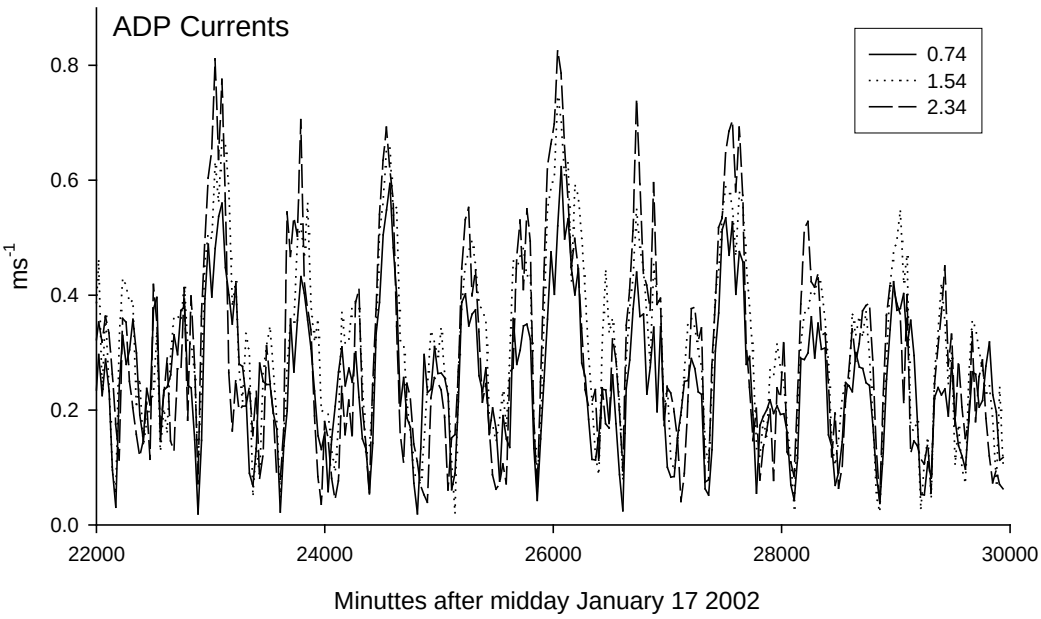


Fig. 4.4. Peak currents in Hog Island Bay at incoming mid-tide, calculated from a 2d Bellamy Kinematic hydrodynamic model. The Map was produced by Lawson (2003) and the model developed by Fugarte and Fridrich (Submitted).

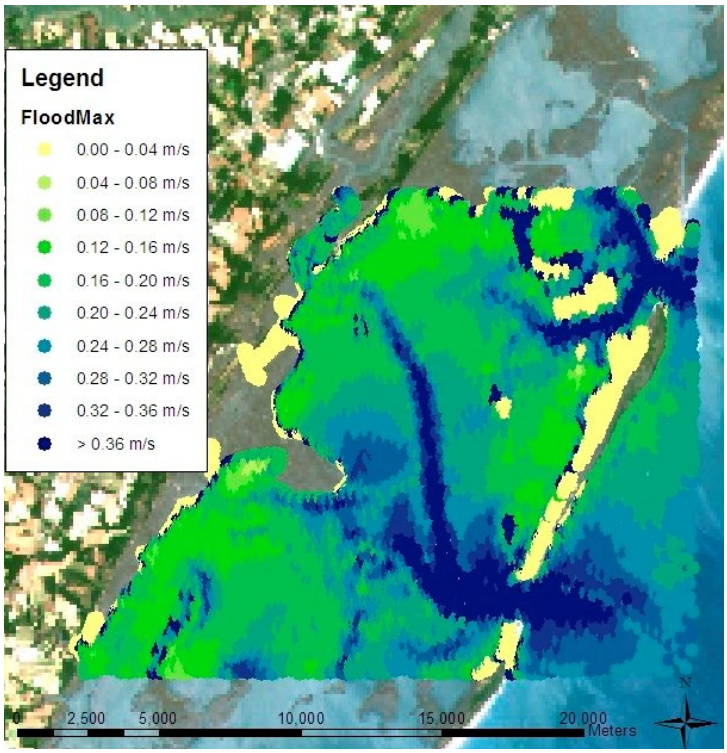
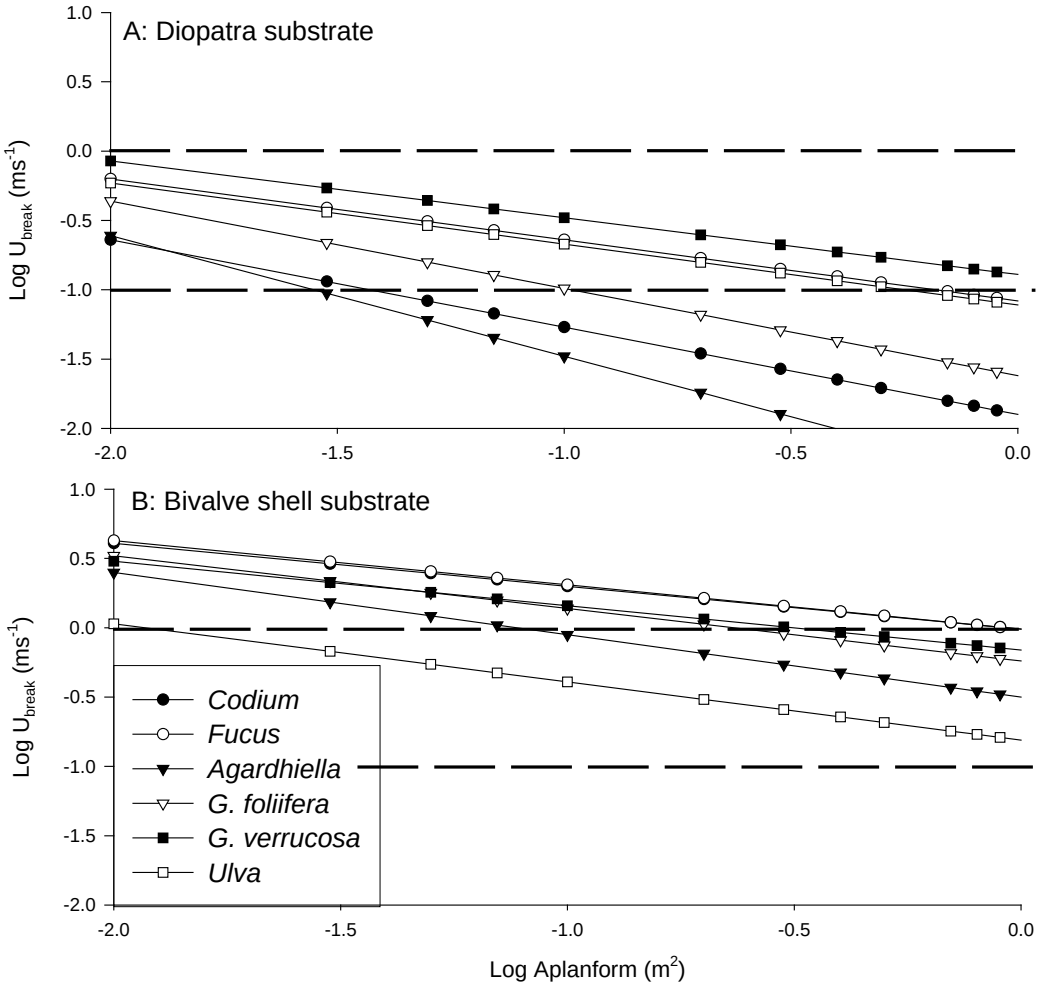


Fig. 4.5. Species-specific allometric Log-models of planform area versus break velocities (cf. Table 4.1) when attached to *D. cuprea* tube caps (A) and bivalve shells (B). The vertical dashed lines shows typical velocity ranges encountered in Hog Island Bay (0.1-1 ms^{-1}). Algae above the top line are 'safe' from breakage, between the lines susceptible to breakage under peak hydrodynamic events, and below the lower line should break in most places and during most tidal cycles.



Chapter 5. The alien *Codium fragile* have low performance characteristics compared to native macroalgae in a soft bottom turbid lagoon, Virginia

Abstract

The chapter investigates whether the successful introduction of the Asian macroalgae *Codium fragile* ssp. *tomentosoides* into Hog Island Bay, a shallow lagoon in Virginia with extensive intertidal areas, can be explained by an ability to perform better than native macroalgae. Hog Island Bay is characterized by high turbidity and high sedimentation rates, high densities of herbivorous mud snails, relatively low nutrient concentrations, and predictable gradients in water quality from mainland to ocean sites. Given a well-documented ability of *C. fragile* to invade soft bottom lagoons we hypothesized that *C. fragile* would perform better compared to native macroalgae. To test this hypothesis, nine growth experiments were conducted between March and August 2002 using drift algal assemblages containing fragments of *C. fragile*, *Fucus vesiculosus*, *Gracilaria verrucosa*, *Agardhiella subulata*, *Hypnea musciformis* and *Ulva curvata*. Contrary to the hypothesis, *C. fragile* performed no better than the native species in all experiments. *C. fragile* were less resistant to sedimentation, were more desiccation prone, showed lower growth rates at either high or low light levels or nutrient concentrations, and were more severely grazed by mud snails than the native species. Although *C. fragile* was able to grow along the entire mainland-ocean gradient, growth was consistently lowest at near-mainland sites, intermediate at near-ocean sites, and highest at mid-lagoon sites. This pattern was most likely due to light limitation at the near-mainland site and nutrient-limitation at the near-ocean site. In comparison, *F. vesiculosus* was resistant to stressful conditions, particularly desiccation, *G. verrucosa* had some stress-tolerant traits, and could sustain higher growth than *C. fragile*, and *H. musciformis* and *U. curvata*, and, to a certain extent, *A. subulata* had opportunistic traits with high growth under high

nutrient and light conditions. These results provide a process oriented basis for why *G. verrucosa* and *U. curvata* are more abundant and have a wider distribution pattern than *C. fragile* within Hog Island Bay. The results also fit into a surface to volume ratio framework (S:V), where growth and growth variability increased with increasing S:V ratio. In conclusion, the commonly reported invasive success of *C. fragile* could not be related to superior growth or stress resistance compared to native species in Hog Island Bay.

Introduction

Invasions of alien species are considered a major threat to global biodiversity because the invaders often outcompete, eat or infect native species (Carlton 1999, Meinesz 1999, Ruiz et al. 1997). Several marine macroalgae have caused dramatic transoceanic invasions. In particular, *Caulerpa taxifolia*, *Undaria pinnatifada*, *Sargassum muticum*, and *Codium fragile* ssp. *tomentosoides* invasions have created adverse effects worldwide by clogging waterways, competing with native algae, altering the nursery habitat for fishes and invertebrates, reducing light penetration in the water column, changing biogeochemical cycles, and suffocating or drifting away with economically important shellfish (Chapman 1999, Den Hartog 1998, Meinesz 1999, Norton 1976, Stæhr et al. 2000, Wallentinus 2002). Often the invasive success of a species has been related to 'super'-traits (e.g. high intrinsic rate of growth, high dispersal capacity and high regenerative abilities, Meinesz 1999, Norton 1976, Rejmánek & Richardson 1996, Stæhr et al. 2000, Trowbridge 1998, Wernberg et al. 2001). It is therefore important to

understand how species traits influence performance if the effects of macroalgal invasions are to be evaluated and future invasions predicted, managed and prevented.

The macroalgal invader *C. fragile* ssp. *tomentosoides* (van Goor) Silva originates from Asia (Trowbridge 1998), but spread to the North American east coast in the 1950s and arrived in Virginia in the 1970s (Hillson 1976). Today, *C. fragile* is the fourth most common species in Hog Island Bay (Chapter 2), a shallow turbid lagoon, which is part of the U.S. Long Term Ecological Research program (Virginia Coast Reserve, Hayden et al. 2000). Due to its high relative abundance, *C. fragile* can be considered successful in Virginian turbid shallow waters. Conclusions about traits that make a species successful have often been interpreted from single-species independent laboratory experiments (e.g. Littler 1980, Lotze & Schamm 2000, Pedersen & Borum 1997, Wallentinus 1984), where extrapolations to multi-species interdependent performance responses are limited. There is a need for multi-species multi-factorial field experiments comparing performance of invasive species to native species to understand invader success.

The lagoonal habitats successfully invaded are typically characterized by low light penetration (Lawson 2003, McGlathery et al. 2001), high meso-grazer densities, especially of mudsnails (this study, Giannotti & McGlathery 2001, Rosinski 2004, Scheltema 1964), high sedimentation and re-suspension rates (Lawson 2003) and often relatively high nutrient concentrations (Goshorn et al. 2001). In addition to these characteristics, two spatial gradients may further influence macroalgal performance in coastal soft bottom systems. On a small vertical scale, tidal changes create the potential

for different desiccation rates, grazing rates, sedimentation levels and light conditions at different elevation levels (Colman 1933, Doty 1946, Lewis 1964). On a large horizontal scale different distances from the mainland results in a gradient in nutrient loading and in water residence time which influence turbidity, nutrient, light, temperature and sedimentation levels (Castel et al. 1996, Lawson 2003, McGlathery et al. 2001). The success of *C. fragile* in low energy lagoons and estuaries (Malinowski & Ramus 1973, Trowbridge 1998) suggests a high tolerance to the variations in physical and chemical characteristics within these lagoons.

The main objectives of this study were to investigate if *C. fragile* performs better in terms of biomass gain relative to native macroalgae under a range of conditions within the lagoon. Specifically, it was hypothesized that *C. fragile* would be superior under low and high levels of mud snail grazing, nutrients, light, desiccation, sedimentation, and at all sites along the distance-gradient. Because the elevation gradient is strong and well-described (high levels = desiccation, Doty 1946, Dromgoole 1980, Lüning 1990) compared to the distance gradient, the latter was of particular interest in this study. To test these hypotheses, nine independent *in situ* experiments were conducted in spring and summer 2002 directly comparing performance of *C. fragile* to native macroalgae in drift algal mini-assemblages. In addition to *C. fragile*, assemblages contained tissue fragments of *Fucus vesiculosus* L., *Agardhiella subulata* (C. Ag.) Kraft et Wynne, *Gracilaria verrucosa* (Hudson) Papenfuss, *Hypnea musciformis* (Wulfen) Lamouroux, and *Ulva curvata* (Kutzing) De Toni, arranged after surface area:volume (S:V) ratio with *C. fragile* having lowest and *U. curvata* highest ratios (Nielsen & Sand-Jensen 1990). These species

were chosen because they are typical components of lagoonal drift algal assemblages along West Atlantic coastlines (Cowper 1978, Goshorn et al. 2001, Thorne-Miller et al. 1983).

Methods

Study site

Hog Island Bay is a ca. 100 km^2 low-energy lagoon on the Delmarva Peninsula on the eastern shore of Virginia, US (McGlathery et al. 2001). Scattered unconsolidated bivalve shells of the oyster *Crassostrea virginica* and clam *Mercenaria mercenaria*, and patchy intertidal oyster reefs provide hard substrate for macroalgal attachment. The average depth is 1.5 m and ca. 80 % of the lagoon is less than 3 m deep (Oertel 2001). Semidiurnal tides move mats of drift algae around within the lagoon (McGlathery et al. 2001, Tyler et al. 2001) at typical flow rates of 0.1-0.3 ms^{-1} (Chapter 4). Mud snails are present year-round in high densities in marshes and on mudflats (Table 5.1, Giannotti & McGlathery 2001, Rosinski 2004). Dissolved nitrogen is typically 15-20 μM and light extinction between 1.7 to 2.2 m^{-1}, with highest values near the mainland and lowest near the ocean (Table 5.1, McGlathery et al. 2001). Sedimentation, re-suspension and suspended solid concentrations are high throughout the lagoon, and storms can add or remove several centimeters of sediment within a few hours (Lawson 2003). *Codium, F. vesiculosus, A. subulata*, *G. verrucosa* and *U. curvata* are relatively common year-round and they potentially compete for substrate, light and nutrients. *H. musciformis* is mainly found in summer months as an entangled epiphyte (Norton & Mathieson 1983), and probably does not compete for substrate. The six algal species constitute more than 90%

of the total algal biomass in Hog Island Bay (Chapter 2), and as such represent the typical drift algal assemblages.

***In situ* experiments**

Seven factorial experiments were conducted to test for effects on tissue performance of species (SPE), distance from mainland (DIS), elevation level (ELE ≈ desiccation), sedimentation/burial (SED), light reduction (LIG), nutrient addition (NUT), and grazer/snail addition (GRA). Two additional experiments were conducted to test for experimental artifact, such as effects of twist-tie wrapping (TWI) and cage enclosure (CAG). Although assemblage experiments can produce statistically biased p-values because of potential interdependence of species they have high predictive value compared to single-species laboratory experiments because of a close resemblance to natural *in situ* conditions (Peters 1991). Details on the experimental design are given in Table 5.2. Apical fragments cut from healthy and fresh algal specimens (0.2 to 2 g WW; species with high S:V ratio had lowest biomass) were collected from drift mats in the mid-lagoon, and allowed 24 hours of wound recovery before field incubation (Ramus & Venable 1987). Wet weight (0.001 g) was measured before and after incubation after blotting with a towel. Performance was defined as percent change in biomass per fragment per incubation period. This measure was preferred over the exponential growth model (Pedersen 1995, Pedersen & Borum 1996) because the latter cannot account for a total biomass loss. Because the main objective was to compare performance of *C. fragile* to native species under a range of environmental conditions, mortality was frequently encountered (=100% biomass loss). Another advantage of the time-integrated

performance measure is that it makes no assumption about temporal development in biomass change. Daily biomass changes can be calculated from incubation time and biomass data (Table 5.2, 5.6). A few fragments and assemblages were lost due to storms resulting in a few slightly unbalanced designs.

Elevation effects

To estimate the relative importance of elevation and distance, two open plot experiments were carried out in spring 2002 (16 and 14 days of incubation). An open plot design eliminate cage artifacts associated with flow reductions. Because *H. musciformis* was not found in spring and *U. curvata* only in minute quantities, these two species were not included. A fragment of *C. fragile, F. vesiculosus, A. subulata* and *G. verrucosa* was attached with a twist-tie which was gently wrapped around the fragment (a maximum of 5% of the fragments were physically covered by the twist tie) and attached to a cable tie to mimic a typical assemblage. The cable ties were then attached at two elevations on PVC poles: Low elevation = 0.8 m and High elevation = 0.0 m below mean sea level. Poles were inserted into the sediment at five near-mainland, five mid-lagoon and five near-ocean sites, each site being separated by a minimum of 500 m (n = 1 pole per site). Because numerous fragments died at the high-treatment in the first experiment a lower high-treatment was used in the second experiment (High = 0.5 m below mean sea level).

Sedimentation effects

To test for resistance to sediment burial, a litterbag decomposition experiment was conducted. Pre-weighed fragments (minus *H. musciformis* which was not present in May 2002) were incubated in 4 mm mesh bags buried under 3 cm sandy sediment in the lower

intertidal zone (0.5 m below mean sea level) at a mid-lagoon mudflat. Litter bags were recovered after 0, 1, 2, 3, 7, 12, 21, 27, 34 and 37 days of burial and wet weight was measured on remaining fragments (n = 3-6 per sampling day). The sediment characteristics at the site were: organic matter = 2.1% DW, sediment molar C:N = 11.8, sediment bulk density 1.51 gcm^{-3} (McGlathery et al. 2001), and mean sediment grain diameter = 63 μm (Lawson 2003).

Cage experiments

Cage experiments were conducted to test for effects of nutrient addition, shading of light, addition of grazing snails and for effects of methodological artifacts of twist tie wrapping and cage enclosure. Each of these experiments were replicated at a near-mainland (Creek 1), a mid-lagoon (Shoal 1) and a near-ocean (Hog 1) site (McGlathery et al. 2001). This design allowed us to test the interactions between the uncontrolled spatial gradient and the controlled treatments listed below. All allocations were random (fragments, treatments, order and position of cages, etc). Fragments were enclosed in 22 cm transparent acrylic cages with 30 two-millimeter perforations to keep grazers out and fragments inside of cages and to ensure a steady water flow. The cages reduced the photosynthetic active radiation (PAR) by 11%, calculated from 10 PAR-measurements taken during a sunny summer day from 10 AM to 6 PM. One fragment of each of the six species was added to a cage and the ends were closed with plastic caps. The mean algal density at the start of these experiments was 130 $gWWm^{-2}$ (n = 230, SD = 33 $gWWm^{-2}$, Max. = 240 $gWWm^{-2}$; Cage densities were calculated by estimating that 40% of the total cylindrical cage surface (= 0.022 m^2) provided substrate for looselying algal fragments).

Cages were kept submerged and aerated until incubation and were incubated horizontally attached to floating PVC frames 15 cm below the water surface.

Light, Nutrient, and Grazer effects

The effect of light reduction was tested by comparing cages covered with white screening nets to cages covered with black but identical screening nets (8 days of incubation). These manipulations corresponded to 32 and 51% reduction in PAR compared to non-caged open plots (PAR-sampling procedure as above, n = 4). The effect of nutrients on growth rates was tested by adding two fertilizer stakes to half of a set of cages in two consecutive experiments (7 and 6 days of incubation). A stake weighed 62 g and contained 4% available phosphate and 2% NO_3^-, 2% urea, 2% other soluble N and 7% water insoluble N (13% total N, Jobe's Fertilizer Spikes™). Similar fertilizer stakes have been applied with success in other enrichment studies (cf. references in Worm et al. 2000). At the end of the experiments their were still minute quantities of the stakes left within the cages. To test for effects of grazers, adult mud snails (*Ilyanassa obsoleta* (Say) were added as 0, 2, 7 and 20 snails per cage following 24 hours of starvation (n = 2). The mudsnails utilized all cage surfaces (top/bottom), and densities were calculated using the total cage surface (0.055 m^2) to 0, 36, 126 and 362 snails m^{-2} corresponding to typical density ranges encountered in Hog Island Bay (Table 5.1, Giannotti & McGlathery 2001, Rosinski 2004). Tissue nitrogen was measured on fragments from the nutrient experiment to verify that the added stakes provided elevated levels of nutrients (algae are typical nitrogen limited in summer month, Lapointe et al. 1992, Pedersen 1995, Pedersen & Borum 1996). In addition, tissue nitrogen was measured in the snail addition experiment

because invertebrates have been shown to enhance growth by excretion of nitrogen-rich waste products (Fong et al. 1997, Williams & Carpenter 1988). Tissue for N-analysis was rinsed in de-ionized water, oven dried at 70°C, ground to homogeneity, and N-content (% of DW) was measured in a Carlo-Erba NA 2500 Elemental Analyzer.

Methodological artifacts

Two experiments were conducted to facilitate comparisons between the cage experiments with looselying unwrapped fragments, and the open plot experiments where fragments were fixed with wrapped twist-tie. In the first experiment, the separate effect of twist-tie was tested by wrapping half of the fragments (± TWI, n = 4). These fragments were incubated looselying within the 22 cm cages. In the second experiment the combined effect of twist-tying, spatial fixation, and cage-enclosure were tested by wrapping and fixing algal fragments onto rebars and then incubating half of the rebars inside and half outside closed cages (± CAG, n = 3).

Data analysis

Fixed factorial ANOVAs were conducted on individual experiments, except for the tests of elevation and nutrient effects, where the second experiment was added as an orthogonal treatment to increase the test-power. To provide a stronger test of distance effects and to compare the integrated performance of *C. fragile* to the native species the six summer experiments were pooled and tested for effect of species, distance and experiment number. This design was balanced and the different experiments had relatively similar designs, procedures, species, sites, replicates, and ambient temperature

and light conditions (experiment number was considered fixed, because it was not of interest to extrapolate time- and design-specific effects). Factor specific contributions of total data variability were calculated within each ANOVA as percent sum of squares out of the total sum of squares (= η^2) (Levine & Hullet 2002). Despite a tendency for η^2 to be slightly biased upwards (Quinn & Keough 2002, Underwood 1993), this measure was preferred over ω^2 because of its simplicity, its analogy to the well-known r^2 in correlation analyses, and its ability to preserve rankings between different sources of variability (Levine & Hullet 2002). To investigate in a formalized way if *C. fragile* had performed better than the native macroalgae, each ANOVA was followed by Student-Neuman-Keul (SNK) pair-wise comparisons on the species-factor (Underwood 1981a). Also, because the emphasis was on *C. fragile* performance, a similar set of ANOVA's was conducted only on *C. fragile* biomass changes, again followed by SNK-tests (here on the distance factor). Because most treatment and species responses could not be transformed to variance homogeneity (Cochran C < 0.05 for Log, $X^{0.5}$, and arcsine transformation for at least one factor in each experiment), analyses were conducted on non-transformed data. ANOVA is relatively robust to violation of variance heterogeneity for balanced designs with large sample sizes (Quinn & Keough 2002, Underwood 1997). For experiments where tissue nitrogen was quantified, treatment effects on percent tissue nitrogen (%N of gDW per fragment) and total nitrogen content per fragment (%N of gDW per fragment * gDW per fragment, applying a DW:WW ratio of 10) were interpreted from graphs. Finally, because decomposition experiments typically are modeled with first order kinetic of time vs. remaining biomass (Bourgues et al. 1996, Enriquez et al. 1993) regression analysis was used. Only samples where biomass remained were included since these

models cannot account for total biomass loss. A co-variance test was conducted following regression, to test if decay slopes differed between species.

Correlation of performances between species

If asymmetric competition between species is strong, negative relationships between species performances should be detectable in correlation analyses. Negative among-sample correlation (sensu Underwood 1997) causes statistical inter-dependency and increases the likelihood of detecting spurious differences, and is therefore important to document. Alternatively, a negative correlation between species-performance could indicate opposite traits to the ambient conditions, in which case samples are independent and p-values unbiased. For example, if *U. curvata* responded positively to nutrient addition whereas *C. fragile* responded negatively, it could either be because *U. curvata* produced allelic substances, shaded out *C. fragile* or depleted nutrient sources (competition), and/or because *U. curvata* was facilitated but *C. fragile* inhibited by high nutrient concentrations (opposite traits). It should be noted that it is problematic to detect symmetric competition with a correlation analysis. Analogous to a negative correlation, a positive correlation could either indicate mutualism, or if no species-interactions occur, indicate similar ecological traits. In this case real differences are less likely to be detected (Underwood 1997). To test if species-specific performances were related, Pearsons correlation coefficients were calculated for all species pairs following each ANOVA, in particular searching for significant negative values. The correlation analyses do not correspond to a rigorous test of competition, mutualism and traits similarities, but can point to the potential merits of these processes.

Significance was determined as $p < 0.05$, and near-significant results as $p < 0.10$. No statistical corrections were applied following multiple testing procedures on the same data set. Instead, exact p-values are reported, with the knowledge that 1 out of 20 will be significant by chance (Anderson 2000). All statistical analysis were conducted in SPSS 8.0.

Results

ANOVA results comparing species performances for each experiment are given in Table 5.3, and the single-species ANOVA testing *C. fragile* performance in Table 5.4. The corresponding SNK-test results of rankings between species and *C. fragile* rankings between sites are described in the text, but summary tables can be found in Appendix 1.5. To facilitate a structured analysis of interaction effects and comparisons between species performances within and between experiments, results were graphed with identical interactions plots (Quinn & Keough 2002) showing performance (% change in biomass) on the ordinate axis and species arranged after S:V ratios on the abscissa (Fig. 5.1-5.7). These interaction plots portray all significant interaction- and single factor effects, except for four interactions of low relevance for the study objectives. Graphs portraying these results are shown in Appendix 1 for completeness.

Effect of elevation

In the elevation experiment there was a significant species * elevation * experiment interaction and several significant lower order-interactions (Table 5.3). The third order interaction effect was caused by the second experiment (Exp. 2, Table 5.2) applying a

lower and less adverse 'high'-treatment. Single factor effects of species, elevation and experiment explained most of the data variability (18%, 14%, and 11%, cf. η^2-column in Table 5.3). The distance factor was unimportant, only being nearly significant in the interaction with elevation (η^2 = 1%). The SNK-test classified *C. fragile* into a low and *F. vesiculosus*, *G. verrucosa* and *A. subulata* into a high performance group, although graphical analysis rather indicated that *F. vesiculosus* was resistant, *G. verrucosa* relatively resistant, and *A. subulata* and *C. fragile* sensitive to high elevations (Fig. 5.1A). *C. fragile* had a significant elevation * experiment interaction (9%, Table 5.4), but it was the elevation factor that dominated the data variability (52%). *C. fragile* had near-zero growth at low elevations but high biomass loss at high elevations (Fig. 5.1A). Although statistically insignificant (SNK-test), there was a tendency for lowest growth at near-mainland sites and highest growth at mid-lagoon sites.

Effect of days of sediment burial

In the burial experiments there was a significant interaction between species and number of days of burial (12%, Table 5.3), but it was the days of burial that explained the majority of the data variability (69%), reflecting different decomposition rates. Fig. 5.1B shows that *C. fragile* and *A. subulata* decomposed faster (within a week) than *F. vesiculosus*, *G. verrucosa* and *U. curvata* that retained biomass for up to three weeks (Fig. 5.1B). This pattern was supported by the SNK-test that grouped *C. fragile* and *A. subulata* into the low performance group. The decay slopes were significant for each species (Table 5.7, Aga > Cod > Gra = Ulv > Fuc) and a co-variance analysis detected heterogeneous slopes, although a post-hoc Tukey-HSD interval test pooled all decay

slopes into one group. The time factor was highly significant for *C. fragile* growth, explaining all of the data variability (100%, Table 5.4).

Effect of shading

The shading experiment had significant species * distance (8%, Table 5.3) and species * light (9%, Table 5.3) interactions, but it was the species factor that was most important (38%). All species grew in the various treatment combinations. However, whereas *C. fragile, F. vesiculosus* and *G. verrucosa* showed little response to shading or distance treatments, *A. subulata*, *H. musciformis* and *U. curvata* had particularly high growth at the mid-lagoon site (Fig. 5.2A) and in the high-light treatment (Fig. 5.2B), indicating opportunistic traits. In the SNK-test, *C. fragile*, *G. verrucosa*, *F. vesiculosus* and *A. subulata* were classified in the lowest, *U. curvata* in the intermediate, and *H. musciformis* in the high performance group. *C. fragile* had a near-significant distance * light interaction (27%, Table 5.4), although the growth effect was small compared to other species. The distance factor was statistically insignificant, although *C. fragile* again had slightly lower growth at the near-mainland site (SNK-Table, Appendix 1).

Effect of nutrient addition

In the nutrient experiments the species * distance interaction was significant (4%, Table 5.3) and the species * experiment and species * nutrient interactions near-significant (1% each). The species factor explained the majority of data variability (62%) compared to other factors. *U. curvata* and *H. musciformis* showed strong treatment effects with highest growth at Shoal 1 (Fig. 5.3A) and in cages with nutrient spikes (Fig. 5.3B), indicating opportunistic traits, compared to the other species that had minimal treatment

effects. *C. fragile*, *F. vesiculosus*, *A. subulata* and *G. verrucosa* were classified into the low, *H. musciformis* into the intermediate and *U. curvata* into the high performance group. *C. fragile* generally had positive biomass changes with significant distance * experiment (9%, Table 5.4) and nutrient * experiment (6%) interaction effects. This suggests that distance and nutrient effects differed on the small temporal scale between the two experiments. Although these interactions were significant, they were minor compared to the similar treatment effects for *H. musciformis* and *U. curvata* performance. *C. fragile* also had a highly significant distance effect (25%), and the SNK-test grouped the near-mainland treatment into a low performance site. The tissue-nutrient graphical analysis showed that percent tissue nitrogen was low at the barrier island site (Fig. 5.3C) and high in nutrient-addition cages for all species, typically raising the tissue level nitrogen content by 0.2-0.4% (Fig. 5.3D). These patterns were similar for the total tissue nitrogen data (Fig. 5.3E and 5.3F).

Effect of snail addition

In the grazer experiment there were significant species * grazer (15%, Table 5.4) and species * distance (5%) effects, although the species factor explained most of the data variability (40%). All species, except for *F. vesiculosus*, had highest performance at the mid-lagoon shoal site and lowest at the near-mainland site (Fig. 5.4A). Additional SNK-tests conducted on the grazer-treatment for each species (pooling the distance factor, Table 5.4) grouped the original four grazer densities into a distinct low (0 and 2 snails per cage) and high (7 and 20 snails per cage) density treatment for all species. Hence, only results based on these two grazer treatments are shown (Fig. 5.4B, n = 4). Graphical and

statistical analysis (Fig. 5.4B, Table 5.4) revealed that *C. fragile* suffered pronounced negative effects of snail additions, *F. vesiculosus* was indifferent, and that *A. subulata*, *G. verrucosa*, *H. musciformis* and *U. curvata* had marked performance enhancement (opportunistic traits). The SNK-test grouped *C. fragile* and *F. vesiculosus* into the low, *A. subulata*, *G. verrucosa* and *H. musciformis* into the intermediate, and *U. curvata* into the high performance group. *C. fragile* had again lowest growth at the near-mainland, although statistically insignificant (SNK-test). Whereas the nitrogen effect was weak on percent tissue content (Fig. 5.4D) the total tissue nitrogen content was clearly highest in high snail density treatments for the fast-growing species (Fig. 5.4F), suggesting that snail-excreted N-compounds facilitated growth.

Effect of twist-tie wrapping and caging

Wrapping algae with a twist-tie had a significant effect (2%, Table 5.3), generally reducing performance with 5-10% (most clearly for *A. subulata*, *H. musciformis* and *U. curvata*, Fig 5.5B, although the species * twist tie interaction was non-significant). Fig. 5.5A shows a tendency for poor performance at the near-mainland site. Despite significant and near-significant interactions of the distance factor, the majority of data variability was explained by the species factor (50%). The SNK-test grouped *C. fragile* and *F. vesiculosus* in the low, *A. subulata*, *G. verrucosa*, and *H. musciformis* in the intermediate, and *U. curvata* in the high performance group. *C. fragile* did not demonstrate any response to twist-tie wrapping, but a significant response to distance (41%, Table 5.4), The latter effect was supported by the SNK-test that classified near-mainland as a low performance site compared to mid-lagoon shoal and barrier island.

Thus, twist tie wrapping did not affect performances in any detrimental way and the results from the elevation experiments should reflect real performance differences.

Enclosing fragments in transparent cages revealed a significant species * distance * cage interaction (10%, Table 5.3), but slightly more important significant factors included species (20%), species * distance (13%) and species * caging (11%). Caging had a complex effect on tissue performance, depending on location and species. Performance of *A. subulata, G. verrucosa, H. musciformis* and *U. curvata* were highest at Shoal 1 and lowest at the near-mainland site (Fig. 5.6A, corresponding to the species * distance interaction) and also highest in open plots for the latter three species (Fig. 5.6B, corresponding to the species * twist tie interaction). The SNK-test grouped *C. fragile*, *F. vesiculosus* and *A. subulata* in the low, *H. musciformis* and *G. verrucosa* in the intermediate and *U. curvata* in the high performance group. For the ANOVA on *C. fragile* performance there was a significant effect of distance (34%, Table 5.4) although the effect were negligible compared the faster growing species. Finally, the SNK-test classified the near-mainland sites as a poor growth site compared to mid-lagoon and near-ocean sites.

Effect of species and distance on pooled experiments

The ANOVA test on species and distance effects conducted on the pooled summer experiments revealed significant interactions between species * experiment number (12%, Table 5.3), species * distance (4%) and distance * experiment (1%). However, the single species factor clearly explained most of the data variability (33%). Thus, *C. fragile*

and *F. vesiculosus* had low, *G. verrucosa* and *A. subulata* intermediate, and *H. musciformis* and *U. curvata* large performance variability between different locations (Fig. 5.7A) and particularly between experiments (Fig. 5.7B). There was generally highest performance at the mid-lagoon and lowest at the near-mainland site, although this pattern was most clear for *A. subulata*, *H. musciformis* and *U. curvata*. The SNK-test again classified *C. fragile* and *F. vesiculosus* in the lowest, *A. subulata* and *G. verrucosa* in the intermediate, *H. musciformis* in the high and *U. curvata* in a very high performance group. The ANOVA test on *C. fragile* performance showed significant effects of experiment (30%, Table 5.4) and distance (4%), and the SNK-test grouped the near-mainland sites into the low and the mid-lagoon and near-ocean sites into the high performance sites.

Performance similarities between species

Out of the 106 test-combinations of species performance pattern 55 were significant and 10 near-significant (Table 5.5). Only 8 of these had negative correlation coefficients (6 significant and 2 near-significant), and each explained a relatively small proportion of the data variability ($r^2 < 0.30$). In the grazing experiment, *C. fragile* performance was negatively related to *H. musciformis* and *G. verrucosa* biomass, probably because *C. fragile* was grazed by mud snails while *H. musciformis* and *G. verrucosa* were facilitated by enhanced nutrients. Based on the few negative correlations with low explanatory powers, asymmetrical interspecific competition within cages is considered unlikely. The overwhelming number of positive correlations instead suggested similar responses between species to environmental conditions.

Discussion

Here we document that, contrary to our hypothesis, *C. fragile* did not have higher growth than native species under environmental conditions characteristic for North-West Atlantic lagoons. Contrary, *C. fragile* was inferior with low growth under benign conditions (high light, lack of grazers, added nutrients, at low elevations and at the mid-lagoon site), and higher biomass loss compared to other species under stressful conditions (low light, high grazer abundance, sediment burial, at high elevations and at the near-mainland site). In particular *C. fragile* was susceptible to burial, mud-snail grazing and desiccation, and it is likely that these trait-limitations will hinder further dominance of *C. fragile* in Hog Island Bay. Instead, *U. curvata* and *H. musciformis* (high S:V ratios) had high growth and high growth variability, *G. verrucosa, A. subulata* medium (and medium S:V), and *F. vesiculosus* and *C. fragile* low growth and growth variability (and low S:V ratios).

Burial effects

Sediment deposition and subsequent burial are fundamental characteristics of coastal lagoons and estuaries (Keddy 2000, Lawson 2003, McManus 1998, Schoellhamer 1996). In Hog Island Bay, sediment cores typically contain a top layer of recognizable seaweed fragments (pers. obs.) and a deeper black organic-rich layers indicating both recent and past burial events (Lawson 2003, Neira & Rackemann 1996), and hence it is important for seaweeds to be resistant to temporary burial (Kamermans et al. 1998, Keddy 2000). We found that *C. fragile* and *A. subulata* decomposed within days compared to *G. verrucosa*, *F. vesiculosus* and *U. curvata* which decomposed within weeks. The

decomposition rates of *C. fragile* and *A. subulata* was also high compared to numerous other red and green algae (Bourgues et al. 1996, Kamermans et al. 1998, Santelices et al. 1984, Trowbridge 1996a). It is noteworthy that *C. fragile* decomposed faster than *U. curvata*, even though its high S:V ratio, simple and thin structure, high protein content, and low C:N ratios should make *U. curvata* susceptible to physical and bacterial break-down (Duarte 1992, Enriquez et al. 1993). Although the ability to resume growth was not measured, pulse-amplified modulated fluorescence yield (Häder et al. 1999, Hader et al. 2000) measured on recovered tissue before biomass determination, indicated a correlation between retrieved biomass and electron transport viability (Appendix 1). Thus, our results suggest that *C. fragile* is inferior to many native species in burial resistance.

Light effects

Lagoons and estuaries are naturally turbid environments and hence it should be advantageous to be optically dense to allow for efficient light absorption. *C. fragile* is considered such an efficient light utilizer (Ramus 1978, Ramus et al. 1976b, a), and should then perform well under low light levels in the shading experiment. Specifically, Ramus (1990) suggested that *C. fragile* could outgrow *U. curvata* at low light levels based on photosynthetic P-I curves measured in single-species laboratory experiments. However, in our study *C. fragile* did not have higher growth compared to native macroalgae under low light, suggesting that native species are equally efficient primary producers. It is interesting that *U. curvata* and *H. musciformis*, actually had higher growth at low light, although these taxa with high saturation and compensation points are typically considered high light adapted (Littler 1980, Littler & Arnold 1982, Pedersen

1995). However, because *C. fragile* and *F. vesiculosus* are positively buoyant and have upright and dense canopies when submerged (Begin & Scheibling 2003, Chapman 1995), these species can have a light advantage that is not reflected in tissue-based comparisons and can potentially shade species of similar size with prostrate morphologies and/or negative buoyancy, e.g. *G. verrucosa*, *A. subulata*, *U. curvata*, and *H. musciformis* (Schneider & Searles 1991).

Nutrients effects

Lagoons and estuaries are naturally nutrient-rich systems, and successful lagoon species should be able to canalize high nutrient concentrations into high growth and/or reproductive outputs. Nutrient rich areas have been particularly susceptible to invasion by *C. fragile* (Hanisak 1979a, b, Trowbridge 1999), and enrichment has been suggested to be of major importance for its invasive success. However, we found *C. fragile* to be indifferent to nutrient additions, but that growth of *H. musciformis* and *U. curvata* with higher S:V ratios were clearly stimulated. This supports the hypothesis that nutrient effects and growth scale with S:V ratios (Nielsen & Sand-Jensen 1990, Pedersen & Borum 1997, Rees 2003, Wallentinus 1984). It is interesting that species with low S:V ratios and without growth response to nutrient additions, nevertheless increased tissue nitrogen content, providing nitrogen storage to sustain growth if nutrients later are depleted (Pedersen & Borum 1996, Pedersen & Borum 1997). In these cases the low intrinsic growth rates, low metabolic demands, and a nitrogen storage pool can ensure a competitive advantage of *C. fragile* and *F. vesiculosus* compared to high S:V-species (Pedersen & Borum 1996, Pedersen & Borum 1997).

Grazing effects

Lagoons and estuaries are occasionally top-down controlled by migrating waterfowl (Rowcliffe et al. 2001) and small herbivorous crustaceans and gastropods (Duffy & Hay 1991b, Duffy & Hay 1991a, Giannotti & McGlathery 2001, Hauxwell et al. 1998, Rosinski 2004). Our results suggested inhibition of *C. fragile* and facilitation of species with high S:V ratios by the omnivorous mudsnail *Ilyanassa obsoleta*, one of the most ubiquitous gastropods in West Atlantic lagoons (Kelaher et al. 2003). This facilitation of species with high S:V ratios was probably caused by uptake of nitrogenous excretory product from the mudsnails, a hypothesis supported by the tissue nitrogen data (Fong et al. 1997, Giannotti & McGlathery 2001, Williams & Carpenter 1988). The inhibition of *C. fragile* was somewhat surprising considering that alien species often are successful in invaded habitats due to grazer escape (Boudouresque & Verlaque 2002, Myers & Bazely 2003), because *C. fragile* in particular has been considered unpalatable and of poor food quality for generalist herbivores (Scheibling & Anthony 2001, Trowbridge 1998), and because high quality food items with high tissue nitrogen content, few chemical deterrents, and low structural complexity were offered as food simultaneously (Cebrián & Duarte 1994, Geertz-Hansen et al. 1993, Karban et al. 1997). Our findings also contrast with results from Giannotti and McGlathery (2001) who reported significant mudsnail grazing on *U. curvata*, but differences probably arise because the former experiment only included *U. curvata* as food source, were laboratory based, and used a different algae-grazer ratio (we used ca. 13gDWm2 vs. 48 g and both studies used typical field densities of 150-300 snails m^{-2}). However, several processes may reduce the ecological importance

of the reported top-down control of *C. fragile*: (1) in natural systems an indefinite sediment supply with microbes, larvae, and detritus are available (2) flow rates are reduced in cages, and hence replacement of nutrients and dilution of excretions should be more important under natural conditions (Hurd 2000), (3) large and upright *C. fragile* canopies may be difficult to 'grab and graze' in tidal currents (Kawamata 1998), and (4) predation by fish and decapods may limit mudsnail grazing efficiency during high tides and in subtidal regions.

Elevation effects

There are several reasons why marine organisms have variable performance at different tidal elevation levels: (1) species have different physiological tolerances (Colman 1933, Stephenson & Stephenson 1949, Williams 1948), (2) interactions are constrained by time of inundation (Connell 1961b, a, Paine 1966), and (3) physical disturbances are linked to the water level and depth (Dayton 1971, Denny & Gaines 1990, Paine & Levin 1981). *C. fragile* occurs in dense intertidal stands in geographical regions where winter freezing is rare (Trowbridge 1999), and was expected to perform well at low and mid-intertidal levels. However, *C. fragile* lost biomass at both 0.0 and 0.5 m below mean sea level, a pattern confirmed in additional experiments (Appendix 1), and reflecting distribution data within Hog Island Bay (Chapter 2). Thus, successful invasion in Virginia and nearby states, should be limited to the lower intertidal zone. Native species that showed similar sensitivity to high elevations were *A. subulata* and *H. musciformis* (cf. Appendix 1). High intertidal elevation levels are particular stressful due to desiccation, the combined effect of temperature and water stress (Doty 1946). The elevation gradient is of particular

importance in flat tidal habitats such as Hog Island Bay because minor differences in tidal level still affect large horizontal areas with notably different emergence levels (Hayden et al. 2000). In Hog Island Bay, the elevation level that corresponds to optimal performance will change with season, the lunar cycle, and storm dynamics. For example, if a low pressure system coincides with offshore winds and spring low tide, up to 80% of the lagoon bottom on the Delmarva peninsula can become emerged (Hayden et al. 2000). If such extreme low waters co-occurred with high temperatures and light levels, effects could be detrimental for desiccation-prone species such as *C. fragile* and *A. subulata* in large geographical areas, and could contribute to annual fluctuations in biomass patterns (Chapter 2). Elevation level is clearly important in understanding algal distribution patterns in shallow coastal systems such as Hog Island Bay.

Distance effects

Horizontal gradients also provide different growth conditions for marine organisms. In particular, terrestrial influences are strongest at near-mainland sites and oceanic influences increase with distance from the mainland, potentially causing performance differences (Castel et al. 1996, Taylor et al. 1995a). One of the main objectives was to cross the manipulative treatments with a distance gradient to test for interaction effects and allows broad predictions about the likelihood of successful invasion by *C. fragile*. Despite a high tolerance to environmental fluctuations (Malinowski & Ramus 1973, Trowbridge 1998, 1999) *C. fragile* had poor performance at near-mainland sites, probably reducing the likelihood of invasions in such habitats. Most native species also had lowest growth at these sites, indicating general poor growth conditions. However,

because environmental factors co-vary along the distance gradient it is difficult to identify a single cause (Table 5.1, Appendix 1, Flindt & Kamp-Nielsen 1997, Morand & Briand 1996, Taylor et al. 1995a). In particular, because nutrient concentrations are highest at these sites, adverse effects on growth are most likely related to a high concentrations of suspended solids, potentially reducing light penetrations and abrading and smothering thallus. Similarly, most species had highest growth a the mid-lagoon site, probably because light, nutrients and flow conditions are favorable compared to near-by locations. It is possible that these results would differ if experiments are repeated as non-caged benthic growth experiments because grazing (Duffy & Hay 1991b, Hauxwell et al. 1998), waves and currents (Hawes & Smith 1995), sedimentation, and smothering by drifting algal mats (Raffaelli et al. 1998) likely are most intense at the mid-lagoon site. Also, because interactions between distance and the manipulated treatments were lacking or weak, extrapolations of treatment effects to large areas are valid.

Methodological artifact and competition

Three aspects may limit inferences: (1) using twist tie wrapping or cage enclosures may have influenced the results, (2) within-assemblage species-interactions may have affected the ecological outcomes, and (3) if such within-assemblage interactions are important, statistical tests involving the species factor could bias p-values. Wrapping algae with twist-tie slightly reduced growth for species with high growth rates, probably due to direct thallus shading or because the thallus was forced into a denser self-shading configuration. Because the high growth could be sustained with twist tie wrapping this method was considered suitable for fixation and not limiting interferences. Cage-structure

artifacts have been debated numerous times (e.g. Navarrete 1996, Parker et al. 1993, Underwood 1997) and cage-control structures are often added to evaluate artifacts (altered flow, sedimentation, grazing, drift algae accumulations, nutrient encounter rates). We ignored cage-controls because co-variation between factors makes it problematic to design a single cage-control (Chapter 6)(Parker et al. 1993, Woodin 1978), because it was imperative to use unattached fragments to simulate the drift algal assemblage (semi-open structures would not retain fragments), and because emphasis was on comparative performance patterns. In the caging experiment, the structural complex and slow growing species with low S:V-ratios (*C. fragile*, *F. vesiculosus*) were indifferent to enclosure, whereas native species with high S:V-ratios had highest growth in open plots, probably because light and nutrient encounter rates were highest outside cages. The lack of negative significant correlation's between species performances indicated that asymmetrical competition was not of major importance within the assemblages (Underwood 1997). The significant positive interactions could instead indicate positive interactions or common responses to the ambient test conditions. Positive relationships are well-known from intertidal studies where desiccation is a main limiting factor (Bruno et al. in press, Dring & Brown 1982, Jenkins et al. 1999, Leonard et al. 1999) and it is possible that test conditions in our elevation experiment would have been harsher if conducted as independent experiments for each species. However, in the other experiments it is more likely that the species reacted to the ambient conditions in similar, but relatively independent ways, i.e. the results were statistically robust (in addition, because results were straightforward to interpret, they are even robust to many errors, Roa 1992). The densities within the experimental cages (130 – 380 gWW m^{-2})

correspond to typical Hog Island Bay densities (Chapter 2, McGlathery et al. 2001), but are low compared to many other systems (Morand & Briand 1996, Raffaelli et al. 1998). This suggest that competition is of low importance in Hog Island Bay, except during times and in localized areas where macroalgae bloom (Chapter 2, 6, Appendix 1).

Performance of *Codium fragile*

C. fragile had slow growth compared to native species with high S:V ratios, and based on these results *C. fragile* is unlikely to be a successful invader. Nevertheless, *C. fragile* gained biomass (1) in all treatments in the light and nutrient experiments, (2) at low elevation in the elevation experiment and (3) in the control treatments of the grazing experiment, and growth can add up to extensive biomass if accumulated during the entire growing season from early spring to late fall (Borum 1996, Trowbridge 1998). However it is clear that such biomass gain will not be possible sites and time periods where sedimentation, mud-snail grazing and desiccation rates are high, limiting areas of potential invasions. In comparison the reported high growth rates and strong competitive abilities of *H. musciformis* and *U. curvata* are less likely to be sustained over long time periods because *U. curvata* regularly produce spores followed by tissue necroses and can be heavily grazed (Casteldelli et al. 2003, Geertz-Hansen et al. 1993, Ramus & Venable 1987) and *H. musciformis* is mainly found in summer months indicating that a low tolerance to cold waters and low light levels (Berchez et al. 1993, Humm 1979). Several other short-term performance studies have documented that ephemeral species with high S:V ratios outperform perennial and larger species (Duarte 1992, Littler 1980, Littler & Arnold 1982, Pedersen & Borum 1996, Pedersen & Borum 1997, Ramus & Venable

1987, Rees 2003) although larger species often dominate lagoonal habitats (Chapter 2, Goshorn et al. 2001). Thus, distribution are clearly also influenced by traits other than rates of nutrient uptake, photosynthesis and intrinsic growth, and for a slow growing species like *C. fragile*, persistence is likely instead accomplished by minimizing biomass loss during adverse conditions alternating with steady, but slow, growth when conditions are benign (Sand-Jensen & Borum 1991). Alternative, but not investigated, explanations to the success of *C. fragile* include (1) morphology (its large size and dense structure can shade competitors, Trowbridge 1998), (2) reproduction (pathenogenesis, one individual can create a population, Churchill & Moeller 1972), (3) recruitment (high recruitment with large holdfast formation, Chapter 6), (4) recovery (all thallus parts have strong recovery potentials, Trowbridge 1998, Yotsui & Migita 1989), and (5) biomechanical (positive buoyancy, high dispersal, strong attachment, Chapter 4, Ben Avraham 1971, Dromgoole 1982) characteristics. Ultimately, these alternatives should be tested in controlled and manipulative field experiments to strengthen our abilities to predict success of *C. fragile* introduced into new locations.

Conclusion

In conclusion, *C. fragile* did not outperform native and common North American macroalgae under conditions reflecting coastal low-energy soft bottom habitats (high sedimentation, high mud-snail densities, high desiccation rates, low-high light availability, low-high nutrient concentrations). Instead it performed worse than most other algae under most test conditions. Thus, other traits and ecosystem properties should be explored to understand how this species can become dominant in certain shallow

lagoons and estuaries. In particular we suggest that successful introduction with sustained high biomass will be limited to areas where mud-snail grazing, sedimentation and desiccation are unimportant, and in addition we consider it unlikely for *C. fragile* to become super-abundant over large-scale areas in Virginian soft bottom lagoons.

Chapter 5. Tables

Table 5.1. Biotic and abiotic characteristics (± SE) in Hog Island Bay at near-mainland (Creek), mid-lagoon (Shoal) and near-ocean (Hog) sites. Water temperature can vary seasonally from 2 to 28°C and air temperature from –5 to 35°C.

	Creek	**Shoal**	**Hog**
[1]*Ilyanassa obsoleta* densities (m^{-2})	16 ± 4	0 ± 0	78 ± 13
[2]DIN (μM)	4.4 ± 0.9	2.3 ± 2.5	1.2 ± 0.4
[2]DON (μM)	15.5 ± 1.9	12.1 ± 3.8	11.8 ± 1.6
[2]DIP (μM)	1.4 ± 0.2	0.8 ± 0.8	0.5 ± 0.1
[2]Light extinction *k* (m^{-1})	2.2 ± 0.6	1.9 ± 0.8	1.7 ± 1.7
[2]Sediment bulk density (g cm^{-3})	0.89 ± 0.09	1.51 ± 0.15	1.78 ± 0.04
[2]Sediment organic content (% DW)	3.8 ± 0.2	2.1 ± 0.3	0.48 ± 0.3
[3]Temperature (°C)	High variability	Medium variability	Low variability
[3]Salinity (‰)	28-34	32-34	34
[3]Fetch (re-suspension, disturbance)	Low	High	Low
[4]Algal biomass (gDW m^{-2})	12.3 ± 1.4	54.2 ± 6.6	4.7 ± 1.2
[4]Algal richness (number 0.15 m^{-2})	0.61 ± 0.03	2.34 ± 0.10	0.73 ± 0.05
[4]*G. verrucosa* biomass (gDW m^{-2})	11. 07 ± 1.34	42.18 ± 5.65	1.86 ± 0.27
[4]*U. curvata* biomass (gDW m^{-2})	0.82 ± 0.27	4.21 ± 0.85	0.24 ± 0.05
[4]*C. fragile* biomass (gDW m^{-2})	0.00 ± 0.00	0.81 ± 0.31	1.01 ± 0.94

[1]Random samples (5-6 sites and 5-8 samples per site) in fall 2002 (unpub. data). [2]Annual averages of samples taken in all four seasons, from McGlathery et al.(2001), [3]Unpub. data. [4]n = 1104, 480, and 792 per location, 27 surveys, 1998-2002, Chapter 2).

Table 5.2. Summary of experiments. Water temperatures were 11°C in Exp_1, 13°C in Exp_2, 24°C in Exp_3, 26°C in Exp_4 and Exp_5 and 27°C in Exp_6, Exp_7, Exp_8 and Exp_9. SPE = species type, DIS = distance from mainland, ELE = elevation level, EXP = experiment number, DAY = days of burial, LIG = light level (shading), NUT = nutrient level, GRA = grazer additions (mudsnails), TWI = twist tie wrapping, CAG = caging.

Exp. #	Factorial Design	Test Objective	Incubation Date	Comments
1 2	4 SPE * 3 DIS * 2 ELE * 2 EXP * 5 REP	Elevation	11/3 to 27/3 and 27/3 to 15/4	Fixed fragments with twist tie in open plots, Exp 1 = 0.8 to 0.0 m below MSL, Exp 2 = 0.8 to 0.5 m below MSL, no *H. musciformis* or *U. curvata*
3	5 SPE * 11 DAY * 2-6 REP	Burial	17/6 to 23/7	Loose fragments in litterbags covered by 2-3 cm sediment, no *H. musciformis*, only conducted at S1
4	6 SPE * 3 DIS * 2 LIG * 4 REP	Light	26/6 to 4/7	Loose fragments in 22 cm closed cages, white vs. black mesh cover.
5 6	6 SPE * 3 DIS * 2 NUT * 2 EXP * 4 REP	Nutrients	9/7 to 16/7 and 12/7 to 19/7	Loose fragments in 22 cm closed cages, 2 or 0 nutrient stakes per cage, nitrogen analysis
7	6 SPE * 3 DIS * 2 TWI * 4 REP	Twist tie	19/7 to 25/7	Loose fragments in 22 cm closed cages, ± twist tie, no mesh, small holes
8	6 SPE * 3 DIS * 4 GRA * 2 REP	Grazers	25/7 to 31/7	Loose fragments in 22 cm closed cages, 0, 2, 5, 20 mud-snails per cage (all survived), nitrogen analysis
9	6 SPE * 4 DIS * 2 CAG * 3 REP	Caging	26/7 to 31/7	Loose fragments in 22 cm closed cages, fixed open plot (on rebar) vs. fixed closed cage (on rebar)

Table 5.3A. ANOVA results on assemblage performance (Exp. 1-6). Significant results are in bold ($p < 0.05$). Levenes test of equality of variances were significant for all tests.

Exp	Source	Df	SS	η^2(%)	F	p
1 & 2	Species (SPE)	3	206960	18	30.29	**0.000**
1 & 2	Elevation (ELE)	1	162754	14	71.47	**0.000**
1 & 2	Experiment (EXP)	1	122714	11	53.88	**0.000**
1 & 2	Distance (DIS)	2	8011	1	1.76	0.175
1 & 2	SPE * ELE	3	82851	7	12.13	**0.000**
1 & 2	ELE * EXP	1	22633	2	9.94	**0.002**
1 & 2	SPE * EXP	3	20784	2	3.04	**0.030**
1 & 2	DIS * ELE	2	12483	1	2.74	0.067
1 & 2	DIS * EXP	2	7373	1	1.62	0.201
1 & 2	SPE * DIS	6	14729	1	1.08	0.377
1 & 2	SPE * ELE * EXP	3	19292	2	2.82	**0.040**
1 & 2	SPE * DIS * ELE	6	24493	2	1.79	0.103
1 & 2	DIS * ELE * EXP	2	4822	0	1.06	0.349
1 & 2	SPE * DIS * EXP	6	11460	1	0.84	0.542
1 & 2	SPE * DIS * ELE * EXP	6	5479	0	0.40	0.878
1 & 2	Error	181	412198	36		
3	Days of burial (DAY)	9	151880	69	112.65	**0.000**
3	SPE	4	22436	10	37.44	**0.000**
3	SPE * DAY	36	25925	12	4.81	**0.000**
3	Error	135	20224	9		
4	SPE	5	611495	38	25.54	**0.000**
4	Light level (LIG)	1	92409	6	19.30	**0.000**
4	DIS	2	103218	6	10.78	**0.000**
4	SPE * LIG	5	137360	9	5.74	**0.000**
4	SPE * DIS	10	124461	8	2.60	**0.007**
4	DIS * LIG	2	7036	0	0.73	0.482
4	SPE * DIS * LIG	10	22752	1	0.48	0.903
4	Error	105	502830	31		
5 & 6	SPE	5	1781988	62	105.97	**0.000**
5 & 6	DIS	2	59707	2	8.88	**0.000**
5 & 6	Nutrients (NUT)	1	18056	1	5.37	**0.021**
5 & 6	EXP	1	15926	1	4.74	**0.031**
5 & 6	SPE * DIS	10	110087	4	3.27	**0.001**
5 & 6	SPE * EXP	5	35546	1	2.11	0.065
5 & 6	SPE * NUT	5	31972	1	1.90	0.095
5 & 6	DIS * NUT	2	8411	0	1.25	0.288
5 & 6	NUT * EXP	1	2220	0	0.66	0.417
5 & 6	DIS * EXP	2	666	0	0.10	0.906
5 & 6	SPE * NUT * EXP	5	19707	1	1.17	0.324
5 & 6	SPE * DIS * NUT	10	25847	1	0.77	0.659
5 & 6	DIS * NUT * EXP	2	269	0	0.04	0.961
5 & 6	SPE * DIS * EXP	10	10123	0	0.30	0.980
5 & 6	SPE * DIS * NUT * EXP	10	11775	0	0.35	0.966
5 & 6	Error	216	726468	25		

Table 5.3B. ANOVA results on assemblage performance (continued from Table 5.3A, Exp. 7-9). Significant ($p < 0.05$) results are in bold. Levenes test of equality of variances were significant for all tests.

Exp	Source	Df	SS	η^2(%)	F	p
7	SPE	5	134416	50	32.69	**0.000**
7	Twist tie (TWI)	1	5263	2	6.40	**0.013**
7	DIS	2	4652	2	2.83	0.064
7	DIS * TWI	2	8697	3	5.29	**0.007**
7	SPE * DIS	10	15561	6	1.89	0.055
7	SPE * TWI	5	5177	2	1.26	0.288
7	SPE * DIS * TWI	10	11834	4	1.44	0.174
7	Error	100	82243	31		
8	SPE	5	552785	40	37.19	**0.000**
8	Grazing (GRA)	3	166662	12	18.69	**0.000**
8	DIS	2	107919	8	18.15	**0.000**
8	SPE * GRA	15	212153	15	4.76	**0.000**
8	SPE * DIS	10	69098	5	2.32	**0.020**
8	DIS * GRA	6	15483	1	0.87	0.523
8	SPE * DIS * GRA	30	46596	3	0.52	0.975
8	Error	72	214054	15		
9	SPE	5	211489	20	7.92	**0.000**
9	Caging (CAG)	1	72105	7	13.50	**0.000**
9	DIS	2	20340	2	1.90	0.157
9	SPE * CAG	5	114067	11	4.27	**0.002**
9	SPE * DIS	10	130549	13	2.44	**0.015**
9	DIS * CAG	2	22663	2	2.12	0.128
9	SPE * DIS * CAG	10	106703	10	2.00	**0.047**
9	Error	68	363282	35		
Sum	SPE	5	2328621	33	108.19	**0.000**
Sum	DIS	2	195322	3	22.69	**0.000**
Sum	EXP	5	163886	2	7.61	**0.000**
Sum	SPE * DIS	10	177596	2	4.13	**0.000**
Sum	SPE * EXP	25	850383	12	7.90	**0.000**
Sum	DIS * EXP	10	84669	1	1.97	**0.034**
Sum	SPE * DIS * EXP	50	268918	4	1.25	0.121
Sum	Error	705	3034706	43		

Table 5.4. ANOVA results on *C. fragile* performance. Significant ($p < 0.05$) results are in bold. Levenes test of equality of variances were not significant for experiment 4, 5, 6, 7 and 9, but were significant for 1 and 2 ($p = 0.021$), 3 ($p = 0.003$) and 8 ($p = 0.000$).

Exp	Source	Df	SS	η^2(%)	F	p
1 & 2	Distance (DIS)	2	1124	1	0.77	0.468
1 & 2	Elevation (ELE)	1	53877	52	74.10	**0.000**
1 & 2	Experiment (EXP)	1	4092	4	5.63	**0.022**
1 & 2	DIS * ELE	2	1480	1	1.02	0.370
1 & 2	DIS * EXP	2	1141	1	0.78	0.463
1 & 2	ELE * EXP	1	9155	9	12.59	**0.001**
1 & 2	DIS * ELE * EXP	2	575	1	0.40	0.676
1 & 2	Error	43	31265	30		
3	Days of burial	10	315000	100	819.14	**0.000**
3	Error	27	1038	0		
4	DIS	2	15	0	0.04	0.959
4	Light level (LIG)	1	255	6	1.42	0.252
4	DIS * LIG	2	1097	27	3.06	0.077
4	Error	15	2692	66		
5 & 6	DIS	2	1246	25	9.14	**0.001**
5 & 6	Nutrients (NUT)	1	4	0	0.06	0.806
5 & 6	EXP	1	332	7	4.87	**0.034**
5 & 6	DIS * NUT	2	61	1	0.45	0.642
5 & 6	DIS * EXP	2	471	9	3.45	**0.042**
5 & 6	NUT * EXP	1	312	6	4.57	**0.039**
5 & 6	DIS * NUT * EXP	2	160	3	1.17	0.321
5 & 6	Error	36	2453	49		
7	DIS	2	488	41	6.42	**0.008**
7	Twist ties (TWI)	1	42	3	1.10	0.310
7	DIS * TWI	2	14	1	0.19	0.833
7	Error	17	647	54		
8	DIS	2	2214	5	0.85	0.453
8	Grazers (GRA)	3	17340	37	4.42	**0.026**
8	DIS * GRA	6	11630	25	1.48	0.264
8	Error	12	15694	33		
9	DIS	2	894	34	5.09	**0.025**
9	Caging (CAG)	1	57	2	0.65	0.434
9	DIS * CAG	2	600	23	3.42	0.067
9	Error	12	1053	40		
Sum	DIS	2	3652	4	3.91	**0.023**
Sum	EXP	5	25724	30	11.03	**0.000**
Sum	DIS * EXP	10	1601	2	0.34	0.967
Sum	Error	116	54110	64	466.47	

Table 5.5. Correlation coefficients ($r_{Pearson}$) for pair-wise comparisons between species performance. Exp = Experiment, Aga = *A. subulata*, Cod = *C. fragile*, Fuc = *F. vesiculosus*, Gra = *G. verrucosa*, Hyp = *H. musciformis*, Ulv = *U. curvata*. Cf. Table 5.6 for number of replicates. Significant results are in bold ($p < 0.05$) and significant negative coefficients further underlined.

Comparison	**Exp**	**r**	**p**	**Exp**	**r**	**p**	**Exp**	**r**	**p**	**Exp**	**r**	**p**
Aga vs. Cod	1 & 2	0.45	**0.00**	3	0.97	**0.00**	4	-0.18	0.23	5 & 6	0.26	**0.04**
Aga vs. Fuc	1 & 2	0.23	**0.04**	3	0.75	**0.00**	4	0.49	**0.01**	5 & 6	-0.09	0.28
Aga vs. Gra	1 & 2	0.36	**0.00**	3	0.62	**0.00**	4	0.59	**0.00**	5 & 6	0.44	**0.00**
Aga vs. Hyp	1 & 2			3			4	0.73	**0.00**	5 & 6	0.30	**0.02**
Aga vs. Ulv	1 & 2			3	0.65	**0.00**	4	0.46	**0.01**	5 & 6	0.04	0.39
Cod vs. Fuc	1 & 2	0.31	**0.01**	3	0.78	**0.00**	4	0.19	0.21	5 & 6	-0.04	0.40
Cod vs. Gra	1 & 2	0.39	**0.00**	3	0.71	**0.00**	4	-0.27	0.13	5 & 6	0.31	**0.02**
Cod vs. Hyp	1 & 2			3			4	0.06	0.40	5 & 6	0.34	**0.01**
Cod vs. Ulv	1 & 2			3	0.67	**0.00**	4	-0.17	0.24	5 & 6	0.33	**0.01**
Fuc vs. Gra	1 & 2	0.57	**0.00**	3	0.83	**0.00**	4	0.58	**0.00**	5 & 6	-0.02	0.45
Fuc vs. Hyp	1 & 2			3			4	0.55	**0.00**	5 & 6	0.08	0.49
Fuc vs. Ulv	1 & 2			3	0.84	**0.00**	4	0.59	**0.00**	5 & 6	0.14	0.17
Gra vs. Hyp	1 & 2			3			4	0.55	**0.00**	5 & 6	0.20	0.08
Gra vs. Ulv	1 & 2			3	0.85	**0.00**	4	0.71	**0.00**	5 & 6	0.11	0.23
Hyp vs. Ulv	1 & 2			3			4	0.50	**0.01**	5 & 6	0.41	**0.00**
Aga vs. Cod	7	0.23	0.15	8	-0.21	0.16	9	0.32	0.10	Sum	-0.19	**<u>0.01</u>**
Aga vs. Fuc	7	-0.31	0.08	8	-0.18	0.20	9	0.53	**0.02**	Sum	-0.14	0.05
Aga vs. Gra	7	0.10	0.33	8	0.65	**0.00**	9	-0.25	0.17	Sum	0.43	**0.00**
Aga vs. Hyp	7	0.44	**0.02**	8	0.57	**0.00**	9	0.13	0.32	Sum	0.41	**0.00**
Aga vs. Ulv	7	-0.03	0.45	8	0.86	**0.00**	9	0.05	0.43	Sum	0.20	**0.01**
Cod vs. Fuc	7	-0.14	0.27	8	0.27	0.10	9	0.44	**0.04**	Sum	0.36	**0.00**
Cod vs. Gra	7	0.30	0.08	8	-0.45	**<u>0.01</u>**	9	0.14	0.29	Sum	-0.33	**<u>0.00</u>**
Cod vs. Hyp	7	0.10	0.32	8	-0.51	**0.01**	9	-0.51	**<u>0.02</u>**	Sum	0.02	0.41
Cod vs. Ulv	7	0.33	0.06	8	-0.26	0.11	9	0.17	0.26	Sum	0.04	0.34
Fuc vs. Gra	7	0.20	0.18	8	-0.28	0.09	9	0.34	0.09	Sum	-0.22	**<u>0.00</u>**
Fuc vs. Hyp	7	0.09	0.36	8	0.02	0.45	9	0.18	0.26	Sum	0.17	**0.02**
Fuc vs. Ulv	7	0.25	0.13	8	-0.21	0.16	9	0.34	0.10	Sum	0.15	**0.04**
Gra vs. Hyp	7	0.29	0.09	8	0.56	**0.00**	9	0.01	0.49	Sum	0.12	0.08
Gra vs. Ulv	7	0.31	0.08	8	0.72	**0.00**	9	0.64	**0.00**	Sum	0.29	**0.00**
Hyp vs. Ulv	7	0.09	0.35	8	0.67	**0.00**	9	-0.02	0.47	Sum	0.30	**0.00**

Table 5.6. Number of replicates (n) and mean (X) and maximum (Max) biomass per fragment at the start (WW-t_0) and the end (WW-t_1) of the experiments.

	T_0						T_1					
Exp	**Cod**	**Fuc**	**Aga**	**Gra**	**Hyp**	**Ulv**	**Cod**	**Fuc**	**Aga**	**Gra**	**Hyp**	**Ulv**
n E1	28	28	28	28			28	28	28	28		
n E2	27	27	27	27			27	27	27	27		
n E3	37	37	37	37		37	37	37	37	37		37
n E4	24	24	24	24	24	24	22	24	24	24	24	24
n E5	24	24	24	24	24	24	24	24	24	24	24	24
n E6	24	24	24	24	24	24	24	24	24	24	24	24
n E7	24	24	24	24	24	24	23	22	23	23	22	23
n E8	24	24	24	24	24	24	24	24	24	24	24	24
n E9	18	18	18	18	18	18	18	18	17	18	17	17
X E1	1.26	0.69	1.04	0.87			0.71	0.76	0.50	0.74		
X E2	1.15	0.70	1.05	0.81			0.86	1.15	0.94	1.33		
X E3	0.40	0.64	0.45	0.45		0.40	0.05	0.20	0.04	0.15		0.12
X E4	0.68	0.48	0.75	0.43	0.22	0.32	0.81	0.52	1.14	0.51	0.66	0.63
X E5	0.68	0.48	0.58	0.43	0.22	0.32	0.82	0.52	0.81	0.60	0.48	1.02
X E6	1.00	0.70	0.85	0.63	0.17	0.25	1.16	0.76	0.73	0.63	0.35	0.78
X E7	0.68	0.48	0.58	0.43	0.18	0.32	0.63	0.50	0.78	0.54	0.25	0.62
X E8	0.68	0.48	0.58	0.43	0.18	0.18	0.60	0.46	1.07	0.82	0.38	0.46
X E9	0.68	0.48	0.58	0.43	0.18	0.18	0.76	0.51	0.82	0.80	0.30	0.39
Max E1	1.61	1.02	1.37	1.23			1.75	1.24	1.58	1.86		
Max E2	1.44	1.06	1.32	1.16			1.54	2.46	5.09	3.72		
Max E3	0.40	0.64	0.45	0.45		0.40	0.41	0.77	0.46	0.46		0.44
Max E4	0.68	0.48	0.75	0.43	0.22	0.32	1.02	0.56	2.71	0.72	1.48	1.81
Max E5	0.68	0.48	0.58	0.43	0.22	0.32	0.96	0.60	1.27	0.86	1.53	1.93
Max E6	1.33	0.93	1.13	0.83	0.22	0.32	1.76	1.06	1.48	1.05	0.70	1.76
Max E7	0.68	0.48	0.58	0.43	0.18	0.32	0.73	0.57	1.18	0.64	0.39	0.92
Max E8	0.68	0.48	0.58	0.43	0.18	0.18	0.93	0.56	2.43	1.45	0.82	0.91
Max E9	0.68	0.48	0.58	0.43	0.18	0.18	0.90	0.58	1.38	1.33	1.29	1.22

Table 5.7: Regressions of remaining biomass (gWW) versus days of burial. Null hypothesis: Slopes ($gWWd^{-1}$) are equal: $F_{4,86} = 2.57$, $p = 0.04$. Null hypothesis: Intercepts are equal: $F_{4,90} = 5.98$, $p = 0.00$. Null hypothesis: Regressions are identical: $F_{8,86} = 4.48$ $p = 0.00$. Multiple comparisons for slopes with 95% Tukey-HSD interval: No pair-wise comparisons were different ($p > 0.05$).

Regression	**Cases**	**Intercept**	**Slope**	**Df**	**SS**	**r^2**	**p**
A. subulata	8	-0.41	-0.35	6	0.89	0.59	**0.03**
C. fragile	11	-0.63	-0.19	9	3.20	0.47	**0.02**
F. vesiculosus	29	-0.26	-0.05	27	1.48	0.80	**0.00**
G. verrucosa	25	-0.22	-0.08	23	2.00	0.78	**0.00**
U. curvata	23	-0.47	-0.08	21	19.74	0.22	**0.03**
Pooled				86	27.31		
Common	96	-0.44	-0.07	90	30.57		
Total	96	-0.57	-0.05	94	38.69		

Chapter 5. Figures

Fig. 5.1. Effect of elevation (A) and burial (B) on *C. fragile* performance (% change in biomass) compared to 5 native macroalgae. A. Effect of incubation at high and low elevation levels for experiment 1 (0.8 m difference) and 2 (0.3 m difference). B. Effects of different burial time intervals (days) under a 2 cm sediment layer. Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description, Exp. 1, 2, 3). Species are arranged from low S:V ratios (left) to high S:V ratios. Cod = *C. fragile*, Fuc = *F. vesiculosus*, Aga = *A. subulata*, Gra = *G. verrucosa*, Hyp = *H. musciformis*, Ulv = *U. curvata*.

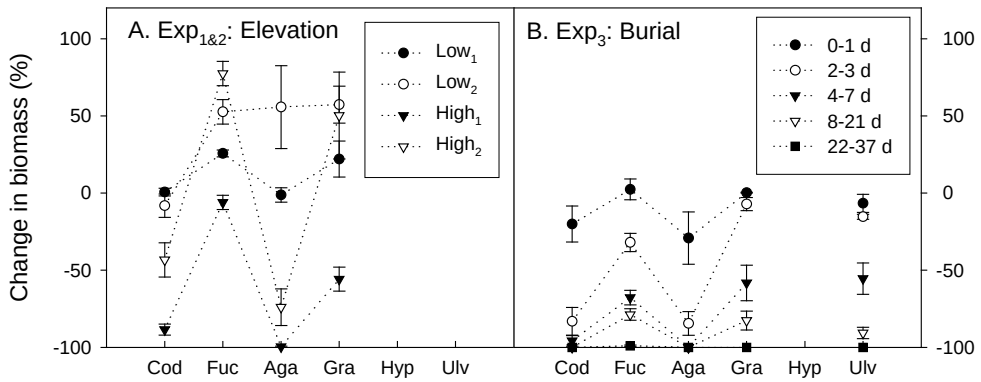


Fig. 5.2. Effect of distance from mainland (A) and shading (B) on *C. fragile* performance (% change in biomass) compared to 5 native macroalgae. Light reduction was obtained by covering cages with black (LIG-) and white (LIG+) screening mesh. Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description, Exp. 4). Species are arranged from low S:V ratios (left) to high S:V ratios.

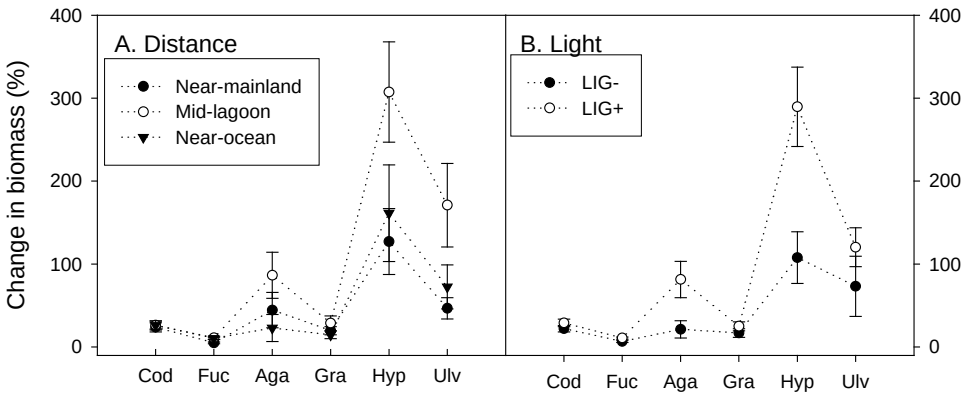


Fig. 5.3. Effect of distance from mainland (left) and nutrient addition (right) on *C. fragile* performance compared to 5 native macroalgae. Left graphs: effect of 3 distances for the nutrient addition experiments data on biomass performance (A), nitrogen concentration (C) and total nitrogen content per species (E). Right graphs: effects of nutrient addition (NUT+) versus controls (NUT-) on biomass performance (B), nitrogen concentration (D) and total nitrogen content per species (F). Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description, Exp. 5, 6). Species are arranged from low S:V ratios (left) to high S:V ratios.

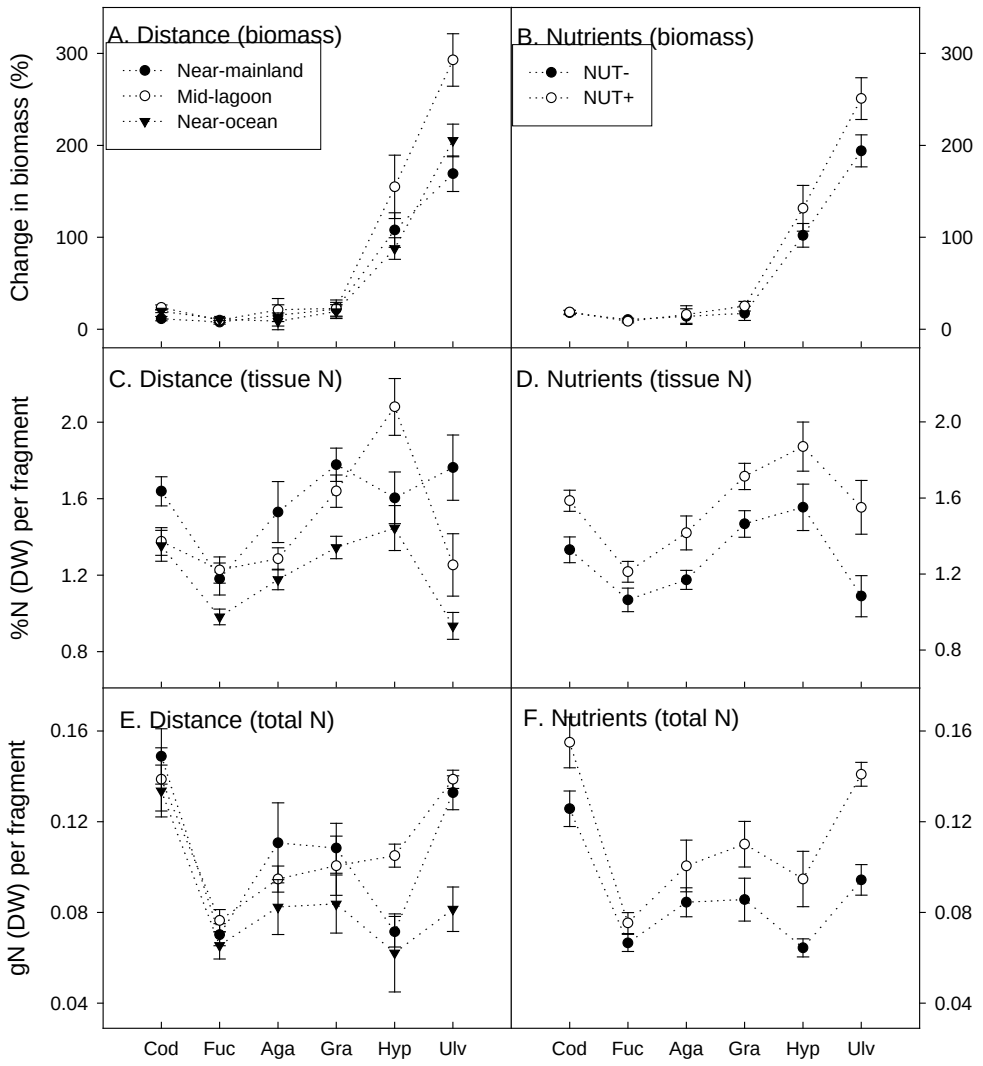


Fig. 5.4. Effect of distance from mainland (left) and snail addition (right) on *C. fragile* performance compared to 5 native macroalgae. Left graphs: effect of 3 distances for the snail (= grazers) addition data on biomass performance (A), nitrogen concentration (C) and total nitrogen content per species (E). Right graphs show effects of snail addition (GRA+, 7 or 20 mudsnails/cage) versus controls (GRA-, 0 or 2 mudsnails/cage) on biomass performance (B), nitrogen concentration (D) and total nitrogen content per species (F). Errors bars are standard errors (cf. Table 5.1 for replicates and design description, Exp. 8). Species are arranged from low S:V ratios (left) to high S:V ratios.

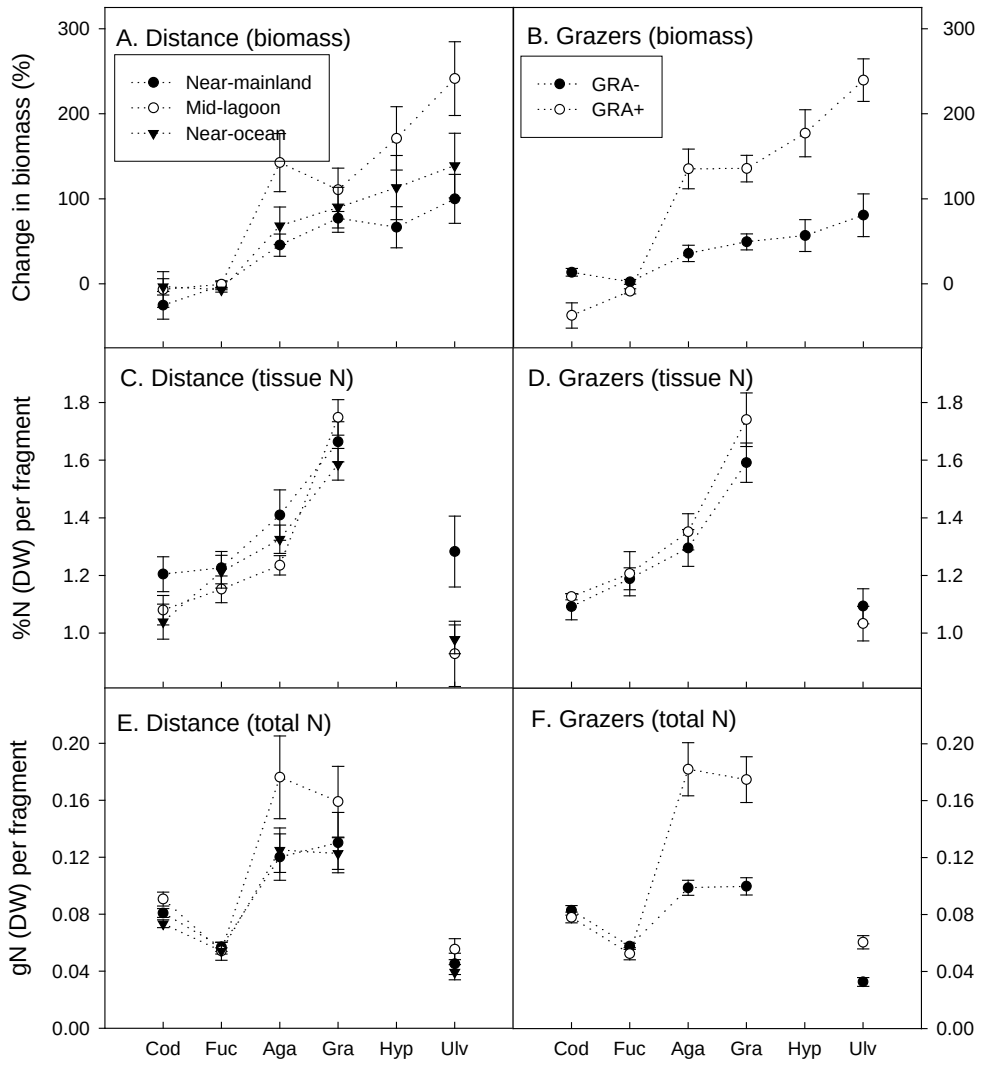


Fig. 5.5. Effect of distance from mainland (A) and twist-tie wrapping (B) on *C. fragile* performance (% change in biomass) compared to 5 native macroalgae. Half of the tissue were wrapped with twist-tie (TWI+) versus non-wrapped controls (TWI-) looselying in cages. Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description, Exp. 7). Species are arranged from low S:V ratios (left) to high S:V ratios.

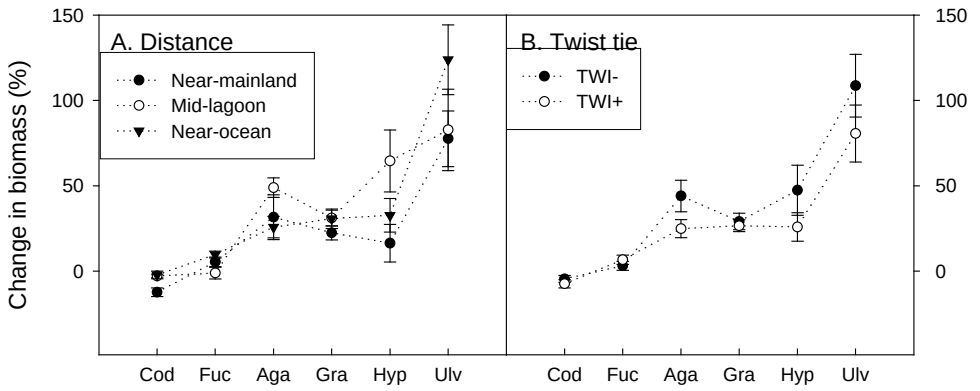


Fig. 5.6. Effect of distance from mainland (A) and caging (B) on *C. fragile* performance (% change in biomass) compared to 5 native macroalgae. Fragments were fixed in space with wrapped twist tie. Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description, Exp. 9). Species are arranged from low S:V ratios (left) to high S:V ratios.

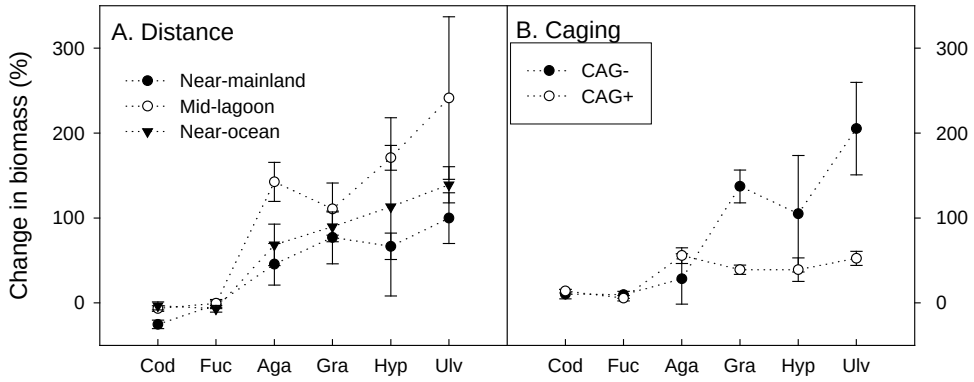
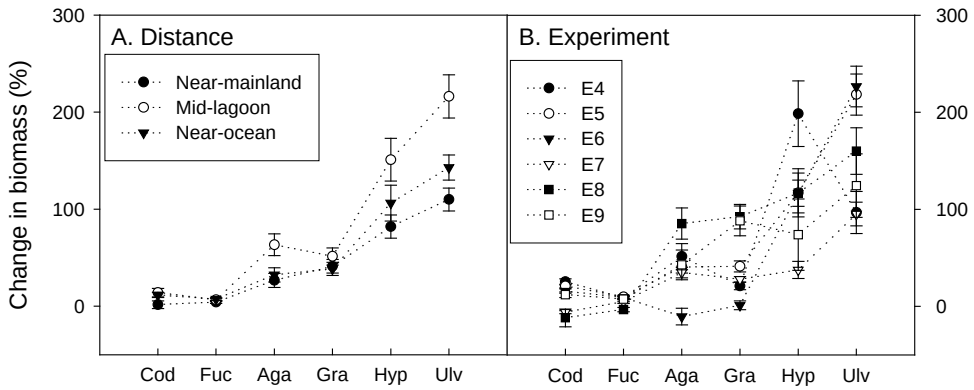


Fig. 5.7. Effect of distance from mainland (A) and experimental design (B) on *C. fragile* performance (% change in biomass) compared to 5 native macroalgae. Errors bars are standard errors (cf. Table 5.1 for number of replicates and design description). Species are arranged from low S:V ratios (left) to high S:V ratios.



Chapter 6. Performance of oyster reef associated sessile organisms: effects of hydrodynamics and accumulations of sediments and drift algae

Abstract

Proliferation of drift algae and enhanced sedimentation are major disturbances in shallow lagoons. It is well known that these disturbances affect seagrass beds and soft bottom fauna, but less is known about how these disturbances affect lagoonal hard bottom assemblages. In soft bottom lagoons the oyster is a foundation species that affects the local biota by altering hydrodynamic conditions and biogeochemical cycles, and by providing substrate for reef-associated organisms. To test if accumulations of drift algae or sediments affected recruitment of oyster reef associated sessile organisms, cages were constructed to trap either algae or sediments on recruitment bricks. The experiment was conducted simultaneously in front, between, and behind a series of oyster reefs at a mid-lagoon shoal site in Hog Island Bay, Virginia. These locations represent different hydrodynamic habitats: wave-exposed, current-exposed and wave- and current-protected. The abundances of attached taxa were mapped on the recruitment bricks four times during a one-year period. There were significant multivariate effects of both cover type and hydrodynamics on the species assemblage, but no interaction effects. The coverage of either algae or sediments explained 2-6 times more of the assemblage variability than hydrodynamics. Bricks with no cover (controls) had high taxonomic richness and abundance of attached organisms. In comparison, bricks with drift algal cover had medium richness and low abundance, and sediment-covered bricks low richness and very low abundance. Overall, the red algae *Gracilaria verrucosa* and *Agardhiella subulata*, the green algae *Codium fragile* ssp. *tomentosoides*, *Ulva curvata* and *Enteromorpha* sp. and the oyster *Crassostrea virginica* were the most abundant taxa, particularly on the control bricks. These taxa followed the pattern described for total abundance, except that

Enteromorpha and *U. curvata* were common under a cover of drift algae. *C. fragile* is an alien macroalgae that some claim has smothered oyster beds. Here, *C. virginica* and *C. fragile* showed similar distribution patterns, but were not observed co-occurring in high abundance, suggesting that they may compete for space. Overall, cover of sediments or drift algae profoundly affected the distribution and abundance of sessile reef-associated organisms, favoring a few small ephemeral taxa. This suggests that drift algae growth and sedimentation that are usually associated with eutrophication will cause an impoverishment of oyster reef assemblages. Because oysters themselves recruited poorly under a cover of drift algae or sediments, longer-term effects may result in diminishing reef structures with potentially negative effects beyond the structure of a patch reef (e.g. less hard substrate for sessile organisms, reduced topographic complexity, less shelter for small invertebrates).

Introduction

In soft bottom lagoons, oysters reefs provide three-dimensional habitats that contain rich and abundant floral and faunal assemblages (Barh & Lanier 1981, Galtsoff 1964). Healthy oyster reefs alter local biogeochemical cycles by their water filtering and sediment-binding capacities (Dame 1993, Haven & Whitcomb 1983, Lenihan 1999, Mann 2000, Möbius 1877). In general, oyster reefs are similar to coral reefs, kelp forests, mangroves, salt marshes, seagrass beds, and mussel beds, in that they are composed of a few foundation species (sensu Dayton 1972) that facilitate the distribution and abundance of a range of associated species (Bruno & Bertness 2001, Bruno et al. in press). Because of ecological and economic benefits associated with healthy and abundant oyster reefs

(Barh & Lanier 1981, Galtsoff 1964, Mann 2000), oysters have been well-studied from an autecological perspective, but synecological field experiments on oyster reef assemblages are surprisingly few (Anderson & Underwood 1997, Underwood & Anderson 1994). Oyster reefs in soft bottom lagoons provide physical relief in an otherwise flat and smooth habitat, and as a result cause local flow accelerations and decelerations (Barh & Lanier 1981, Lenihan 1999). Oyster reefs can thereby influence processes that depend on hydrodynamic conditions and that affect biological performance, such as sedimentation and resuspension rates (Airoldi 2003, Lawson 2003, Lenihan 1999), drift algae accumulations (Chapter 4, Raffaelli et al. 1998), grazing rates (Duggins et al. 2001, Kawamata 1998) and nutrient/particle encounter rates (Hurd 2000, Lenihan et al. 1996, Wheeler 1988).

Lagoonal oyster reefs are threatened by diseases, over-harvesting, and natural predators (Barh & Lanier 1981, Haven & Whitcomb 1983, Luckenbach et al. 1999, Mann 2000, McCormick-Ray 1998). Urbanization, agricultural runoff, coastal development and increased boat traffic are additional stressors that may also impact oyster reefs. The impact on the oyster reefs include: (1) enhanced sedimentation/sediment instability (Airoldi 2003, Koch & Gust 1999, McManus 1998), (2) nutrient enrichment followed by enhanced drift algae accumulations (Fletcher 1996, Morand & Briand 1996, Raffaelli et al. 1998), and (3) introduction of alien species (Moyle 1999, Ruiz et al. 1997, Ruiz et al. 1999).

Sedimentation, nutrient-enrichment and drift algae accumulations severely reduce the productivity, depth penetration and spatial extent of rooted habitat-forming angiosperms (Hauxwell et al. 2001, Holmquist 1997, Morand & Briand 1996, Nelson & Lee 2001, Raffaelli et al. 1989, Sand-Jensen & Borum 1991, Valiela et al. 1997). These stresses also limit infaunal and epifaunal species richness and abundance by suffocation, development of anoxia, limiting larvae from reaching the substratum, reducing flow rate, and interfer with feeding behaviors (Hull 1987, Norkko 1998, Norkko & Bonsdorff 1996c, a, Raffaelli et al. 1998). However, it is not known if and how sediment and drift algae stresses interfere with hard bottom assemblages, within soft bottom systems. The severity of these disturbances is most likely linked to local hydrodynamic conditions. For example, strong currents can reduce sedimentation rates and flush out algal mats, thereby reducing adverse effects of increased stresses (Flindt et al. 1997a, Hiscock 1983, Raffaelli et al. 1998, Salomonsen et al. 1997). On the other hand accumulations of drift algae and sediments may be elevated in low energy habitats, i.e. with potential enhanced stresses on associated reef organisms. Thus, it is possible that the influence of oyster reefs on hydrodynamics can moderate or accelerate the effects of these stresses (Lenihan 1999).

In addition to enhanced sedimentation and drift algae accumulations, alien pests have repeatedly invaded North American lagoons and estuaries, and some of these invasions have previously been linked to nutrient enrichment (Moyle 1999, Ruiz et al. 1999). The macroalgae *Codium fragile* ssp. *tomentosoides* has been a particular successful invader in many low energy eutrophic lagoons and estuaries where oyster reefs are abundant

(Fralick & Mathieson 1973, Malinowski & Ramus 1973, Ramus & Venable 1987, Trowbridge 1998). The dispersal and success of *C. fragile* has typically been associated with oysters (Campbell 1999, Churchill & Moeller 1972, Garbary et al. 1997, Trowbridge 1998) and it has been suggested that *C. fragile* can smother and suffocate oysters, as well as drift away with oysters attached to its holdfast (Fralick & Mathieson 1973, Hillson 1976, Mathieson et al. 2003, Trowbridge 1998, 1999). To have a significant negative effect on oyster reefs, *C. fragile* must recruit onto reefs in high densities and grow fast compared to native reef associated organisms. To our knowledge, there have been no studies that have compared recruitment of *C. fragile* to that of native sessile oyster reef taxa. The main study objectives were therefore threefold: (1) to test for effects of sediments and drift algae on the recruitment, survival, and growth of oyster reef-associated sessile organisms, (2) to test if oyster reef structures create different hydrodynamic regimes and thereby influence sedimentation, drift algae accumulations and recruitment of reef organisms, and (3) to test if the invasive *C. fragile* is a stronger recruiter, compared to native reef organisms, under different conditions of drift algae and sediment accumulation and hydrodynamic regimes.

Methods

Study site

Hog Island Bay is located in the Virginia Coast Reserve on the Delmarva Peninsula and is part of the US Long Term Ecological Research Program (Hayden et al. 2000). Hog Island Bay is a dynamic system that has changed considerably during the last 70 years with extinction of extensive sediment-binding seagrass meadows in the 1930's due to

storms and diseases (Hayden et al. 2000, Ralph & Short 2002), decimation of filter feeding oyster populations in the 1940-1960's by disease and overharvesting (Gottlieb & Schweighofer 1996, Mann 2000), accumulations of drift algal mats in the 1960-1970's (Goshorn et al. 2001, Truitt 2002) and invasions of alien species in the 1970-1990's (Hayden et al. 2000, Hillson 1976, Monti 1993). The macroalgal pest *C. fragile* ssp. *tomentosoides* originates from the northwest Pacific (Chapman 1999, Trowbridge 1999) and arrived in Virginia and Hog Island Bay in the 1970's (Hillson 1976, Monti 1993). Although not dominant in absolute biomass terms on the lagoonal scale, *C. fragile* is today the fourth most abundant macroalgae in the bay, and is particularly common below 0.6 m above mean sea level at mid-lagoon sites (Chapter 3, Appendix 1).

Experimental design

Preliminary experiments showed that sessile species typically found attached to oyster shells could recruit onto clay bricks (20 * 8 * 6 cm, Appendix 1). Because we were interested in taxonomic richness and detection of 'rare' species, the percent cover method was chosen over the more time-consuming method of determining species occurrence at 30 random pin points (Dethier et al. 1993). Before recording percent cover, each brick was gently cleaned of sediments to ensure that small and buried sessile taxa were observed. Cover could exceed 100% if organisms occupied different vertical layers and/or covered more than 184 cm^2 (the area of a single recruitment brick). To minimize observer variability a training session, estimating cover of computer generated screen patterns was conducted prior to a sampling event, and a sample-frame divided into 20

rectangles was used to aid in cover estimations (10 rectangles covered the brick, and 10 covered the brick peripherals).

An orthogonal experiment was designed to test if a cover of sediments or drift algae, and hydrodynamic conditions affected recruitment of attached organisms. First, plots were allocated to areas in front, between, and behind a series of scattered oyster reefs in the mid-lagoon (Shoal site, McGlathery et al. 2001). Spatial location was hypothesized to reflect hydrodynamic regime (Lenihan 1999) and was used as a natural experimental treatment. Areas in front of oyster reefs were subject to the largest fetch and had the steepest slope, and were hypothesized to be susceptible to waves generated under windy conditions (hereafter 'wave-exposed' sites). Areas between reefs were hypothesized to have elevated tidal currents (hereafter 'current-exposed' sites). Finally, areas behind reefs were hypothesized to be protected from both waves and currents (hereafter 'protected' sites). All plots were positioned within the 0.6-0.8 m below mean sea level depth contour where *C. fragile* had been observed to recruit with success (Appendix 1.6). Two random sites were allocated in front, between and behind oyster reefs, situated to the east of and parallel to the Machinpongo channel (Hayden et al. 2000, Oertel et al. 2000). These six sites were separated by a minimum of 30 m. Within each site 2 open control plots, 2 sediment cages and 2 drift algae traps, were systematically allocated, each plot/cage separated by approximately one meter. Sediment-cages were constructed of 65*50*50 cm plastic boxes to reduce tidal currents and thereby trigger sediment deposition on small spatial scales. The cages were transparent to minimize shading at low solar angles, but resulted in a 5% light reduction accumulated over an entire day (Table 6.1). Cages were

fixed with rebar which was inserted through holes drilled in the corners and center of the cages. Five cm depth of mixed sediments and unconsolidated oyster shells was added to the cages to mirror the ambient benthic habitat, and small holes were drilled in the side walls to ensure normal tidal fluctuations in water level. Cage-roofs were not added because these structures get fouled within days by drift algae, sediments and epiphytes, and as a result reduce light penetration and sedimentation. This design allowed access for mobile grazers. Drift algae cages were constructed of four corner rebars connected by a top-string (65*50*50 cm) in order to trap drift algae. This open-structure design, did not affect light conditions (Table 6.1) or water flow (Table 6.5N, 6.5O, Table 6.6). It is unlikely that the corner rebars by themselves should have affected sedimentation or accessibility for mobile herbivores and predators (pers. obs.). Finally, non-caged open control plots were established to quantify recruitment of attached organisms with low background levels of sediments and drift algae covers. The experiment was initialized in July 2002 by placing three bricks in each of the 36 plots (3 plots with different hydrodynamic regimes * 3 plots with different cover types * 4 replicated plots). Attached taxa were identified and percent cover was recorded on each brick on March 7, April 14, June 11, and July 30 2002. The three within-plot bricks were separated by a few centimeters and were treated as sub-replicates, i.e. species abundance per plot was calculated as the mean abundance for the three bricks.

The cover of sediments, the cover of drift algae, hydrodynamic forces and potential co-varying factors, were quantified. First, accumulated sediment depth was recorded with a ruler to the nearest mm at 3 random sub-sites on each brick on March 7, June 11, and July

30, 2002. The average sediment depth per plot (3 bricks/plot * 3 sub-brick areas) was used for the data analysis. In addition, sedimentation rates were measured in 20 cm PVC tube traps, with an inner diameter of 50 mm^2. A tube was placed in the center of each plot and inserted ca. 10 cm into the sediment on the 17 of June 2002. On the 28 of June, the tubes were brought to the laboratory and dried at 70°C to a constant weight. Because of the closeness of the tube opening to the sediment surface, these sedimentation rates include re-suspended sediments. Second, accumulated drift algae were collected in 60 * 50 cm sample frames (0.3 m^2, similar to plot area) from each plot on five sampling dates (July 17, December 15 2001, January 4, July 16, August 5 2002). Algae were brought to the lab, blotted with a towel and the wet weight was measured. To test for hydrodynamic effects three response variables were measured. First, tidal currents were measured in the center of each plot after removal of drift algae with a Marsh-McBinney electromagnetic current meter on July 17 (12:56, water level rising, 20 cm water depth) and June 25, 2002 (13:30, falling water level, 35 cm). Second, maximum water forces (Jones & Demetropoulus 1968) were measured with drag meters (Bell & Denny 1994) centered in each plot on July 20 and December 13, 2001 after 1 day of incubation. A 5 cm stainless steel spring, 15 cm long when experiencing 125 g force, was inserted into a 20 cm PVC tube. The spring was connected to a practice golf ball via a fishing line that extended five centimeters outside the tube, and a piece of rubber was used as a ‘marker’ to record maximum spring extension during each incubation period. See Bell and Denny (1994) for specific design details. Each drag meter tube was placed into the sediment. Drift algae can entangle the line and the practice golf ball and thereby increase drag, a high value could be indicative of either high water forces or entanglement by the algae. Third, wave

heights were estimated on several occasions under different weather conditions by recording the wave height using a 2 m ruler as a reference marker (i.e. subtracting wave trough heights from wave peaks) in front, between and behind reefs.

Water temperatures, oxygen levels and salinity were measured in the 36 plots on July 24, 2001 with an Orion DO meter and a refractometer, but none of these variables differed between treatments (28-29ºC, 5-6 mg O_2L^{-1}, 34 ppt) i.e. even if these variables changed in time, treatments are unlikely to differ. In addition, light reducing effect of cage structures versus open plots was measured with an Apogee Quantum Meter 5 times from early morning to mid-afternoon on August 4, 2002 in plot centers and corners (n = 2 per time). Light differences between cage structures and open plots were minor, and mean values are simply listed in Table 6.1 (time pooled).

Data analysis

Treatment effects were tested with repeated two-factorial ANOVAs on sediment accumulation, sedimentation rate (no repeated component), drift algae accumulation, current velocity, and maximum hydrodynamic force (Table 6.2), followed by SNK-tests to group specific single-factor treatments (Underwood 1997). Since the data resolution of the visually determined wave height data is poor, these are only discussed qualitatively. To test if cover type and hydrodynamic regime had affected the recruited assemblages, two-factorial non-parametric multivariate ANOVAs were conducted on each of the four sampling times (Table 6.3, NPMANOVA do not allow a repeated design, Anderson 2001, Anderson & Ter Braak 2003), followed by pair-wise permutation t-tests to suggest

treatment differences (Table 6.4). To explore which species contributed most to the assemblage variability within and between treatments, similarity percentages were calculated on the hydrodynamics and cover factors separately with time pooled (SIMPER does not allow for multi-factorial testing, Clarke & Warwick 1994). Treatment effects were also tested with repeated measure ANOVAs on key assemblage summary variables (taxonomic richness and total percent cover) for animals and plants respectively, followed by SNK-tests on each factor to group specific treatments. Animals and plants were kept separated because of potentially different treatment responses. Finally, treatment effects were tested on individual taxa of special interest including (1) the reef building oyster, *Crassostrea virginica*, (2) the alien algae *C. fragile*, (3) the two dominant red coarsely branched algae *Gracilaria verrucosa* and *Agardhiella subulata* (Chapter 2, Goshorn et al. 2001), and (4) the two opportunistic sheet-like green algae *Enteromorpha* spp. and *Ulva curvata* that typically proliferate under stressed conditions (Fletcher 1996, Morand & Briand 1996). Also, to explore if the abundance of *C. fragile* was related to the abundance of *C. virginica* (Carlton & Scanlon 1985, Fralick & Mathieson 1973), Pearsons correlation coefficient was calculated, using each brick as a replicate. All data for ANOVA tests were Log(x+1) transformed prior to analysis to reduce variance heterogeneity and the influence of outliers, and back-transformed for graphical display. Inspection of box-plots and comparisons of Cochran's C-values showed that transformations successfully reduced variance heterogeneity, although some variables remained with heterogeneous variances despite the transformation (i.e. $p < 0.05$). Because ANOVA is robust to minor variance heterogeneity, particularly for large samples sizes and balanced designs (as in this study) these tests were included (Quinn &

Keough 2002, Underwood 1997), but marked with an asterisk after reported significant p-values (cf. ANOVA tables, non-significant p-values remain statistically valid also with variance heterogeneity). Eta square (η^2) was calculated to compare the relative contribution of each test-factor to the total data variability (Levine & Hullet 2002, Welden & Slauson 1986). Because the emphasis was on the between-subject effects, i.e. effects of cover type and hydrodynamics, and less on within-subject time effects (Trial factor), reporting of the results focuses primarily on the significant between-subject effects. However, because temporal effects were important in most univariate ANOVAs on recruitment, time differentiated abundance patterns were nevertheless visualized on graphs.

Results

Drift algae accumulations, sedimentation and hydrodynamics

There were significant effects of accumulated sediment depth on the recruitment bricks for Cover and Cover * Hydrodynamics, with Cover being by far most important (Table 6.2A). The SNK-test showed that sediment depth accumulated over a 3-4 month period and was largest in PVC-cages (6.8 mm), intermediate in open plots (2.2 mm) and smallest in drift algae cages (1.2 mm) (Fig. 6.2A). Also, the magnitude of these effects depended on the ambient hydrodynamic regime and were most pronounced in wave-exposed plots and least in current-exposed plots. For sedimentation rate, there were significant effects of both Cover and Hydrodynamics, with the majority of data variability explained by the Cover factor (Table 6.2B). The SNK-test indicated that sedimentation was higher in control and sediment plots (0.029 $gDWmm^{-2}d^{-1}$) compared

to drift algae plots (0.021), and that current-exposed plots had higher sedimentation rates (0.030) compared to wave-exposed plots (0.026) and protected plots (0.024)(Fig. 6.2B). Drift algae accumulations were affected significantly by Cover, Hydrodynamics and Cover * Hydrodynamics, again with the majority of data-variability explained by Cover (Table 6.2C). The SNK-test showed that drift algae accumulations were highest in the rebar-cages (1770 $gWWm^{-2}$), medium in the PVC cages (767 $gWWm^{-2}$) and lowest in the open control plots (192 $gWWm^{-2}$). Also, there was significantly more drift algae in the protected and wave-exposed plots compared to the current-exposed plots (Fig. 6.2C). There were significant effects on current velocities of Cover, Hydrodynamics, and Cover * Hydrodynamics, with the two single factors explaining most of the data variability (Table 6.2D). The SNK-test showed that velocities were largest in current-exposed plots (5.5 ms^{-1}), intermediate in wave-exposed plots (1.0 ms^{-1}), and lowest in protected plots (0.6 ms^{-1}). Also, control plots and rebar cages had significant higher velocities (3.5 ms^{-1}) compared to the PVC cages (0.1 ms^{-1}) (Fig. 6.2D). Since the trapped drift algae was removed from the rebar cages before the measurements were made, these results indicated that the rebar structure did not by itself influence free-stream velocity. There was a near-significant effect of Cover on drag forces, but with low η^2, probably due to the relatively low hydrodynamic forces within Hog Island Bay (Table 6.2E, Fig. 6.2E). Finally, wave heights were highest in the wave-exposed plots, intermediate at current-exposed plots, and smallest in the protected plots. These results are relevant for northeastern, northern and northwestern windy conditions or when boat wake activity was high; southern winds only generated ripples at all locations.

Recruitment

The community structure of oyster reef-associated sessile organisms was significantly affected by sedimentation and drift algae accumulations, and to a lesser extent, by differences in hydrodynamic conditions. The NPMANOVA on the species assemblages showed significant single factor effects of both cover of substrate and hydrodynamic regime for each sampling time, but no significant interaction effects (Table 6.3). Cover explained 2-6 times more of the data variability compared to hydrodynamics (η^2 = 41-68 vs. 11-19%). Of the pair-wise comparisons, all 12 were significant for Cover and 10 were significant for Hydrodynamics (Table 6.3), indicating that each cover type and hydrodynamic regime had a distinct assemblage at each sampling time. Graphical analysis of species-abundance curves for individual treatments for both the Cover and Hydrodynamic factors showed different dominance patterns between and within test factors (Fig. 6.1). Open control plots represented typical recruitment patterns within the 0.8-0.6 m below MSL depth contour, and were dominated by *G. verrucosa*, followed by *C. virginica*, *A. subulata*, *C. fragile*, *Ectocarpus* spp., *Enteromorpha* spp. (epiphytic on *G. verrucosa*) and *U. curvata* (Fig. 6.1A). In contrast, sediment-covered bricks had very low abundance of any organisms, and the most common species were *G. verrucosa*, *Enteromorpha* and the filter feeders *C. virginica*, *Membranipora* spp., *Amathia vidovici*, *Molgula* sp., *Hydroides dianthus*, and *Bugula turrita* (Fig. 6.1B). The drift algal covered assemblages had low abundance, except for the opportunistic *Enteromorpha* spp. and *U. curvata* (Fig. 6.1C). The differences between assemblages exposed to different hydrodynamic regimes were less obvious. Wave and current protected plots had a relatively even distribution of many taxa, including *G. verrucosa*, *C. virginica*, *A.*

subulata, *C. fragile*, *Ectocarpus* spp. (epiphytic), *Enteromorpha* spp., *U. curvata* and *Punctaria latifolia*, all with 2-4% cover (Fig. 6.1D, Time and Cover pooled). Wave-exposed plots were primarily dominated by *G. verrucosa*, *Enteromorpha* sp., *C. virginica* and *C. fragile* (Fig. 6.1E), whereas current exposed plots mainly were dominated by *G. verrucosa* and *Enteromorpha* spp. (Fig. 6.1F). The SIMPER analysis (Table 6.5) indicated that few species contributed to the majority of assemblage data variability, with *G. verrucosa*, *C. virginica* and *Enteromorpha* spp. being the dominant taxa. Most invertebrate taxa were relatively unimportant within the different assemblages, but when added together contributed to a relatively large proportion of the between group variability (*B. turrita*, *A. vidovici*, *Membranipora* spp., *Molgula* sp., *H. dianthus*, and various hydroids).

Species richness and abundance were also affected by sedimentation, drift algae accumulations, and hydrodynamic conditions. There was a significant interaction effect between cover and hydrodynamics for animal richness, but with a low η^2-value (Table 6.6A). Due to the lack of significant single factor effects, the SNK-test did not differentiate between treatments (overall mean of 2 animals/brick). In particular, it was noteworthy that sediment-covered plots supported as many animal taxa as algal-covered and control plots (Fig. 6.3A-D). Plant species richness was significantly affected by Cover and near-significantly affected by Hydrodynamics (Table 6.6B). The SNK-test showed highest plant richness in control plots (4.8 plants/brick), intermediate in drift-algae treatments (3.3) and lowest in sediment treatments (2.1). Also, plant richness was significantly higher in protected and current-exposed plots (3.6) compared to wave-

exposed plots (3.2, Fig. 6.3E-H). Animal abundance was significantly affected by Cover and by the interaction between cover and hydrodynamics, with most of the variability explained by Cover (Table 6.6C). The SNK-test showed that control plots had higher abundance of animals (6.2% cover/brick) compared to plots covered by drift algae or sediments (2.2%) (Fig. 6.4A-D). For plant abundance, there were significant effects of both Cover and Hydrodynamics, with Cover explaining the majority of the data variability (Table 6.6D). Thus, plant abundance was highest in control plots (28%), intermediate under a cover of drift algae (10%), and lowest under sediment cover (1.6%), Current exposed plots (16%) had higher plant abundance compared to protected and wave-exposed plots (12%). The interaction plots (Fig. 6.4E-H) showed a peak in abundance in early summer, largely because of high abundance of *G. verrucosa* and *Enteromorpha* sp.. Sessile algae were in general more abundant than sessile animals (Fig. 6.4). It should be noted that recruitment bricks were never fully occupied, indicating that space was not a limiting resource during the 1 yr study period. Typically, 20-40% of the space was occupied on bricks in open plots, 5-20% in drift algal covered plots and 2-5% in sediment covered plots.

As with the assemblage response, all 6 taxa of interest were affected by sedimentation and drift algae accumulations, and to a lesser extent by hydrodynamic conditions. The reef-building oyster, *C. virginica*, was significantly affected by Cover (Table 6.7A), with higher abundance in control plots (4.5%) compared to algal or sediment covered plots (0.7%). Within the open plots recruitment were highest in wave-exposed plots at time 1 and 2 (Fig. 6.5A-B), but shifting to highest abundance in protected plots at time 3 and 4

(Fig. 6.5C-D). Similarly, the alien *C. fragile*, was significantly affected by Cover (Table 6.7B), and control plots had higher abundance (3.4%) compared to sediment and drift-algae covered plots (0.0%). The interaction plots showed slightly lower abundance in current-exposed plots compared to wave-exposed and protected plots (Fig. 6.5E-H). Of all the mapped bricks, *C. fragile* occupied a maximum of 40% of a single brick. Also, of the 144 observations on sediment-covered bricks (1/3 of 432 brick observations), *C. fragile* recruits were found on 8, and all later died. Similarly out of drift-algal covered bricks *C. fragile* was observed 14 times, again with 100% mortality. In contrast *C. fragile* was observed 96 times, i.e. on 67% of the open block bricks. Of these 96, 38 were on bricks behind reefs, 27 between reefs, and 31 in front of reefs. Despite similar abundance patterns between *C. fragile* and *C. virginica*, they were not significantly correlated ($r = 0.01$, $p = 0.90$, $n = 324$). No bricks were found with high abundances of both species (Fig. 6.6).

The ubiquitous coarsely-branched red alga *G. verrucosa* was significantly affected by Cover and Hydrodynamics, with Cover being particularly important (Table 6.7C). *G. verrucosa* was significantly more abundant in the control plots (14.1%) compared to drift algae or sediment covered plots (ca. 1.0%), and also had higher abundance in current-exposed plots (7.2%) compared to wave-exposed and protected plots (ca. 4.2%). Also, *G. verrucosa* had a pronounced peak at sampling time 2 compared to times 1, 3 and 4 (Fig. 6.7A-D). For the other coarsely-branched red alga, *A. subulata*, there were significant effects of both Cover and Hydrodynamics and a near significant interaction effect between Cover and Hydrodynamics, although variance heterogeneity was relatively

pronounced for this data. The three factor-combinations explained roughly equal amounts of the data variability (i.e. 18, 11, 15%, Table 6.7D). The SNK-test showed that *A. subulata* was significantly more abundant in control plots (7.8%) compared to alga or sediment covered plots (0.0%). Also, *A. subulata* had highest abundance in protected plots (2.7%), intermediate in current exposed plots (1.2%) and lowest in wave-exposed plots (0.0%, Fig. 6.7E-H). The opportunistic green algae *Enteromorpha* spp. was significantly affected by Cover and Hydrodynamics, with the highest η^2 for Cover (Table 6.7E), and the highest abundance at sampling time 2 (Fig. 6.8A-D). *Enteromorpha* spp. was significantly more abundant under a drift algae cover (6.2%), intermediate in control plots (1.4%) and lowest under a sediment cover (0.4%). *Enteromorpha* spp. also was more abundant at current- and wave-exposed plots (3.2%) compared to protected plots (1.7%). Finally, the opportunistic green alga *U. curvata* was significantly affected by Cover (Table 6.7F), and the SNK-test showed that abundance was highest in control plots and under a cover of drift algae (1.6%) compared to the sediment cover (0.3%). In addition, a SNK-test on the Hydrodynamic factor suggested that *U. curvata* was more abundant in current-exposed and protected plots (1.4%) compared to wave-exposed plots (0.8%). However, the interaction plots indicated a complex pattern with treatment effects changing between all sample times (Fig. 6.8E-H). Thus, *U. curvata* was mainly present at times 1 and 2 in current-exposed control plots, at time 3 in most plots, and at time 4 in current-exposed drift algal-covered plots and protected control plots. This confirmed that *U. curvata* was an opportunistic species able to recruit onto hard substrate for short time periods in most seasons and habitats.

Discussion

Quantifying succession and recruitment of sessile organisms has been a goal for benthic ecologists for decades, and these processes have been well documented in rocky intertidal and subtidal systems (e.g. Buschmann 1990, Connell 1961b, a, Dean & Connell 1987c, b, Hirata 1986, 1987, Leonard et al. 1999, Parker et al. 1993, Petraitis & Latham 1999). Relatively few studies have considered succession and recruitment of sessile organisms in soft bottom lagoons and estuaries, where oyster reefs, mussel beds and man-made constructions provide patches of hard substrate, which typically support a rich associated flora and fauna (Albrecht 1998, Anderson 1999a, Connor 1980, Dean & Hurd 1980, Lenihan 1999, Rhodes 1970, Underwood & Anderson 1994, Wells 1961). We document that accumulations of sediments and drift algae negatively affect recruitment, survival and growth of sessile oyster reef assemblages. Since eutrophication typically enhances drift algae and sediment instability/sedimentation, increasing human pressures on coastal systems are likely to cause impoverished oyster reef assemblages on large spatial scales.

Effects on sediments, drift algae and hydrodynamics

It is well-established that sedimentation structures sessile benthic assemblages (Airoldi 2003, Airoldi & Virgilio 1998, Rogers 1990). However, Airoldi (2003) reviewed the literature and concluded that most impact studies only measured net accumulation or sedimentation rates (or nothing at all). In the present study, both sediment accumulation and sedimentation rates were quantified, and because patterns differed slightly both should be reported as a general rule (Airoldi 2003). We believe that accumulated sediments is the more ecologically relevant estimate of sediment stress that can reduce

adhesion strength (Charters et al. 1973, Devinny & Volse 1978) or bury and suffocate sessile recruits (Airoldi 2003, Berger et al. 2003). The relative high sedimentation rate in the control plots, compared to the amount of accumulated sediments, was likely caused by the sediment tube structure itself which would induce small-scale turbulence, reduce flow, and trigger sediment out-fall. This effect was most pronounced in the wave and current-exposed plots where sediments frequently become resuspended or where encounter rates are high (McManus 1998, Schoellhamer 1996). Drift algal densities in eutrophied shallow systems commonly exceed 1 $kgWWm^2$ (Menedez & Comin 2000, Norkko & Bonsdorff 1996a, Peckol & Rivers 1996, Raffaelli et al. 1998, Tagliapietra et al. 1998) and experiments testing for drift algal effects on soft bottom in and epi-fauna have typically applied densities above this value, using green or brown sheet-like or filamentous algae (Hull 1987, Norkko & Bonsdorff 1996a, Norkko et al. 2000, Osterling & Pihl 2001, Raffaelli et al. 1989). We found minor effects of hydrodynamic differences on the amount of accumulated drift algae, although there was a tendency for lowest accumulations where currents were strongest (Flindt et al. 1997a, Martins et al. 2001, Raffaelli et al. 1998). The accumulated drift algal mats were composed primarily of the coarsely branched red algae *G. verrucosa* (Humm 1979), i.e. taxonomically and structurally different from the aforementioned drift-algae impact studies. It should also be noted that our trap approach in the low intertidal did not seem to cause algal decomposition or development of anoxia. Velocities were low but not unusual for lagoons (Hawes & Smith 1995, Lawson 2003, Schanz et al. 2000), and the accelerated currents between the oyster reefs reflected that the reef structures altered local hydrodynamics on small spatial scales (Barh & Lanier 1981, Lenihan 1999). It is

interesting that the mean velocities in the current-exposed plots were below 0.1 ms^{-1}, which was suggested by Hurd (2000) to demarcate low water motion regimes where metabolic processes may be transfer limited. This suggests that in our experiment, nutrient limitation may differ between treatments. The velocities were not measured when the reefs were inundated, but it is likely that currents would be smaller (Lawson 2003). The wave climate was also affected by the reef structures, with 20-30 cm wind and wake generated waves breaking in front of the reefs, and being non-existent behind. Waves were also only observed before the reefs became inundated. Because benthic wave stress decrease with water depths (Denny 1985), the measured wave heights probably constitute near-maximal wave influences, although benthic stress may be higher under extra-tropical storms (Dolan 1996, Hayden et al. 2000, Lucy et al. 1986). The waves were observed to resuspend sediments, thereby increasing turbidity on small spatial and temporal scales and also influencing light conditions (Lawson 2003, Schoellhamer 1996, Ward et al. 1984).

We did not apply cage-controls because in systems where hydrodynamic regimes affect nutrient and suspended solid encounters rates, sedimentation, resuspension, light conditions, drift algae transport, dislodgment, propagule dispersal, and grazing (Chapter 2, 4, 5, Christensen 2000., Kastler & Wiberg 1996, Lawson 2003), such structures will inevitable alter many factors simultaneously. Our open and simple drift algal trap structure minimized the possibility of confounding for this treatment (similar to typical cage-controls, Parker et al. 1993, Rosinski 2004, Woodin 1978), whereas the sediment cages could be confounded by drift algae accumulations (quantified) or altered

accessibility of herbivores and predators (not quantified). However, because sediment accumulations were lower under a cover of drift algae compared to controls (this study), opposite to the effect of the sediment cages, it is likely that the imposed algae effect within the sediment cages was minimal.

Recruitment in open plots

The orthogonal design between cover and hydrodynamics allowed for tests of interaction effects, but because few interaction effects were significant, single factor effects could be interpreted independently. Also, because the cover factor treatment was more severe than the hydrodynamic factor, data could be interpreted as recruitment in open control plots vs. drift algae covered plots vs. sediment covered plots. The taxa in the control plots are common along the North American east coast, and have been observed attached to oyster shells or recruitment panels (Connor 1980, Dean & Hurd 1980, Gosner 1978, Humm 1979, Lippson & Lippson 1997). However, in comparison to recruitment studies from similar systems (Albrecht 1998, Anderson 1999a, Dean & Hurd 1980, Underwood & Anderson 1994), macroalgae and growth of primary producers were more dominant in Hog Island Bay (Barh & Lanier 1981, Dame et al. 1989, Dame 1992, Dame 1993). Many algae commonly found in the drift assemblage, e.g. the filamentous *Bryopsis plumosa*, *Ectocarpus* spp., *Polysiphonia* spp., *Ceramium* spp., *Champia parvula* and the coarsely branched *Hypnea musciformis* (Chapter 2, 3, 4) did not recruit onto the bricks, but were mainly observed entangled or epiphytic on larger primary attached algae. Thus, these species mainly thrive unattached and epiphytic. Overall, *G. verrucosa* was the most abundant species, adding a high recruitment ability to an array of previously described

successful lagoon adaptations, including high stress tolerance (Chapter 5, Stokke 1956), high growth and recovery potential (Chapter 5, Hanisak et al. 1979, McLachlan & Bird 1986) and strong association with the polychaete facilitator *Diopatra cuprea* (Chapter 3), together explaining the ubiquity of this species in North American east coast lagoons (Cowper 1978, Goshorn et al. 2001, Chapter 2, Humm 1944, Peckol & Rivers 1996). The larger algal species (*A. subulata, C. fragile, G. verrucosa*) generally recruited in high densities, with large and small individuals being intermixed. Individuals of these species can grow into large thalli within a few months under benign conditions (Chapter 5, McLachlan & Bird 1986, Pedersen & Borum 1996, Poole & Raven 1997). However, large individuals are susceptible to dislodgment and pruning by hydrodynamic forces (Chapter 4, Blanchette 1997, Gaylord et al. 1994, Thomsen & Wernberg submitted), and hydrodynamic forcing may frequently generate fragments to the drift algal assemblages (Chapter 2, 3, 4). Also, because unattached algae in general do not become reproductive (Norton & Mathieson 1983), the algae attached to the oyster reefs ensures that a propagule bank is constantly produced (Santelices et al. 1995). Thus, reef attached algae probably reduce the likelihood of local extinctions on the mudflats (where waves and currents constantly remove algae) by providing a continuous supply of fragments.

The only animal that was space dominant on the bricks was the oyster *C. virginica*. This is similarly to other soft bottom studies that also observed local oyster species to be efficient recruiters (Anderson 1999a, Lenihan 1999, Underwood & Anderson 1994). Other recruited animals were filter feeding subdominants (e.g. *H. dianthus, Membranipora* spp., *Molgula* sp.) and seasonally fluctuating taxa (e.g. *B. turrita, A.*

vidovici) that generally perform relatively well in high depositional environments (Barh & Lanier 1981, Dean & Hurd 1980, Lippson & Lippson 1997). We noted that a large proportion of the oysters died within a few months of recruitment, probably due to predation or diseases (Anderson 1999a, Barh & Lanier 1981, Lenihan 1999, O´Beirn et al. 1996). Despite a high mortality, the shells of the recruited oysters still caused increased topographic complexity, and may thereby have increased available space (Barh & Lanier 1981, Connor 1980, Rhodes 1970).

The experiment was conducted on a small spatial scale within a hydrodynamic well-mixed area, and propagules were probably distributed uniformly in the water masses (Norton 1992, Santelices 1990). However, small-scale differences in hydrodynamic process could cause different encounter rates between propagules and the experimental substrates. Abundance patterns may thereby have reflected different propagule encounter rates, different likelihood of attachment, and/or differential survival and growth rates. Current-exposed plots should have encountered most propagules (Lenihan 1999, Leonard et al. 1999), whereas wave-exposed plots may have had highest attachment success because orbital water motion increases contact rates between suspended propagules and the recruitment bricks (Denny 1988). Oyster reefs have previously been suggested to influence local hydrodynamic conditions (Barh & Lanier 1981, Brooks 1996, Galtsoff 1964, Mann 2000). In particular Lenihan (1999) documented that reef sizes, reef shapes and reef elevation influenced the local hydrodynamic regime, and thereby partly explained survival and growth of oyster recruits. However, effects on recruitment of oysters positioned at different elevations likely differed due to both effects associated

with the reef-structure (alteration of flow and flow-associated variables) and to effects uncoupled from the reef-structure (e.g. light levels, orbital wave velocities, sedimentation rates and re-suspension levels (Chapter 5, Appendix 1). In the present study, all plots had similar elevations, and changes in physical conditions and assemblage patterns could thereby only be attributed to the structure of the oyster reefs. We documented that the reef position in itself caused significantly different sessile assemblages, although the effects were less obvious compared to the effects of drift algae or sediment accumulations (cf. η^2 values in ANOVA models). Thus, even within apparently uniform low-energy lagoons (< 0.1 m/s, Hurd 2000), different hydrodynamic regimes induce differential performance patterns on small spatial scales. Species-specific performance patterns are typically inter-related in assemblage based field experiments. Thus, successful recruitment may be related to the abundance of other taxa already present (Connell & Slatyer 1977, Petraitis & Latham 1999, Sutherland 1974, Underwood & Anderson 1994), although inhibitory or facilitative effects probably were relatively unimportant due to the low covers of sessile organisms. The limited success of *C. fragile* and *C. virginica* in these plots could be caused either by spatial inhibition by *G. verrucosa* or by a low tolerance to current induced drag and/or entanglement of drift algae clumps. The main taxa-specific hydrodynamic effects were the absence of *A. subulata* in front of reefs, a high abundance of *G. verrucosa* between reefs and relative low abundance of *C. fragile*, *C. virginica* and *A. subulata* between reefs. The absence of *A. subulata* was likely caused by frequent wave-induced thallus breakage because it has a low adhesion strength (Chapter 4), but large drag when growing into a large organism (Chapter 4, Denny 1995, 1999, Gaylord et al. 1994). *G. verrucosa* could be most

dominant between reefs because this species likely is the least susceptible to entanglement by drift algae clumps (Chapter 4, Holmquist 1997), a potential detrimental process where currents and drift algae transport are high (Flindt et al. 1997a, Martins et al. 2001, Salomonsen et al. 1997). Transplantation experiments and improved biomechanical measurements are needed to support these explanations.

Recruitment under drift algae

Eutrophication and subsequent increased drift algae abundance (Fletcher 1996, Morand & Briand 1996, Raffaelli et al. 1998) may limit oyster recruitment (this study), and thereby threaten reef maintenance process in coastal systems worldwide. Because the oyster is a foundation species facilitating numerous associated organisms, and alter biogeochemical cycles and abiotic conditions (Barh & Lanier 1981, Bruno & Bertness 2001, Bruno et al. in press), detrimental effects of drift algae proliferation may have system wide consequences. A cover of drift algae significantly affected the sessile assemblages. These effects were manifested through poor plant richness, and low cover of plants and animals. In particular, the algal assemblage lacked large perennial taxa. Recruits of these species were occasionally observed, but did not survive, potentially due to light limitation or smothering/abrasion by the algal mat (Krause-Jensen et al. 1996, Norkko & Bonsdorff 1996b, Raffaelli et al. 1998). Few oysters recruited onto these bricks and those few that did recruit had 100% mortality. The effects of the drift algae cover were not related to anoxia development as observed in other studies (Norkko & Bonsdorff 1996a, Raffaelli et al. 1998), rather the drift cover effects were likely due to reduced light penetration (Krause-Jensen et al. 1996, Peckol & Rivers 1996), filtering of

propagules (Olafsson 1988), reduced currents (Escartin & Aubrey 1995), and interference with feeding apparatus (Norkko & Bonsdorff 1996a), as well as positive effects associated with reduced desiccation. The green algae *Enteromorpha* spp. and *U. curvata* were the most common space-occupying taxa, although only as mm-cm small individuals. These taxa are ephemeral subdominants on primary substrates, but have high growth and reproductive outputs (Littler 1980, Nielsen & Sand-Jensen 1990, Poole & Raven 1997). *U. curvata* and *Enteromorpha* spp. were thus probably dominant because of reduced grazing (Geertz-Hansen et al. 1993, Giannotti & McGlathery 2001, Poole & Raven 1997), dislodgment (Chapter 4, Hawes & Smith 1995, Martins et al. 2001, Thomsen & Wernberg submitted) and competition from canopy-forming algae.

Recruitment under sediments

Enhanced sedimentation is increasingly threatening coral reefs, rockweed beds and kelp forests (Airoldi 2003, Devinny & Volse 1978, Johansson et al. 1998, Rogers 1990). Here it is documented that sessile organisms in soft bottom lagoons also are detrimentally affected by enhanced sedimentation. Enhanced sedimentation can be caused by decreased abundance of sediment stabilizers, climatic changes, coastal construction projects, changed agricultural practices, and reduction of sediment traps such as salt marshes (Airoldi 2003). On the eastern shore of Virginia, these mechanisms already have caused, or are likely to cause, enhanced sedimentation (Haven & Whitcomb 1983, Hayden et al. 2000, Ralph & Short 2002). The accumulation of 4-10 mm of sediment per 1-4 month periods was sufficient to decrease the abundance of plant and animals, although animal richness was unaffected, demonstrating that species did recruit onto the bricks but did not

survive, or had reduced growth. Sediment effects were particularly detrimental to the algal assemblage, with the opportunistic *U. curvata* being the only species to occupy small amounts of space for short times periods. The effects were also adverse for filter feeders, although less so in current exposed plots where sediment accumulations were smallest. Many filter feeding animals are relatively resistant to small amounts of sediments (Dean & Hurd 1980), although eventually feeding structures will clog or become buried. Oysters occasionally recruited onto these bricks, but did not survive. Thus, the long term effects would again, similar to the drift algae treatments, be diminished reef structures with potentially wide-ranging ecological effects.

Temporal recruitment effects

Temporal effects are the cornerstone of succession studies (Clements 1936, Connell & Slatyer 1977, Cowles 1899), and temporal effects in recruitment patterns of sessile marine organisms are well-studied (e.g. Dean & Connell 1987b, a, Hirata 1986, 1987, Parker et al. 1993, Petraitis & Latham 1999). Although temporal effects could be deduced from the present study, they were of secondary interest compared to effects of cover stress and hydrodynamics. Because the experiment was unreplicated within and between seasons, temporal interpretations also suffer from problems of auto-correlation and carry-over effects (Anderson 1999a, b, Anderson & Underwood 1997, Underwood & Anderson 1994). Thus, studies by Anderson and Underwood (cf. above) specifically replicated incubation panels in different seasons and found different assemblages. However, most of these studies had incubation time of less than six months, making it possible that assemblages could converge given several cycles of recruitment and life-history turnover

(Petraitis & Latham 1999, Sutherland 1974). Because the bricks in the present study had low cover, independent recruitment was possible, although the available area would shrink and expand depending on the performance of neighboring attached organisms. The importance of temporal effects was apparent from the interaction plots and ANOVA tests. Temporal changes were likely caused by lunar cycles (different emergence times, different peak tidal currents), seasons, (temperature, light, storms) and life-history strategies (length, intensity and timing of propagule supply)(Appendix 1, Santelices 1990, Schneider & Searles 1991). Our study lasted for one year, but it is possible that inclusion of several life-history turnovers could alter the conclusions.

Recruitment of *C. fragile*

Our finding that the invasive *C. fragile* was the fourth most dominant recruiter in control plots supports the claim that *C. fragile* is a successful recruiter onto barren space and a strong space occupier on hard substrates in lagoons and estuaries (Fralick & Mathieson 1972, 1973, Malinowski & Ramus 1973), partly explaining its success as an invader (Begin & Scheibling 2003, Chapman 1999, Hillson 1976, Mathieson et al. 2003). The ability to recruit and survive on bricks positioned at various oyster reef locations indicates tolerance to a range of hydrodynamic conditions (Mathieson et al. 2003, Trowbridge 1998). *C. fragile* and *C. virginica* had similar distribution patterns, but they were not found in high densities together, suggesting possible competition for space. However, longer-term data, and specific experimental designs manipulating densities are necessary to document negative effects of *C. fragile*. Our study also demonstrated that *C. fragile* performed poorly under high sediment and drift algae accumulations, which are

important ecological stresses in eutrophied soft bottom systems, and factors that likely will limit future success of the invader. Because sedimentation and drift algae accumulations were also detrimental to the substrate provider *C. virginica*, (Carlton & Scanlon 1985, Churchill & Moeller 1972, Dromgoole 1982, Garbary et al. 1997), eutrophication and coastal development could have an even greater negative effect on *C. fragile* distribution and abundance.

Conclusion

In conclusion, a sediment cover strongly reduced recruitment, survival and growth of most organisms, particularly the space-dominant perennial macroalgae *G. verrucosa*, *A. subulata* and *C. fragile*, and the filter feeding oyster *C. virginica*, but less so for a few rare stress-tolerant and ephemeral animals. A cover of drift algae also decreased the abundance of the space-dominant organisms, but the opportunistic green algae *Enteromorpha* sp. and *U. curvata* proliferated in these habitats. The effects of the hydrodynamic regime were less dramatic, but nevertheless demonstrated that *G. verrucosa* was abundant in current-exposed plots, that *A. subulata* was absent from wave-exposed plots and that several co-dominants were relatively evenly distributed in protected plots. The invasive macroalgae *C. fragile* was the fourth most abundant organism in the open control plots, being common under all hydrodynamic regimes, but non-existent under sediment and drift algae covers. The former observations suggest that *C. fragile* potentially can be a competitor to *C. virginica* whereas the latter observation implies reduced invasion success as eutrophication progress. Because the reef-building *C. virginica* also performed poorly under cover of sediments and drift algae, increased

eutrophication, sediment destabilization, and sediment enhancement may have wide-ranging effects on oyster reefs in general, and thereby also negative effects on associated flora and faunas, including the invasive *C. fragile*.

Chapter 6. Tables

Table 6.1. Light reduction in different cage designs. The '%' column correspond to the light received compared to the mean of all the control plots.

COV		PAR	%	SD	n
Control	Center	1081	101	729	10
Control	Corner	1070	100	705	40
Cages	Center	1008	94	778	10
Cages	Corner	887	82	684	40
Rebars	Center	1074	100	735	10
Rebars	Corner	1059	98	700	40

Table 6.2. ANOVA on Log(x+1) cover of sediments (A), sedimentation rates (B), cover of drift algae (C), current velocities (D), and drag on practice golf balls (E). Significant values are in bold. Asterisk indicate that Cochran's C was significant for that factor.

Test	Factor	DF	SS	η^2(%)	F	p
A. Sediment accumulations	Hydrodynamics (HYD)	2	0.01	0	0.20	0.817
	Cover (COV)	2	4.94	44	84.49	**0.000***
	HYD*COV	4	0.49	4	4.20	**0.009**
	Error Between	27	0.79	7		
	Time (TIM)	2	1.97	18	23.71	**0.000**
	HYD*TIM	4	0.04	0	0.22	0.928
	COV*TIM	4	0.29	3	1.74	0.154
	HYD*COV*TIM	8	0.35	3	1.06	0.404
	Error Within	54	2.25	20		
B. Sedimentation rates (in tubes)	HYD	2	0.06	13.9	5.30	**0.011**
	COV	2	0.17	41.3	15.83	**0.000**
	HYD*COV	4	0.04	9.6	1.83	0.152
	Error	27	0.15	35.3		
	Total	35	0.42	100.0		
C. Drift algae accumulations	HYD	2	1.57	2	3.99	**0.030***
	COV	2	42.84	46	108.73	**0.000***
	HYD*COV	4	2.26	2	2.87	**0.042**
	Error Between	27	5.32	6		
	TIM	4	2.74	3	3.22	**0.016**
	HYD*TIM	8	4.30	5	2.53	**0.015**
	COV*TIM	8	8.44	9	4.96	**0.000**
	HYD*COV*TIM	16	2.20	2	0.65	0.839
	Error Within	108	22.98	25		
D. Current velocities	HYD	2	2.61	30	52.42	**0.000***
	COV	2	3.45	39	69.27	**0.000***
	HYD*COV	4	1.37	16	13.75	**0.000**
	Error Between	27	0.67	8		
	TIM	1	0.03	0	2.47	0.128
	HYD*TIM	2	0.06	1	2.39	0.111
	COV*TIM	2	0.23	3	8.46	**0.001**
	HYD*COV*TIM	4	0.04	0	0.74	0.576
	Error Within	27	0.36	4		
E. Drag (on practice golf balls)	HYD	2	0.00	0	0.22	0.804*
	COV	2	0.04	6	2.69	0.086*
	HYD*COV	4	0.04	5	1.19	0.339
	Error Between	27	0.21	29		
	TIM	1	0.11	15	9.38	**0.005**
	HYD*TIM	2	0.01	2	0.58	0.568
	COV*TIM	2	0.00	0	0.14	0.875
	HYD*COV*TIM	4	0.03	4	0.66	0.629
	Error Within	24	0.27	38		

Table 6.3. NPMANOVA on Log(x+1) transformed percent cover of attached organisms (total assemblage data). Significant values are in bold ($p < 0.05$).

Group	Source	Df	SS	η^2(%)	F	p
Time 1	Cover (COV)	2	23154	55	27.90	**0.001**
	Hydrodynamics (HYD)	2	6368	15	7.67	**0.001**
	COV*HYD	4	1396	3	0.84	0.620
	Error	27	11203	27		
Time 2	COV	2	30109	68	52.13	**0.001**
	HYD	2	4878	11	8.45	**0.001**
	COV*HYD	4	1456	3	1.26	0.251
	Error	27	7798	18		
Time 3	COV	2	18646	48	18.76	**0.001**
	HYD	2	6351	16	6.39	**0.001**
	COV*HYD	4	449	1	0.23	1.000
	Error	27	13421	35		
Time 4	COV	2	16074	41	15.27	**0.001**
	HYD	2	7440	19	7.07	**0.001**
	COV*HYD	4	1773	4	0.84	0.640
	Error	27	14214	36		

Table 6.4. Pair-wise comparisons (permutation t-tests) for assemblage data following significant single factor effects from NPMANOVA. Significant values are in bold ($p < 0.05$).

	Time 1		Time 2		Time 3		Time 4	
Comparison	**t**	**p**	**t**	**p**	**t**	**p**	**t**	**p**
Sediment vs. Control	5.09	**0.001**	6.23	**0.001**	3.64	**0.001**	3.78	**0.001**
Sediment vs. Drift	4.11	**0.001**	4.98	**0.001**	3.68	**0.001**	3	**0.001**
Drift vs. Control	4.08	**0.001**	6.54	**0.001**	4.55	**0.001**	3.27	**0.001**
Protected vs. Current	1.64	**0.026**	1.41	0.122	1.68	**0.026**	1.7	**0.04**
Protected vs. Wavy	1.76	**0.016**	1.66	**0.048**	2.1	**0.008**	2.21	**0.005**
Current vs. Wavy	1.74	**0.032**	1.14	0.249	1.51	**0.048**	1.91	**0.008**

Table 6.5. Taxa contributing to 90% of within and between group variability, using Bray-Curtis similarity coefficient on Log(x+1)-transformed percent cover data (similarity percentages = SIMPER, time pooled). SIM = average similarity within groups and DIS = average dissimilarity between groups, Pro = protected plots, Cur = current exposed plots, Wav = wave exposed plots, Sed = sediment covered plots, Dri = drift algae covered plots, Con = non-covered control plots.

	Pro	**Cur**	**Wav**	**Sed**	**Dri**	**Con**	**Wav vs. Cur**	**Wav vs. Pro**	**Cur vs. Pro**	**Dri vs. Sed**	**Dri vs. Ope**	**Sed vs. Ope**
SIM/DIS	28.2	32.9	26.1	27.6	34.2	42.2	71.4	73.7	70.7	76	71.4	76.9
Gracilaria	30.6	42.1	29.8	39.3	19	40.8	19.9	16	17.5	13.2	19.5	22
Agardhiella	3.4							4.6	5.4		5.2	5.5
Codium	3.4		2.4			12.7	6.6	6.8	6.7		10.5	11.8
Enteromorpha	15.9	20.8	28.1	18.2	43.2	8.3	13.8	13.2	12	21.5	12.2	6.5
Ulva	7.6	6.7	7		11	7.4	8.3	8.3	8.7	10.7	7.9	7.1
Ectocarpus	4.2	5.9	4.3		5.2	6.2	7.9	6.8	7.6	6.5	7.9	8.1
Punktaria					3.6		2.9	3.9	3.9	2.6	4.2	4.1
Ralfsia								2.1		2.4		
Crassostrea	24.2	11.8	16.7	22.2	9	16.8	11	13.2	10.9	10.9	10.8	12.1
Hydroides			3.3				3.3	3.9	3.3	4.6	3.2	2.4
Amathia	2.7	3.6		4.7			6.5	5.4	6.6	6.9	4.8	5.3
Bugula				2.6			2.1		2	2.3		1.8
Membranipora				3.2			4.5	3.9	4.1	6.1	3.1	2.3
Molgula							2.2	2.1	2.5	2.7		2.2
Hydroids							1.9				1.4	

Table 6.6. Repeated ANOVA on Log(x+1) transformed animal richness (A), plant richness (B), total cover of animals (C) and total cover of algae (D). Significant values are in bold ($p < 0.05$). Asterisk after p-values effects indicate that Cochran's C was significant for that specific factor.

Test	Factor	Df	SS	η^2(%)	F	p
A. Animal Richness	Hydrodynamics (HYD)	2	0.03	1	0.59	0.560
	Cover (COV)	2	0.03	1	0.57	0.570
	HYD*COV	4	0.36	14	3.23	**0.027**
	Error Between	27	0.75	28		
	Time (TIM)	3	0.34	13	13.46	**0.000**
	HYD*TIM	6	0.14	5	2.85	**0.015**
	COV*TIM	6	0.17	7	3.48	**0.004**
	HYD*COV*TIM	12	0.13	5	1.34	0.216
	Error Within	81	0.67	26		
B. Plant Richness	HYD	2	0.08	2	2.85	0.076
	COV	2	1.85	44	3.53	**0.000***
	HYD*COV	4	0.10	2	1.69	0.180
	Error Between	27	0.39	9		
	TIM	3	0.66	16	29.07	**0.000**
	HYD*TIM	6	0.09	2	1.94	0.085
	COV*TIM	6	0.29	7	6.30	**0.000**
	HYD*COV*TIM	12	0.12	3	1.35	0.206
	Error Within	81	0.61	15		
C Animal Cover	HYD	2	0.06	0	0.27	0.767
	COV	2	3.15	23	13.82	**0.000**
	HYD*COV	4	1.26	9	2.77	**0.048**
	Error Between	27	3.08	22		
	TIM	3	1.53	11	15.38	**0.000**
	HYD*TIM	6	0.74	5	3.70	**0.003**
	COV*TIM	6	0.34	2	1.73	0.124
	HYD*COV*TIM	12	1.00	7	2.51	**0.008**
	Error Within	81	2.68	19		
D. Plant Cover	HYD	2	1.15	3	6.40	**0.005**
	COV	2	22.83	65	126.73	**0.000**
	HYD*COV	4	0.31	1	0.86	0.500
	Error Between	27	2.43	7		
	TIM	3	3.54	10	32.43	**0.000**
	HYD*TIM	6	0.69	2	3.17	**0.008**
	COV*TIM	6	1.20	3	5.48	**0.000**
	HYD*COV*TIM	12	0.27	1	0.62	0.823
	Error Within	81	2.95	8		

Table 6.7. Repeated ANOVA on the Log(x+1) transformed abundance of *C. virginica* (A), *C. fragile* (B), *G. verrucosa* (C), *A. subulata* (D), *Enteromorpha* spp. (E) and *U. curvata* (F). Significant values are in bold ($p < 0.05$). Asterisk after p-values effects indicate that Cochran's C was significant for that specific single factor.

Factor	**Df**	**SS**	**η^2(%)**	**F**	**p**	**SS**	**η^2(%)**	**F**	**p**
			A. *C. virginica*				**D. A. subulata**		
Hydrodynamics (HYD)	2	0.20	1	0.49	0.618	1.43	11	3.35	**0.050***
Cover (COV)	2	6.25	38	15.74	**0.000***	2.40	18	5.63	**0.009***
HYD*COV	4	1.06	6	1.34	0.281	2.06	15	2.42	0.073
Error Between	27	5.36	33			5.75	42		
Time (TIM	3	0.21	1	2.35	0.079	0.11	1	2.32	0.082
HYD*TIM	6	0.43	3	2.44	**0.032**	0.14	1	1.44	0.210
COV*TIM	6	0.17	1	0.94	0.474	0.19	1	1.96	0.081
HYD*COV*TIM	12	0.38	2	1.08	0.391	0.14	1	0.70	0.752
Error Within	81	2.41	15			1.31	10		
			B. *C. fragile*				**E. *Enteromorpha* sp.**		
HYD	2	0.15	1	0.59	0.561	0.48	2	6.18	**0.006**
COV	2	7.15	53	28.63	**0.000***	6.36	31	82.71	**0.000***
HYD*COV	4	0.45	3	0.89	0.482	0.17	1	1.11	0.371
Error Between	27	3.37	25			1.04	5		
TIM	3	0.25	2	4.06	**0.010**	7.14	35	97.45	**0.000**
HYD*TIM	6	0.03	0	0.27	0.950	0.14	1	0.97	0.454
COV*TIM	6	0.46	3	3.70	**0.003**	2.60	13	17.73	**0.000**
HYD*COV*TIM	12	0.07	0	0.27	0.992	0.46	2	1.57	0.118
Error Within	81	1.67	12			1.98	10		
			C. *G. verrucosa*				**F. *U. curvata***		
HYD	2	1.60	5	4.47	**0.021**	0.14	1	1.95	0.163
COV	2	20.05	63	55.95	**0.000**	2.13	19	28.97	**0.000***
HYD*COV	4	0.48	2	0.67	0.616	0.23	2	1.53	0.222
Error Between	27	4.84	15			0.99	9		
TIM	3	0.61	2	7.07	**0.000**	2.94	26	62.76	**0.000**
HYD*TIM	6	0.26	1	1.51	0.184	0.60	5	6.41	**0.000**
COV*TIM	6	1.43	4	8.27	**0.000**	2.40	21	25.59	**0.000**
HYD*COV*TIM	12	0.39	1	1.12	0.355	0.68	6	3.61	**0.000**
Error Within	81	2.34	7			1.27	11		

Chapter 6. Figures

Fig. 6.1. Species-abundance patterns for single factor treatments (+SE, n = 48). Rhodophyta: Gra = *G. verrucosa*, Fol = *G. foliifera*, Aga = *A. subulata*, PolD = *Polysiphonia denudata*, PolN = *P. nigrescens*, Cer = *Ceramium rubrum*; Phaeophyta: Ect = *Ectocarpus* spp., Pun = *Punctaria latifolia*, Scy = *Scytosiphon lomentaria*, Fuc = *F. vesiculosus*, Lea = *Leathesis differmis*, Ral = *Ralfsia* sp.; Chlorophyta: Cod = *C. fragile*, Ent = *Enteromorpha* spp., Ulv = *U. curvata*; Porifera: Hal = *Halichondra bowerbanki*; Cnidaria: Hyd2 = unknown hydroids; Crustacea: Bal = *Balanus* spp.; Mollusca: Cra = *Crassostrea virginia*, Cre = *Crepidula fornicata*; Polychaeta: Hyd = *Hydroides dianthus*; Bryozoa: Ama =*Amathia vidovici*., Bug = *Bugula turrita*, Mem = *Membranipora* sp.; Chordata: Mol = *Molgula* sp., Asc = ascidia sp.. The most rare taxa has been omitted.

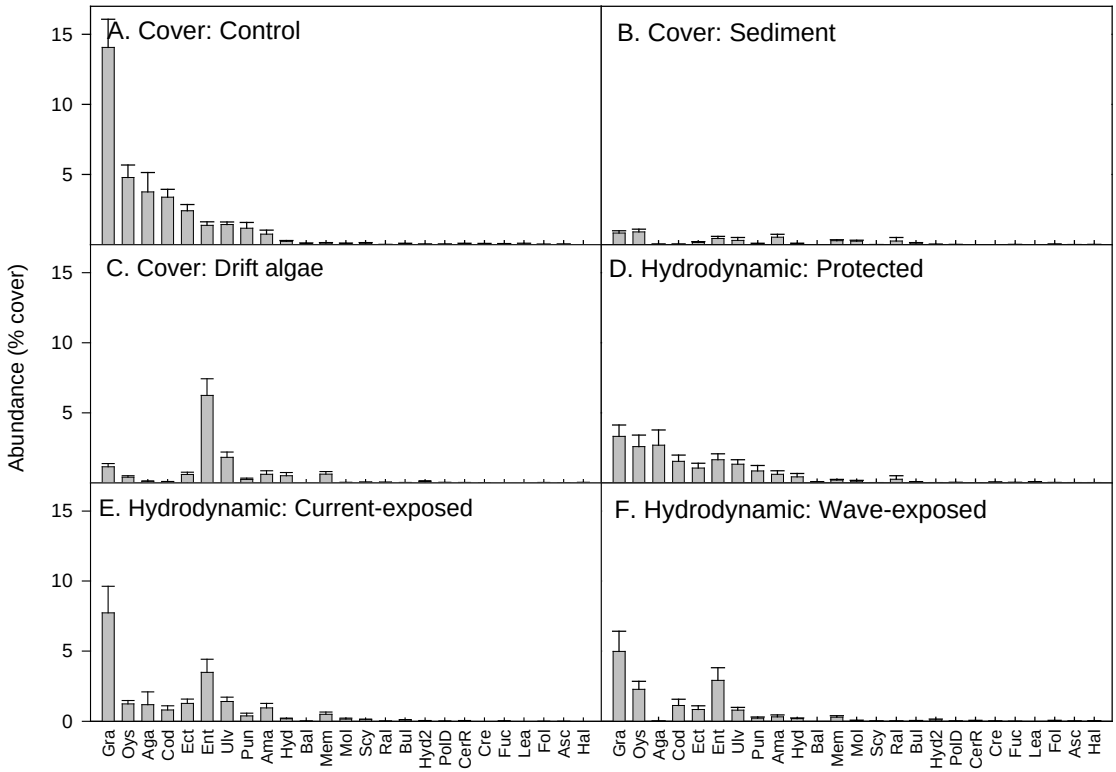


Fig. 6.2. Interaction plots of A. Accumulated sediments on bricks (n = 12), B. Sedimentation in PVC-tubes (n = 4), C. Accumulated drift algae (n = 20), D. Current velocities (n = 8) and E. Hydrodynamic drag on practice golf balls (n = 8). The time factor was pooled, ± SE.

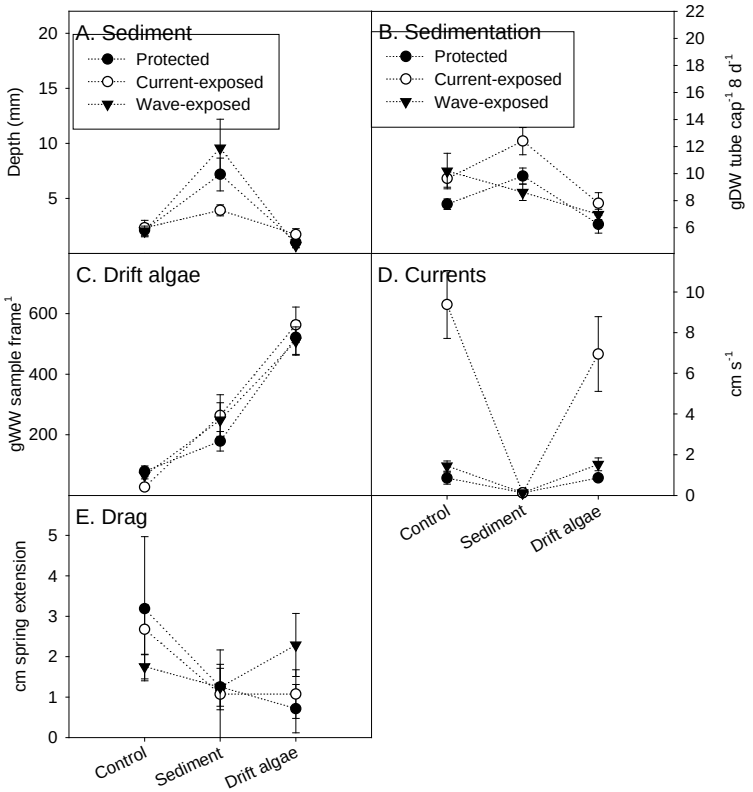


Fig. 6.3. Interaction plots of animal (A-D) and plant richness (E-H) per recruitment brick for separate sampling times (± SE, n = 4).

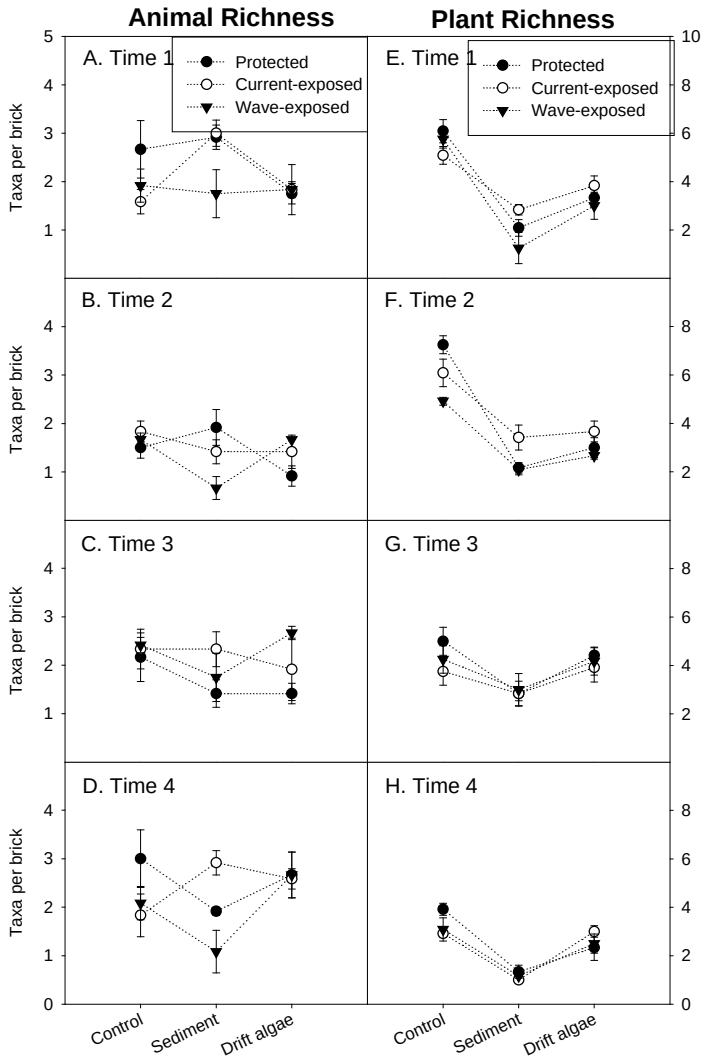


Fig. 6.4. Interaction plots of percent cover of animals pooled (A-D) and plants pooled (E-H) for separate sampling times (± SE, n = 4).

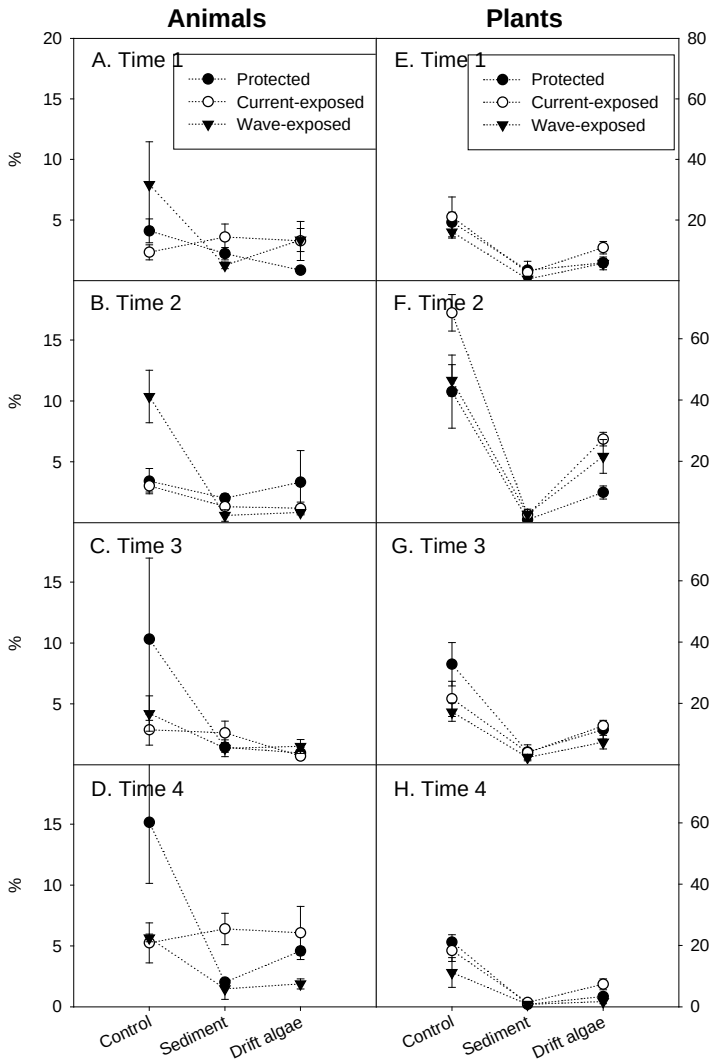


Fig. 6.5. Interaction plots of percent cover of *C. virginica* (A-D) and *C. fragile* (E-H) for separate sampling times (± SE, n = 4).

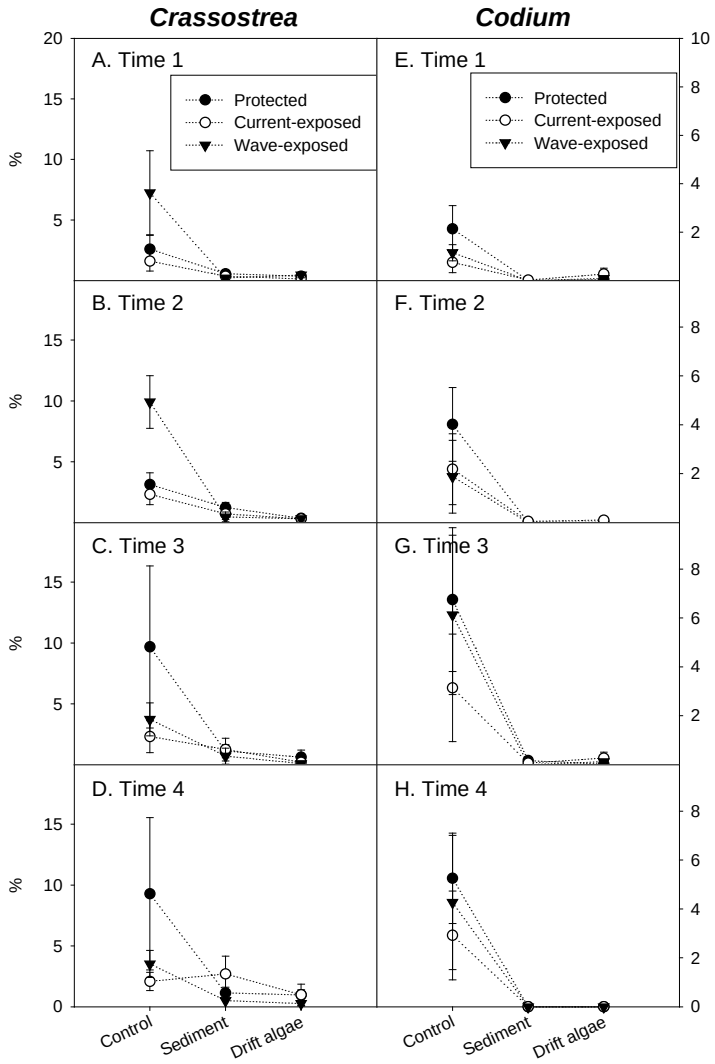


Fig. 6.6. Percent cover of *C. fragile* versus *C. virginia* on all recruitment bricks (n = 432).

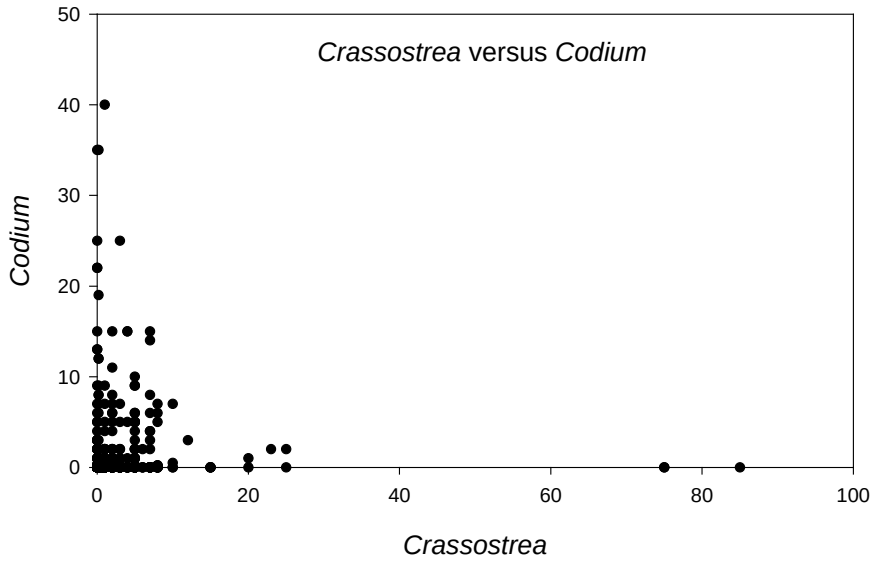


Fig. 6.7. Interaction plots of percent cover of *G. verrucosa* (A-D) and *A. subulata* (E-H) for separate sampling times (± SE, n = 4).

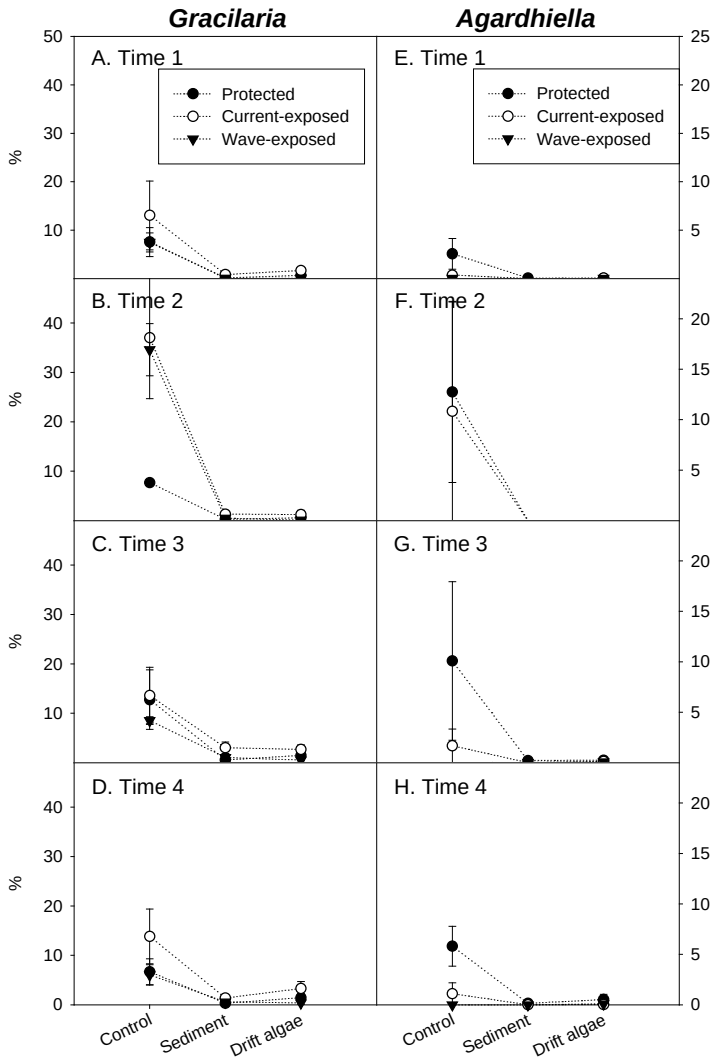
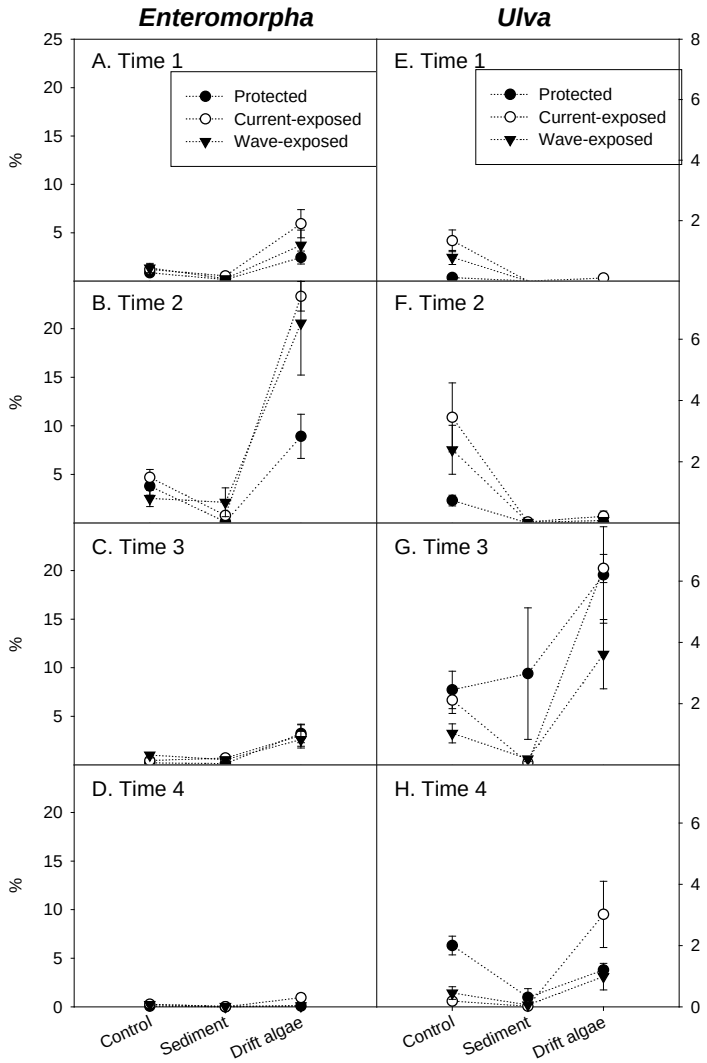


Fig. 6.8. Interaction plots of percent cover of *Enteromorpha* spp. (A-D) and *U. curvata* (E-H) for separate sampling times (± SE, n = 4).



Discussion

Is *Codium fragile* 'superior' in low energy soft bottom lagoons?

Invasions by alien marine organisms have accelerated in the last century often, with unknown ecological and economic consequences (Carlton 1996b, Carlton 1999). The macroalga *Codium fragile* ssp. *tomentosoides* has been reported to be a dominant species in numerous invaded low energy estuaries and lagoons (Campbell 1999, Fralick & Mathieson 1973, Malinowski & Ramus 1973, Wassman & Ramus 1973). However, few direct quantitative comparisons exist of the distribution and performance of *C. fragile* and native macroalgae, but without inter-specific comparisons, it is difficult to evaluate the success of *C. fragile*. I investigated aspects suggested to be of importance for the invasive success of *C. fragile*, with an emphasis on environmental factors, gradients and conditions typical of west Atlantic estuaries and lagoons. Based on the previously reported success of *C. fragile* my main prediction was that *C. fragile* would perform better than the native species under a range of low energy soft bottom lagoonal conditions (cf. hypothesis, Chapter 1). Performance was interpreted broadly to include distribution range and abundance, interactions (or lack of) with key invertebrates, biomechanical properties, tissue resistance to adverse conditions, tissue growth rates under benign conditions, and survival and growth of recruits under various *in situ* conditions.

Wider distribution and higher abundance?

My first hypothesis was that *C. fragile* would be more abundant and more widely distributed in space and time within a recently invaded Virginian lagoon (Hog Island Bay), compared to native species. This hypothesis was only partially supported. Based on data from a large monitoring program (Chapter 2), *C. fragile* was the fourth most

abundant alga in terms of biomass. This is in itself a success criterion considering that *C. fragile* was absent from the system 30 years ago (Hillson 1976). However, this dominance was based on a few samples with large and heavy individuals, and *C. fragile* would be considered less successful if data had been evaluated as presence-absence appearances (Chapter 2). Additional surveys showed that *Codium* was the second most abundant alga in terms of biomass in drifting summer algal assemblages (Chapter 4), and the third most abundant algae (% cover), recruiting onto settling bricks in the vicinity of oyster reefs (Chapter 6). *C. fragile* was mainly dominant at sites in the open mid-lagoon shoal areas and near the barrier islands (Chapter 2, 6, Appendix 1), and on hard substrate at wave-protected sites in the shallow subtidal zone (Chapter 6, Appendix 1). *C. fragile* was not found attached to tube caps of the ubiquitous polychaete *Diopatra cuprea*, an important alternative substrate occupied directly or indirectly by many native algae (Chapter 2, 3), and was only rarely observed at near-mainland sites or in the mid to upper intertidal zone (Chapter 2, Appendix 1). In comparison, many other algae within Hog Island Bay (*e.g. Gracilaria verrucosa, Agardhiella subulata, Ulva curvata, Enteromorpha* spp., *Bryopsis plumosa*, *Ceramium* spp., *Polysiphonia* spp., *Ectocarpus* spp., *Fucus vesiculosus*, *Ralfsia verrucosa*, *Punctaria latifolia* and *Scytosiphon lomentaria)* typically had wider distributions, were found in more samples (as smaller individuals), and/or were more common in the intertidal zone and/or at near-mainland sites (Chapter 2, 3, 6, Appendix 1). Thus, the belief that *C. fragile* is a successful invader due to its ability to occupy a wide range of environmental conditions and habitats (e.g. Campbell 1999, Carlton & Scanlon 1985, Hanisak 1979a, Malinowski & Ramus 1973) is only partially true. Although *C. fragile* is relatively successful in Hog Island Bay in terms

of biomass it was restricted in distribution, and its environmental tolerance cannot be considered high compared to filamentous or sheet-like cosmopolitans (Lüning 1990).With the exception of a narrow spatio-temporal window, the data from Hog Island Bay does not concur with the common observation that *C. fragile* has taken over space in many invaded systems (Fralick & Mathieson 1972, 1973, Hanisak 1979b, Prince 1988). Specifically, spatial domination of *C. fragile* in Hog Island Bay is associated with (1) locations where wave and current regimes are reduced and where oyster shells provide abundant substrates; (2) in the depth interval of ca. –0.6 to –1.5 m above MSL where desiccation and sediment burial is limited but light adequate; and (3) in later summer-early fall before winter fragmentation reduces individual thallus sizes (Chapter 2, 6, Appendix 1).

Strongest facilitation by *Diopatra cuprea*?

In many ecosystems, some species have disproportionately large effects on associated organisms and enhance their distribution and abundance. It has even been suggested that invasions may be facilitated by such species (Bruno & Bertness 2001, Bruno et al. in press, Ruiz et al. 1997). My second hypothesis was that *C. fragile* would be facilitated more by the polychaeta *D. cuprea*, one of the most conspicuous and ubiquitous invertebrates in north American soft bottom coastal habitats (Chapter 2, Lippson & Lippson 1997, Mangum et al. 1968, Myers 1972). *D. cuprea* is particularly well-known for its gardening behavior, where it incorporates algae and shell material to its sediment-extruding tube caps (Chapter 3, Bell & Coen 1982a, Bell & Coen 1982b, Brenchley 1976, Myers 1972). This hypothesis would be supported if *C. fragile* was more abundant on its

tube caps (based on mapping data) and if *C. fragile* was fragmented and incorporated more (based on preference experiment) compared to native species. However, the hypothesis was rejected because *C. fragile* was extremely rare on tube caps and because *C. fragile* rarely was incorporated and never fragmented by *D. cuprea* (Chapter 2, 3). In addition, *C. fragile* had a patchy distribution pattern (Chapter 2), are positively buoyant (Dromgoole 1982), and typical have a large thallus size (Chapter 4, Malinowski & Ramus 1973), suggesting low encounter rates and a high likelihood of dislodgment if fragments/individuals are incorporated (Chapter 3, 4). Species that benefited from *D. cuprea* incorporation included *G. verrucosa*, *U. curvata*, and to a lesser extent *G. foliifera* and *A. subulata* (Chapter 3). *G. verrucosa* and *U. curvata* were highly abundant within Hog Island Bay, were fragmented, and were incorporated (Chapter 2, 3, 4). In addition these species get entangled around tube caps when their negatively buoyant fragments tumble along the bottom with the tides (Harwell & Orth 2001, Holmquist 1994). Finally, both *G. verrucosa* and *U. curvata* are relatively resistant to desiccation and sedimentation, important traits in habitats where *D. cuprea* is abundant (Bell & Coen 1982a, Bell & Coen 1982b, Brenchley 1976, Chapter 5, Appendix 1, Mangum et al. 1968, Vermaat & Sand-Jensen 1987).

Highest resistance to water forces?

The hypothesis that *C. fragile* would be superior in resisting water forces compared to native species when attached onto typical substrates within Hog Island Bay (bivalve shells and tube caps), was approached with correlative biomechanical measurements implementing simple hydrodynamic modeling (Blanchette 1997, Denny 1995,

Shaughnessy et al. 1996). Again, *C. fragile* could not be considered superior to other perennial macroalgae within Hog Island Bay, on either substrate (but superior to *U. curvata* on shells, Chapter 4). Large individuals of *C. fragile* attached to bivalve shells had the highest measured break forces, compared to *G. verrucosa*, *G. foliifera*, *F. vesiculosus*, *A. subulata* and *U. curvata* (Chapter 4). However, because *C. fragile* also had the largest hydrodynamic drag, it had the smallest break velocities (more susceptible to dislodgment, Chapter 4). These calculations supported the observation that *C. fragile* mainly form dense stands with large individuals on either unconsolidated oyster shells or on low energy oyster reefs (Chapter 6, Appendix 1). Entrainment of the entire algae-oyster complex is probably a common process (Ben Avraham 1971, Dromgoole 1982, Hillson 1976), partly because *C. fragile* is often attached to unconsolidated oyster shells, and partly because the oyster reefs may be friable because of weak cementation, small attachment surfaces and weakening by boring sponges or diseases (Barh & Lanier 1981). Indeed entrainment has been suggested to be of key importance in secondary dispersal, following long-range introductions by ship hull transport or transplanted oysters (Carlton & Scanlon 1985, Trowbridge 1998). Another important consequence is that *C. fragile* can bring its own hard substrate and thus can occupy space in habitats where suitable substrate is otherwise lacking, such as mudflats. Because *C. fragile*, as well as other algal species, had low and size-independent attachment forces when incorporated into *D. cuprea* tube caps (because break forces were controlled by the strength of tube cap and not the algae), the likelihood of dislodgment on this substrate increases dramatically with thallus size. Thus, only algae with small sizes, high fragmentation rates (Chapter 3), and/or high recovery rates can survive on tube caps on longer time scales (Chapter 3, 4).

This implies that *C. fragile* and *F. vesiculosus* were most prone to dislodgment and would be least favored by *D. cuprea*, compared to more fragile and fast-growing sheet-like and coarsely-branched algae. These predictions should eventually be tested with flume and *in situ* tagging experiments (Bell 1999, Hawes & Smith 1995).

Highest short-term tissue survival and growth?

The fourth hypothesis predicted that *C. fragile* would have higher growth rates under benign conditions and less biomass loss under stressful conditions compared to native species, and that *C. fragile* would perform equally well from near-mainland sites to near-ocean sites. Benign conditions were defined as high light and nutrient levels, low grazer density, and constant submergence, and stressful conditions were defined as desiccation, sediment burial, low light and nutrient levels, and high grazer densities. Again, the results were opposite to the predictions. *C. fragile* had the lowest growth rates and generally the least resistance to environmental stress of all the algae tested (Chapter 5). When compared to *F. vesiculosus*, *A. subulata*, *G. verrucosa*, *Hypnea musciformis* and *U. curvata*, *C. fragile* decomposed faster when buried, grew slower at both high and low levels of nutrients and lights, was more desiccation prone, and was the only species negatively influenced by the mud snail *Ilyanassa obsoleta* (Chapter 5). This latter result was particularly interesting because *C. fragile* has been considered an unattractive food for generalist herbivores (Chapman 1999, Scheibling & Anthony 2001), and because more palatable species (e.g. *U. curvata*) were present as alternative food choices (Cebrián & Duarte 1994, Geertz-Hansen et al. 1993). *C. fragile* performed particularly poorly at near-mainland sites and at intertidal elevations, reducing the likelihood of becoming

dominant in these habitats. These results reflect the distribution (Chapter 2) and recruitment (Appendix 1) patterns of *C. fragile*, and illustrate that these habitats are dominated by opportunistic and/or stress tolerant taxa like *G. verrucosa*, *U. curvata*, *Enteromorpa* spp., *Ceramium* spp., *Polysiphonia* spp. and *Ectocarpus* spp. It should be noted that *C. fragile* had net biomass gain at low elevations (below 0.6 m above MSL), in shading and nutrient addition experiments, and along most experimental sites. If low growth rates of perennial species are sustained over a long season, substantial biomass can be produced (Borum 1996, Pedersen 1995) whereas populations of species with high growth rates and S:V ratios (Nielsen & Sand-Jensen 1990) are more likely to collapse due to storms (Denny 1995), grazing (Geertz-Hansen et al. 1993, Rosinski 2004), lowered temperature and light levels or by propagule production (Ramus & Venable 1987, Santelices 1990). Thus, these tissue experiments can only demonstrate the short term response and do not necessarily reflect the outcome of exposure to long-term environmental fluctuations.

Highest long-term recruitment onto hard substrate?

The last hypothesis predicted that *C. fragile* would occupy more space on hard substrate (Dromgoole 1982, Scheibling & Anthony 2001) compared to native species under environmental conditions typical of the lagoon, including high sedimentation and drift algae accumulations and under different hydrodynamic regimes. This hypothesis was supported in that *C. fragile* was one of the most dominant species recruiting successfully onto hard substrates protected from tidal currents, although *C. fragile* was nearly completely absent on substrates covered by a layer of drift algae or sediments, like most

other sessile organisms (Chapter 6). Under control conditions, *C. fragile*, *G. verrucosa*, *A. subulata*, and *Crassostrea virginica* (American oyster) were the main space-dominant recruiters. These species tolerated annual temperatures fluctuations of 2-28ºC and short-term desiccation at low spring tides. Observations one and five month after the last sampling supported the recruitment dominance of *C. fragile*, as several recruitment bricks had even changed into pronounced *C. fragile* monocultures (Appendix 1).

Conclusions

In conclusion my data suggest that *C. fragile* is successful compared to native species in eastern North American turbid lagoons by having high tolerance to annual temperature and light fluctuations, by having moderate growth over a long growing season, and by being an effective colonizer of hard substrates in the shallow subtidal zone. On the other hand, *C. fragile* is unsuccessful at near-mainland sites and/or in the intertidal zone where it is less stress tolerant than *G. verrucosa*, *F. vesiculosus*¸ *A. subulata*, *H. musciformis*, *U. curvata* and *Enteromorpha* spp. (Chapter 2, 5, 6, Appendix 1). Overall, *C. fragile* was inferior to many native taxa when considering the effects of polychaete facilitation, mudsnail grazing, intertidal desiccation, enhanced nutrient levels, and cover of drift algal or sediments. The two latter stresses are associated with anthropogenic impacts, and were also detrimental to the oyster *C. virginica* (Chapter 6). Since *C. virginica* is an important facilitator of *C. fragile* (Carlton & Scanlon 1985, Churchill & Moeller 1972, Dromgoole 1982, Garbary et al. 1997) increased eutrophication and coastal development could have an even more pronounced negative effect on *C. fragile* distribution and abundance. In addition to my findings, I suggest that the effects of traits like salinity tolerance,

buoyancy, regenerative abilities, modes of reproduction, alternations of life stages, and life-span of holdfast, on performance patterns should be investigated using a similar multi-species multi-factorial framework, to provide further clues to what habitats can be invaded, what native species, if any, can be out-performed, and in particular under what set of environmental conditions *C. fragile* can be considered superior.

Some implications and general future research directions

The introduction of *C. fragile* to Hog Island Bay, and the findings presented in the thesis emphasize four key aspects of marine plant introductions and invasions. First, most estuarine systems are open and susceptible to invasions. This depart from the old vision of ecosystems being niche-packed habitats with highly competitive and well-adapted species (Moyle 1999, Ruiz et al. 1997, Williamson 1996). Local dispersal mechanisms, hydrodynamic conditions, physical stress, recovery/regeneration processes and biological facilitation are likely major factors determining the success of post-introduction colonization (Bruno et al. in press, Meinesz 1999, Rueness 1989, Ruiz et al. 1997, Walker & Kendrick 1998, Wallentinus 2002). Second, marine plant invaders are not necessarily opportunistic species (Littler 1980, MacArthur 1960, Myers & Bazely 2003). However, it is likely that opportunistic taxa have been and still are being translocated continuously on a global scale (Carlton 1999, Minchin & Gollasch 2002), but that invasions may go unrecognized in part because these taxa are notoriously difficult to identify, in part because these organisms may have been introduced regularly within the last five centuries. In these cases boom and bust cycles that are typically associated with

fluctuations of native species may instead reflect rapid population growth following invasions (Carlton 1996c, b).

Third, it is clear that invasive success is not a deterministic result of a species/population possessing a few simple super-traits, and that screening for such traits (e.g. growth rate, size, grazing resistance) cannot be used as a simple means to predict future invasions (Mack 1996, Myers & Bazely 2003, Williamson & Fitter 1996). Thus, today, there is no simple answer to why the macroalgae *C. fragile* ssp. *tomentosoides, Sargassum muticum, Caulerpa taxifolia, and Undaria pinnatifida,* out of hundreds of related taxa are they key global invaders. More multi-species comparisons are clearly needed with taxonomic and form-functional related taxa to better understand what makes a marine algae an invader (Trowbridge 1998). It is likely that the answer is at least in part associated with (1) the degree of openness of the system, (2) the ability to disperse in association with anthropogenic vectors, and (3) the ability to establish a new population by simple means (e.g. asexual, parthenogenic or monoecious reproduction). Thus, at least three of the four main algal invaders are well adapted to being translocated with imported oysters or on ship hulls (Critchley & Dijkema 1984, Rueness 1989, Trowbridge 1998, Walker & Kendrick 1998, Wallentinus 2002). In addition, after translocation three of the four are characterized as being able to establish new populations from a single fragment and have high regenerative potential (Meinesz 1999, Rueness 1989, Trowbridge 1998, Vroom & Smith 2001, Wallentinus 2002).

Overall species traits and not system characteristics appear to be of primary importance in determining whether a species is a potential invasive species, even though the physical conditions of temperature, salinity, nutrients and light ultimately set constrains for some invasions (Mack 1996). This was particularly clear in the present thesis where few of the conditions typically encountered in soft-bottom systems favored the invader, yet the species was considered successful to native species under highly specific conditions.

Appendix. Additional graphs, photos and tables

This appendix contain additional data, graphs and tables related to the chapters presented in the thesis. All **Appendix Figures** and **Appendix Tables** are in bold to facilitate cross-referencing, and to distinct them from figures and table presented in the main thesis chapters.

Appendix 1. Introduction

Distribution of *Codium fragile*

Fig. A1 was added to show approximate distribution of *Codium fragile*, the various subspecies and outlining major invasion routes. It should be noted that the populations of several of the subspecies have never been recognized in their native range. While the subspecies match morphology of thalli most closely in those regions, populations of the subspecies do not seem to exist as recognizable entities (pers. com. Trowbridge, 2004). Also other relatively similar *C. fragile* species are naturally present in north-east Atlantic, and many tropical regions. The notion of *C. fragile* ssp. *tomentosoides* in Chile is based on pers. com. Trowbridge (2004).

Appendix 2. Mapping

Fig. A2 was added to shows in detail the results of the attachment survey, i.e. what species were found, how many observations of each species, and with what attachment types. It is clear that the *Diopatra cuprea* association with *Gracilaria verrucosa* and *Ulva curvata* is particularly important. It should be noted that the applied methodology (randomly locating nearest visible macroalgae, Chapter 2) favor sampling of large

conspicuous species, and hence may underestimate the commonality of small epiphytic taxa.

Appendix 3. *Diopatra cuprea*

Figures were added to (a) visualize the extent of the *D. cuprea-G. verrucosa* interaction (**Fig. A3-A4**), (b) to document that *C. fragile* can be incorporated into tube caps, although only very rarely, in particularly if no alternative incorporation material is present (**Fig. A4-A5**), and (c) to show algal biomass changes during the two day incubation period in the 'Preference' experiments (**Fig. A5**). Note that *Fucus vesiculosus* and *G. verrucosa* had positive biomass changes on the intertidal mudflat during the short incubation period. It is suggested that *U. curvata* was partially consumed by *D. cuprea* (*U. curvata* typically have high growth also in the lower intertidal zone, Cf. **Fig. A14-A17**), although experiments with proper controls are need to verify this interpretation.

Appendix 4. Biomechanics

Fig. A6 was added to show typical *C. fragile* morphologies in June and November. In June there are no tissue constrictions, tissue is thick and strong, and there are short distances between dichotomies. In November thallus is weaker, with long distances between dichotomies and with numerous constrictions (cf. Fig. 1 in Fralick & Mathieson 1972) from where fragmentation and breakage occurred in biomechanical pull tests (50 breakage at the constrictions out of 50 extension pulls, unpublished data).

Appendix 5. Tissue performance

Performance experiments conducted along distance gradient (Chapter 5).

Various figures and tables were added as supplements to data presented in Chapter 5. However, in the appendix original experimental numbers are used (for future referencing). Hence experiment 1-9 in Chaper 5, correspond to experiment 13, 15, 19, 24, 27, 29, 30, 34 and 37. **Fig. A7** was added to show the applied methodologies of the performance experiments presented in Chapter 5, and **Fig. A8** to show interaction plots corresponding to the significant interactions that was not shown graphically (cf. Fig. 5.1-5.5 and Table 5.3). SNK-test results following ANOVA on entire assemblages (Table 5.3) and following ANOVA of *C. fragile* performance (Table 5.4) are presented below in **Table A1** and **Table A2** respectively. It is clear that *C. fragile* performed poorly compared to the native species and particularly so at near-mainland sites.

Fragmentation (breakage of a fragment) commonly occur in seaweeds either due to external or internal causes. Major external causes are water forces and grazing, whereas internal causes may be related to reproduction or seasonal cues. Fragmentation is often considered adverse if caused by external factors but beneficial if caused by endogenous triggers (Blanchette 1997, Duggins et al. 2001, Fralick & Mathieson 1972, Padilla 1993). Fragmentation were measured in E27, E29, E30, and E34 by counting the number of tissue per species in each cage after incubation (1 fragment was added per cage at T0). The fragmentation rate was calculated as (FragmentsT1 - 1) / 1 * 100%. Thus, 100% fragmentation correspond to a fragment that during incubation broke into two pieces. The total species-specific fragmentation rate is shown in **Table A3** with the four experiments pooled. Also, **Fig. A9** shows interaction plots of tissue fragmentation rates for different

species along the distance from mainland gradient. The plots and experiments are similar to Fig. 5.1-5.5. It is clear that based on these closed-cage experiments, *C. fragile* and *F. vesiculosus* did not fragment, *U. curvata* and *G. verrucosa* fragmented rarely, *Agardhiella subulata* relatively often, and *Hypnea musciformis* very often.

In addition, fluorescence yield was measured with a Mini-Pam using the default settings (9 mm beam distance, 45 degree beam angle)(Heinz 1999) on wet/moist-fragments after experimental incubation. Fragments were exposed to dim laboratory light for at least 1 hour prior to measurements (ca. 5-10 $\mu Em^{-2}s^{-1}$). Yield was measured on tissue after incubation in E19, E24, E27, E29, E30, E34 and E37. **Fig. A10** and **Fig. A11** shows interaction plots of fluorescence yield for different species incubated at different locations along the distance from mainland gradient. The E_{All} graph on **Fig. A9** correspond to the cage-experiments pooled (E24, E27, E29, E30, and E34) and grouped into '+treatments' (added nutrients, black mesh, twist-tie wrapping, grazers) and '-treatments' (no nutrients, white mesh, no twist tie wrapping, no mudsnails). In general there were very small differences in fluorescence yield between species and treatments (**Fig. A11**). Clearly fluorescence yield did not reflect growth or biomass loss in a strict sense (compare to Fig. 5.1-5.5). Only the burial experiment (E19) demonstrated clear yield effects with decreasing yield as a function of burial time.

Macroalgal reattachment (Perrone & Cecere 1997, Santelices & Varela 1994, Smith & Walters 1999, Vroom & Smith 2001, Walters & Smith 1994) was measured in E24, E27, E29, E30, and E34, by counting the number of generated reattachment structures per

species in each cage before measuring fragmentation, fluorescence and wet weight. **Fig. A12** shows examples of reattachment of *C. fragile* and *H. musciformis*. However, *H. musciformis* was the only species to reattach in the five cage experiments, often following entanglement by a newly produced apical hook (**Fig. A12**). The structure whereto *H. musciformis* reattached was also recorded (specific algal species or cage/mesh structure). Although *C. fragile* was not observed reattaching in any *in situ* performance experiment (**Fig. A13**, **Table A4**), reattachment was observed twice in November 2002 in an outdoor aquarium (5-10ºC, no aeration, no water exchange, 2 weeks incubation) where two fragment reattached to the cage bottom and two fragments reattached to *U. curvata* fragments (**Fig. A12**). Thus, this type of reattachment appeared directly from the differentiated macroalgal structure (Fralick & Mathieson 1973, Yotsui & Migita 1989). **Table A4** shows the mean number of produced reattachment structures for single *H. musciformis* fragments, divided into the different types of available substrates. Also, **Fig. A13** show interaction plots of reattachment along the distance from mainland gradient. It is clear that *H. musciformis* did not reattached to *C. fragile* fragments, only rarely onto *A. subulata* and *F. vesiculosus*, often onto *G. verrucosa* and the cage-structure, and most often on *U. curvata*. It should be noted that the area available for attachment differed between species, experiments and treatments. For example, because of the eradication of *C. fragile* by mudsnails in E34, no *C. fragile*-substrate were available for reattachment. On the other hand, within the same cages, *U. curvata* had high growth and high biomass. Thus, by combining the high *U. curvata* biomass with its high S:V ratio, the available *U. curvata* surface area were relatively high.

Additional performance experiments conducted along elevation gradient

In addition to the performance experiments conducted along the distance from mainland gradient and described and analyzed in Chapter 5 and in the previous section, a similar set of experiments were performed along an elevation gradient. The same methodologies were applied: algae were incubated either looselying in cages, fixed by twist-tie wrapping onto rebars inside cages, or fixed by twist-tie wrapping onto PVC poles outside cages (cf. Chapter 5). **Table A5** show the summary table of each of these experiments (compare to table 5.2). Most of these additional performance experiments (except E16) also crossed the elevation treatment with an additional treatment: E28 = 2 levels of shading, E33 = 2 cage hole sizes (≈ flow rates ≈ sediment levels), E38 = 0 vs. 70 g wet sediment added as a wet slurry to each cage, E39 = '1-large' vs. '3-small' numbers of fragments per species per cage (same biomass per species), E40 = 0 vs. 20 mudsnails added per cage, and E41 = caged and looselying fragments vs. non-caged, twist-tie wrapped and fixed fragments. **Fig. A14-A17** shows the interaction plots of these extra experiments with performance of the six algal species for (a) different experiments, (b) different elevations and (c) crossed with different treatments (compare to Fig. 5.1-5.5). **Fig. A14** and **Fig. A15** show the same data, but emphasize different multi-factorial combinations of the interactions. Also, ANOVA analysis, SNK-test and correlation analysis were conducted on these experiments analog to the data analysis described in Chapter 5. Thus, **Table A6** shows the ANOVA conducted on the entire assemblages, **Table A7** the corresponding SNK-test that arrange species into different performance groups, **Table A8** the ANOVA tests conducted on *C. fragile* performance, **Table A9** the corresponding SNK-tests that arrange *C. fragile* performance into different groups along different elevation levels, and **Table**

A10 the correlation analysis that relate performance patterns between the different species. Each of these tables and figures can be directly compared to the results presented in Chapter 5. It is clear that *C. fragile* again show inferior performances, but also that *H. musciformis* and *A. subulata* performed worse compared to the experiments presented in Chapter 5. These three species were particularly sensitive to desiccation (E16, E28, E40, E41). It should be noted that hardly any intertidal emergence occurred in E33, E38, and E39 (cf. **Table A5**). In addition, *H. musciformis* and *A. subulata* are 'fragile' species, that probably suffered more from being fixed with twist tie-wrapping to a vertical positioned pole, compared to the other species (E16, E28, E41, cf. fragmentation rate tables). These experiments confirmed that *U. curvata* and *G. verrucosa* can have high growth and at the same time posses stress-tolerant traits. They also add information about the high desiccation tolerance of *F. vesiculosus* and itt was confirmed that the mudsnail *Ilyanassa obsoleta* can have detrimental effects on *C. fragile* performance (E40).

Fragmentation, fluorescence yield and reattachment of *H. musciformis* were also measured in several of these extra performance experiments. Thus, **Table A11** summarizes the fragmentation rates, fluorescence yield and *H. musciformis*-reattachment summed for each experiment and species, and summed over all experiments. These processes were described in the previous section, and correspond to the data shown in **Table A3**, **Fig. A13** (Fragmentation), **Fig. A14-A15** (Yield) and **Table A4, Fig. A12-A17** (Reattachment). Again, it is clear that mainly *A. subulata* and *H. musciformis* fragmented, that yield results did not differ much between species and experiments, and that *H. musciformis* mainly reattached to *U. curvata* and *G. verrucosa*, and cage

structures. Note that because *H. musciformis* were more stressed in these elevation experiments, compared to being looselying constantly submerged near the water surface (Chapter 5), reattachment was more common with the latter incubation method. Also note that *H. musciformis* in these experiments reattached to *C. fragile*, but mainly as a few high values in E33. Although the cages and experimental designs in general were outlined in Chapter 5 a major difference was that the transparent tube-cages in the elevation experiments were tilted 90º, i.e. positioned vertically instead of horizontally. This created less available space particularly for the non-neutrally buoyant fragments, and hence competition or mutualism may have been of more importance (tube-geometry is provided in Chapter 5, i.e. densities can be calculated because initial biomass were similar to start-biomass described in Chapter 5). In addition, light penetration also differed between cage-positions. Hence, **Table A12** show light reduction for the various cage positions (horizontal vs. vertical) and with or without shading materials used to manipulate light levels (Cf. Chapter 5 and **Table A5**).

Appendix 6. Recruitment

Recruitment experiment conducted around oyster reefs (Chapter 6)

Fig. A18 was added to visualize typical hydrodynamic regimes around the scattered patch oyster reefs at the mid-lagoon site (S1). This figure also show accumulations of drift algae that potentially entangle attached algae and thereby add drag. It also depict the habitat most successfully invaded by *C. fragile*: below 0.7 m above mean sea level, behind oyster bars, with scattered oyster shells available for propagule attachment at the mid-lagoon Shoal 1 site. **Fig. A19** was added to show topographic variation around these

oyster reefs as well as position of the 36 plots described in Chapter 6. **Fig. A20** show a typical recruitment brick (open control plot, behind oyster reefs) in early April 2002, i.e. ca. 9-10 month after incubation. Note several centimeter long *C. fragile* recruits. In addition this figure show the same brick turned into a *C. fragile* monoculture in late August. Similar *C. fragile* dominance were observed on several, but not all, open plot bricks behind oyster reef. **Fig. A21** show the same data as depicted in Fig. 6.3-6.7, but with the time factor pooled. This summary graph demonstrate that accumulations of sediments and drift algae reduce the abundance of most dominant and conspicuous taxa compared to open plots. **Fig. A22** show recruitment data from Chapter 6, at different sampling times but with the Cover and Hydrodynamic factors polled. Recruitment at sampling time 1 was characterized by *G. verrucosa*, *Ectocarpus* sp, *Enteromorpha* sp. and *C. virginica*, at sampling time 2 by *G. verrucosa*, *A. subulata*, *Enteromorpha* sp. and *C. virginica*, sampling time 3 by *G. verrucosa*, *U. curvata*, *C. virginica* and *C. fragile*, and sampling time 4 by *G. verrucosa*, *C. virginica*, various hydroids and *C. fragile*. Finally, **Table A13** and **Table A14** was added to show the SNK-based rankings following univariate ANOVAs presented in Chapter 6.

Additional recruitment experiment conducted along elevation and distance gradients

In addition to the recruitment bricks incubated around oyster reefs (Chapter 6), similar bricks were incubated to test for recruitment effects of elevation and distances from the mainland. Sampling methodologies are described in Chapter 6. To estimate elevation effects on recruitment at a high diversity, high abundance algal site, 40 bricks were incubated from -0.8 to –0.2 m above MSL (mean = 0.59 m) in summer 2001 at the mid-

lagoon Shoal 1 site. Bricks were incubated in a partly systematic, partly random design along a zig-zag transect crossing a line of scattered oyster reefs (front, top, back, top, front, etc), and the elevation of each brick was measured with differential GPS. Bricks were subsequently divided into three elevation classes; Low (0.83-0.70 m below MSL, n = 13, x = 0.76 m, SD = 0.04 m); Mid (0.69-0.50 m below MSL, n = 16, x = 0.59 m, SD = 0.06 m); and High (0.49-0.20 m below MSL, n = 10, x = 0.39 m, SD = 0.09 m). Percent cover of recruited (=attached) organisms were estimated *in situ* in March, June and July 2002. One brick was lost in winter 2001 and data analysis restricted to 39 bricks. **Fig. A23** show the abundance patterns of the sessile recruited reef associated taxa at different elevation levels. Taxa only recorded in minute quantities were removed from the graphs for clarity. These excluded taxa were: Yellow sponge from July (mid elevation); *Cladophora* sp. from June (mid elevation); *Lomentaria bauylina* from July (low elevation), *Polysiphonia* sp. from March (low and mid elevations); *Polysiphonia denudata* from June (low elevation); *Champia parvula* from June (low elevation); *Leathesia difformis* from March (mid elevation), and *Crepidula foernicata* from June and July (low elevations). **Fig. A23** show that *F. vesiculosus* was space-dominant at high elevations, that *G. verrucosa, Crassostrea virginica* and *U. curvata* and *Enteromorpha* sp. were dominant at mid-elevations, and that *G. verrucosa* and *C. virginica* and to some extent *A. subulata* dominant at low elevations. It is interesting that *C. fragile* only was observed on few low elevation bricks, although these low brick in were positioned slightly higher than the bricks described in Chapter 6.

To test if *C. fragile* could recruit at near-mainland and near-ocean sites recruitment bricks were also incubated around oyster reefs near the Creek 1 site (0.8-0.2 m below MSL, x = 0.68 m, SD = 0.13 m, n = 14) and the Hog 1 site (0.8-0.2 m below MSL, x = 0.64 m, SD = 0.19 m, n = 20) and compared to the bricks at Shoal 1 (cf. elevation bricks described above: 0.8-0.2 m below MSL, x = 0.60 m, SD = 0.16 m, n = 39). Because bricks at each oyster reef had the same elevation-distribution, recruitment differences within a site due to elevation effects were ignored. **Fig. A24** shows the abundance patterns of the sessile recruited reef associated taxa at different positions along the distance from mainland gradient. Taxa observed in minute quantities were removed from the graphs for clarity. These excluded taxa were: *Ceramium strictum* at H1 in March, *C. parvula* at S1 in June, *H. musciformis* at H1 in July, *Cladophora* sp. at S1 in June, *Membranipora* sp. at H1 in March, Yellow boring sponge at S1 in July, *Bryopsis plumosa* at C1 in March. **Fig. A24** showed that the dominant species at C1 were *G. verrucosa*, *Enteromorpha* sp., *Ectocarpus* sp., *C. virginica, U. curvata* and *Balanus* sp. whereat at H1 it was *G. verrucosa, C. virginica* and *F. vesiculosus*. No *C. fragile* were observed recruiting at the near-mainland or near-ocean site.

To test if *C. fragile* was a superior recruiter in the lowest intertidal zone (cf. Chapter 6) 33 bricks were incubated in summer 2001 behind an oyster reef at Shoal 1 in a 2*2 m^2 plot (bricks separated by ca. 20 cm) at 0.8 m below MSL. These bricks were sampled at the shoal sites on 24 of June 2002 and *C. fragile* was found to be the third most abundant recruiter (**Fig. A25**). The propagule and larval supply is probably uniform within a site because of strong tidal mixing (Chapter 6), but likely varies between sites (Chapter 2).

Thus, recruitment at different sites can reflect either differences in supply or post-settling processes. To test if post-recruitment processes create different communities between sites, 11 of the 33 bricks were transplanted to C1, 11 to H1 and 11 back-transplanted to S1 on June 25 2002. To ensure that the transplantation treatments (ca. 1 hour of transport in moist and dark coolers) did not affect survival and growth differentially between sites, the bricks that were back-transplanted to S1 underwent similar manipulation. These transplanted bricks were sampled on July 30 and November 2 2002. **Fig. A25** shows the abundance patterns of sessile recruited reef associated taxa transplanted to different positions along the mainland gradient (C1, S1, H1) after being incubated at the mid-lagoon site. Taxa only recorded in minute quantities were removed from the graphs for clarity. These excluded taxa were: *Polychaeta* sp. at S1 in November; *B. plumosa* at C1 in July; Yellow boring sponge at S1 in November; *Polysiphonina nigrescens* at S1 in June; and *Ceramium rubrum* at S1 in June. The dominant species at the mid-lagoon site (the founder assemblage) and the near-ocean site were *G. verrucosa, C. virginica, C. fragile* and *A. subulata* (in concordance with open plot bricks described in Chapter 6). However at the near-mainland site only *G. verrucosa* and *C. virginica* persisted. Hence, whole individuals of *C. fragile* did indeed grow well (and recruited, pers. obs.) at the near-ocean site, but not at the near-mainland site, in agreements with abundance (Chapter 2) and performance data (Chapter 5).

Finally to investigate if a low elevation limit exist for recruitment in Hog Island Bay, **10 "deep-water" bricks** were incubated in summer 2001 in front of the oyster reefs at 2 m below MSL. However, because all the bricks were completely buried by sediments when

sampled in spring 2002, no sessile attached species were recorded, and not statistical data analysis was conducted. The interpretation was straightforward: high sedimentation at low elevations limit recruitment onto low relief hard substrate at Shoal 1.

Appendix 7. VCR/LTER water quality monitoring data

In 1992 the VCR/LTER (Hayden et al. 2000) initialized a water quality monitoring program with 10 permanent station (**Fig. A26**). The 10 sites correspond to the mouth of Phillips Creek (PCm, near-mainland creek), the head of Phillips Creek (PHh, near-mailand creek), Green Creek (GC, near-mainland creek), Oyster Harbor (OH, near-mainland harbor), Red Bank (RB, transition point from near-mainland creeks to open lagoon), No name Creek (NC, back-barrier island creek, i.e. may be influenced by marsh run-off), mouth of Cattle Shed creek (CSm, back-barrier island creek, i.e. may be influenced by marsh run-off), Quinby Inlet (QI, near-ocean inlet), Machinpongo Inlet (MI, near-ocean inlet) and South Hog (SH, near-ocean inlet). Some of the key variables that are sampled on a regular basis include salinity (here presented as the mean of refractometer and SCT-meter values), dissolved oxygen, water temperature (mean from DO and SCT-meters), total suspended solids (each sample based on 3 sub-replicates per site of 300 ml surface waters filtered through GC filters and oven dried at ca. 100ºC), and secchi depth. I digitized and compiled the data from 1999-2002 (collected by Kathleen Overman, Jason Restein, Phillips Smith and Jimmy Spitler), that temporally match most of the data presented in Chapter 2-6. Survey dates include (d/m/y): 31/03/99, 28/04/99, 25/05/99, 30/06/99, 31/07/99, 09/09/99, 29/09/99, 03/11/99, 30/11/99, 02/12/99, 27/01/00, 24/02/00, 27/03/00, 26/04/00, 28/06/00, 08/11/00, 06/12/00, 07/02/01,

08/03/01, 05/04/01, 02/05/01, 04/06/01, 15/08/01, 12/09/01, 12/10/01, 14/11/01, 10/12/01, 22/01/02, 21/02/02, 26/03/02, 26/04/02, 21/05/02, 21/06/02, 22/07/02, 20/08/02, 30/09/02, 17/10/02. Not all variables were sampled on all survey dates. **Fig. A27-A31** shows the temporal development for each of the 10 sites for suspended solids (**Fig. A27**), temperature (**Fig. A28**), secchi depth (**Fig. A29**), salinity (**Fig. A30**) and dissolved oxygen (**Fig. A31**). Each of these figures are divided into a top figure representing 'typical near-mainland sites', a middle figure representing 'typical near-ocean sites', and a lower figure of sites that may have characteristics in-between the two 'extremes'. **Fig. A32** shows temporal development for each of the five variables pooled over all 10 sites. Finally, **Table A15** compare each of the 10 sites to the five variables (i.e. pooling individual surveys). The total suspended solid data were characterized by a few surveys with very high values (**Fig. A27**). Also there was a tendency for higher values at the near-mainland creeks compared to the near-ocean open sites (**Fig. A27**, **Table A13**). Temperature varied from 2ºC in winter months to 35ºC in summer months, and there were only minor differences between near-mainland creeks and ocean sites, although there was a tendency for highest variability at the former sites (**Fig. A28**). Secchi depth fluctuated from ca. 40 to 200 cm with a tendency for highest values at the near-ocean sites (**Fig. A29**, **Table A13**). Salinity varied from ca. 15 to 34 ppt at near-mainland sites (majority of values between 25 and 32) and from 28 to 35 ppt at the near-ocean sites (majority of values between 30 and 32) (**Fig. A30**). Finally, dissolved oxygen varied from ca. 2 to 12 mg/L (**Fig. A31**) with highest values in winter months and lowest in summer months (**Fig. A32**). There were no obvious differences in dissolved oxygen between sites. Thus, it is likely that differences in macroalgal distribution, abundance,

and performance along the distance from mainland gradient (Chapter 2, 3, 5, Appendix 1) is caused by a complex set of interacting factors including nutrients (Chapter 5), grazer abundance (Chapter 5, Rosinski 2004), salinity (this section), light regime (Chapter 5, this section), hydrodynamic regimes and sedimentation levels.

Appendix Tables

Table A1. SNK-tests of all species along distance gradient. Net growth for each species from each experiment (treatments pooled) arranged from lowest to highest growth. The '#' column refers to SNK-groupings.

Exp	SPE	n	%	#	Exp	SPE	n	%	#
13 & 15	*Codium*	57	-34.1	1	34	*Codium*	24	-11.7	1
13 & 15	*Agardhiella*	58	-27.7	2	34	*Fucus*	24	-3.2	1
13 & 15	*Gracilaria*	57	21.7	2	34	*Agardhiella*	24	85.4	2
13 & 15	*Fucus*	57	38.4	2	34	*Gracilaria*	24	92.4	2
19	*Agardhiella*	37	-90.6	1	34	*Hypnea*	24	116.8	2
19	*Codium*	37	-88.6	1	34	*Ulva*	24	160	3
19	*Fucus*	37	-69.1	2	37	*Fucus*	17	7.4	1
19	*Ulva*	37	-68.8	2	37	*Codium*	18	12.1	1
19	*Gracilaria*	37	-65.9	2	37	*Agardhiella*	17	42.7	1 & 2
24	*Fucus*	24	8.8	1	37	*Hypnea*	17	73.9	2
24	*Gracilaria*	24	21	1	37	*Gracilaria*	18	88.1	2
24	*Codium*	21	25.4	1	37	*Ulva*	17	124.4	3
24	*Agardhiella*	24	51.3	1	Sum	*Fucus*	135	6.1	1
24	*Ulva*	24	96.7	2	Sum	*Codium*	134	9.9	1
24	*Hypnea*	24	198.6	3	Sum	*Agardhiella*	136	40.7	2
27 & 28	*Fucus*	48	9.4	1	Sum	*Gracilaria*	137	43.6	2
27 & 28	*Agardhiella*	48	14.9	1	Sum	*Hypnea*	135	113.1	3
27 & 28	*Codium*	48	18.3	1	Sum	*Ulva*	136	155.5	4
27 & 28	*Gracilaria*	48	21.2	1					
27 & 28	*Hypnea*	48	116.8	2					
27 & 28	*Ulva*	48	222.4	3					
30	*Codium*	23	-5.9	1					
30	*Fucus*	22	4.8	1					
30	*Gracilaria*	23	27.9	2					
30	*Agardhiella*	23	34.8	2					
30	*Ulva*	23	95.2	3					
30	*Hypnea*	22	37.6	2					

Table A2. SNK-test of *C. fragile* performance along distance. Net growth for *C. fragile* from each experiment along DIS gradient (treatments pooled) arranged from lowest to highest growth. The '#' column refers to SNK-groupings.

EXP	DIS	n	%	#	EXP	DIS	n	%	#
13 & 15	C1	20	-39.3	1	34	C1	8	-25.2	1
13 & 15	H1	15	-38.6	1	34	S1	8	-6.6	1
13 & 15	S1	20	-28.9	1	34	H1	8	-3.4	1
24	C1	7	23.7	1	37	C1	6	3.4	1
24	H1	7	26.1	1	37	H1	6	12.1	2
24	S1	7	26.3	1	37	S1	6	20.7	2
27 & 29	C1	16	11.5	1	30	C1	8	-12.3	1
27 & 29	H1	16	19.6	2	30	H1	8	-2.2	2
27 & 29	S1	16	23.7	2	30	S1	7	-2.8	2

Table A3. Percent fragmentation (based on E27, E29, E30, E34).

Species	% Frag.	n	SD
Codium	0	95	0
Fucus	1.1	95	10.3
Agardhiella	61.1	95	168.4
Gracilaria	11.6	95	43.4
Hypnea	187.2	94	199
Ulva	5.3	95	26.8

Table A4. *H. musciformis* reattachment. Mean number of produced reattachment structures on different available substrata from E24, E27, E29, E30, and E34 pooled.

Substrate	**X**	**SD**	**n**
Codium	0	0	116
Fucus	0.51	1.25	118
Agardhiella	0.26	1.09	118
Gracilaria	1.24	1.82	118
Ulva	2.32	4.99	118
Cage	1.7	4.24	118
Total	1.01	2.97	706

Table A5. Summery of additional performance experiments along an elevation gradient. All experiments, except E16, test for effect of elevation crossed with an additional treatment.

Exp	Design	Pole depth (m)	Lowest depth (m)	Diff. between levels (m)	Treat	Date (2002)	Comments
16	4 SPE * 7 ELE * 4 REP	-2.2	-2.1	0.2	Open [OPE]	29/3-10/4 (12)	Open and fixed on PVC poles at different elevations. Twist tie wrapped onto cable tie. No cages. No *Hypnea* or *Ulva*
28	6 SPE * 4 ELE * 2 LIG * 3 REP	-1.15	-1.05	0.2	Light [-LIG]	9/7-17/7 (8)	Black (shading) vs. no mesh around cages. Fixed with twist tie on metal flag marker. Large holes in cages. High mortality. High drift algae entanglement.
33	6 SPE * 3 ELE * 2 FLO * 4 REP	-1.36	-1.26	0.4	Sediment (flow) [+SED]	23/7-29/7 (6)	Small cage holes vs. large (= high sedimentation) holes. White mesh. Poor cap drainage, i.e. cages remained moist. Generally high low-tides.
38	6 SPE * 3 ELE * 2 SED * 4 REP	-1.36	-1.26	0.4	Sediment [+SED]	30/7-5/8 (6)	70 g wet sediment added to half of the cages. No mesh. Generally high low-tides. 1 pole moved to C1 for 2 days. Some sediment lost in cap holes.
39	6 SPE * 3 ELE * 2 FRA * 4 REP	-1.36	-1.26	0.4	Frag. [+FRA]	31/7-5/8 (5)	Half of cages with 1 Large vs. half of cages with 3 small fragments of each species. White mesh. Generally high low tide. 1 pole moved to C1 for 2 days. No *Ulva* or *Gracilaria* in cage 13-24 (i.e. lost 2 rep).
40	6 SPE * 2 ELE * 2 GRA * 3 REP	-0.88	-0.48	0.3	Grazing [+GRA]	1/7-7/8 (6)	20 mudsnails/cage in half of the cages. No mesh. Small cage holes. Lost cage 1, 2 and 5, 6 (1 rep). All snails survived.
41	6 SPE * 2 ELE * 2 CAG * 6 REP	-0.88	-0.50	0.3	Caging [OPE]	1/7-7/8 (6)	Half in cages vs. half in open plots, all fixed. Lost plot 1, 2 and 5, 6 (2 rep). Re-used control tissue from E40 as caged tissue.

Table A6A. ANOVA on assemblages on additional performance experiments along elevation gradient. Significant results are in bold ($p < 0.05$). Analysis procedures as in Chapter 5.

Exp	Source	Df	SS	η^2(%)	F	p
16	SPE	3	128780	38	61.48	**0.000**
16	ELE	8	82947	24	14.85	**0.000**
16	SPE * ELE	24	65483	19	3.91	**0.000**
16	Error	89	62143	18		
28	SPE	5	231148	69	85.18	**0.000**
28	ELE	3	8682	3	5.33	**0.002**
28	LIG	1	18422	6	33.94	**0.000**
28	SPE * ELE	15	7819	2	0.96	0.502
28	SPE * LIG	5	7095	2	2.61	**0.029**
28	ELE * LIG	3	4139	1	2.54	0.061
28	SPE * ELE * LIG	15	5340	2	0.66	0.820
28	Error	93	50476	15		
33	SPE	5	316178	43	48.76	**0.000**
33	ELE	2	98014	13	37.79	**0.000**
33	FLO	1	4130	1	3.18	0.077
33	SPE * ELE	10	149408	20	11.52	**0.000**
33	SPE * FLO	5	12117	2	1.87	0.100
33	ELE * FLO	2	11566	2	4.46	**0.014**
33	SPE * ELE * FLO	10	5876	1	0.45	0.916
33	Error	108	140058	19		
38	SPE	5	60095	18	7.52	**0.000**
38	ELE	2	26547	8	8.30	**0.000**
38	SED	1	7947	2	4.97	**0.028**
38	SPE * ELE	10	14650	4	0.92	0.521
38	SPE * SED	5	24358	7	3.05	**0.013**
38	ELE * SED	2	15002	5	4.69	**0.011**
38	SPE * ELE * SED	10	6019	2	0.38	0.954
38	Error	108	172703	53		
39	SPE	5	85639	37	18.59	**0.000**
39	ELE	2	27525	12	14.94	**0.000**
39	FRA	1	1194	1	1.30	0.258
39	SPE * ELE	10	17645	8	1.92	0.054
39	SPE * FRA	5	14189	6	3.08	**0.013**
39	ELE * FRA	2	287	0	0.16	0.856
39	SPE * ELE * FRA	10	9357	4	1.02	0.438
39	Error	83	76469	33		

Table A6B. ANOVA on assemblages on additional performance experiments along elevation gradient (continued from Table 6A). Significant results are in bold ($p < 0.05$). Analysis procedures as in Chapter 5.

Exp	Source	Df	SS	η^2(%)	F	p
40	SPE	5	174804	57	20.82	**0.000**
40	ELE	1	17083	6	10.18	**0.003**
40	GRA	1	1898	1	1.13	0.293
40	SPE * ELE	5	8932	3	1.06	0.392
40	SPE * GRA	5	21664	7	2.58	**0.038**
40	ELE * GRA	1	277	0	0.17	0.686
40	SPE * ELE * GRA	5	3287	1	0.39	0.852
40	Error	48	80588	26		
41	SPE	5	133283	47	37.83	**0.000**
41	ELE	1	12821	5	18.19	**0.000**
41	CAG	1	35405	12	50.24	**0.000**
41	SPE * ELE	5	5923	2	1.68	0.148
41	SPE * CAG	5	23360	8	6.63	**0.000**
41	ELE * CAG	1	341	0	0.48	0.488
41	SPE * ELE * CAG	5	14041	5	3.98	**0.003**
41	Error	84	59196	21		
All	SPE	5	427562	15	66.68	**0.000**
All	ELE	4	44266	2	8.63	**0.000**
All	EXP	6	472697	17	61.44	**0.000**
All	SPE * ELE	16	47263	2	2.30	**0.003**
All	SPE * EXP	28	501094	18	13.96	**0.000**
All	ELE * EXP	9	171329	6	14.84	**0.000**
All	SPE * ELE * EXP	41	196477	7	3.74	**0.000**
All	Error	744	954087	34		

Table A7. SNK-test on species performance along elevation gradient. Test of seven experiments for species, elevation (1-9) and experiment (E16, E28, E33, E39, E40, E41).

Exp	Treatment	n	%	Group	Exp	Treatment	n	%	Group
16	*Codium*	31	-33	1	16	1	8	-65	1
16	*Fucus*	32	37	3	16	2	16	-33	2
16	*Agardhiella*	32	-43	1	16	3	16	-6	3
16	*Gracilaria*	30	17	2	16	4	14	13	3
28	*Codium*	24	-63	2	16	5	16	19	3
28	*Fucus*	23	-4	3	16	6	16	19	3
28	*Agardhiella*	23	-95	1	16	7	16	7	3
28	*Gracilaria*	23	1	3	16	8	15	-4	3
28	*Hypnea*	24	-84	1	16	9	8	-50	1
28	*Ulva*	24	-2	3	28	1	34	-52	1
33	*Codium*	24	-14	1	28	2	35	-47	1 & 2
33	*Fucus*	24	-27	1	28	3	36	-31	3
33	*Agardhiella*	24	13	2	28	4	36	-38	2 & 3
33	*Gracilaria*	24	25	2	33	1	48	55	3
33	*Hypnea*	24	15	2	33	2	48	19	2
33	*Ulva*	24	119	3	33	3	48	-9	1
38	*Codium*	24	-25	1	38	1	48	14	2
38	*Fucus*	24	-23	1	38	2	48	14	2
38	*Agardhiella*	24	24	2	38	3	48	-15	1
38	*Gracilaria*	24	20	2	39	1	40	-5	2
38	*Hypnea*	24	12	2	39	2	40	-12	2
38	*Ulva*	24	19	2	39	3	39	-46	1
39	*Codium*	24	-53	1	All	-1.9	23	-20	1
39	*Fucus*	24	-49	1	All	-1.5	32	13	2
39	*Agardhiella*	24	3	3	All	-1.1	201	-19	1
39	*Gracilaria*	12	17	3	All	-0.7	293	-14	1
39	*Hypnea*	23	-19	2	All	-0.3	305	-14	1
39	*Ulva*	12	11	3	All	E16	125	-6	3
40	*Codium*	12	-63	1	All	E28	142	-42	1
40	*Fucus*	12	-60	1	All	E33	144	22	5
40	*Agardhiella*	12	-50	1	All	E38	144	5	4
40	*Gracilaria*	12	56	2	All	E39	119	-21	2
40	*Hypnea*	12	-71	1	All	E40	72	-27	2
40	*Ulva*	12	27	2	All	E41	108	-47	1
41	*Codium*	18	-71	1	All	*Codium*	157	-43	1
41	*Fucus*	18	-45	2	All	*Fucus*	157	-18	3
41	*Agardhiella*	18	-78	1	All	*Agardhiella*	158	-30	2
41	*Gracilaria*	18	2	3	All	*Gracilaria*	143	18	4
41	*Hypnea*	18	-91	1	All	*Hypnea*	125	-35	2
41	*Ulva*	18	0	3	All	*Ulva*	114	32	5

Table A8. ANOVA on *C. fragile* performance on additional performance experiments along elevation gradient. Significant ($p < 0.05$) results are in bold.

Exp	Source	Df	SS	η^2(%)	F	p
16	ELE	9	71114	89	20.42	**0.000**
16	Error	22	8512	11		
28	ELE	3	2993	12	1.84	0.180
28	LIG	1	11782	48	21.78	**0.000**
28	ELE * LIG	3	899	4	0.55	0.653
28	Error	16	8653	36		
33	ELE	2	13184	30	8.73	**0.002**
33	FLO	1	13464	30	17.82	**0.001**
33	ELE * FLO	2	4419	10	2.92	0.079
33	Error	18	13599	30		
38	ELE	2	25872	67	36.00	**0.000**
38	SED	1	34	0	0.10	0.761
38	ELE * SED	2	6218	16	8.65	**0.002**
38	Error	18	6468	17		
39	ELE	2	21553	54	20.88	**0.000**
39	FRA	1	6151	15	11.92	**0.003**
39	ELE * FRA	2	2985	7	2.89	0.081
39	Error	18	9289	23		
40	ELE	1	85	0	0.53	0.487
40	GRA	1	18264	93	113.62	**0.000**
40	ELE * GRA	1	85	0	0.53	0.487
40	Error	8	1286	7		
41	ELE	1	335	1	1.89	0.191
41	CAG	1	20615	88	116.14	**0.000**
41	ELE * CAG	1	9	0	0.05	0.823
41	Error	14	2485	11		
All	EXP	6	52345	18	15.83	**0.000**
All	ELE	4	24404	8	11.07	**0.000**
All	TRE	1	57006	19	103.46	**0.000**
All	EXP * ELE	9	61928	21	12.49	**0.000**
All	EXP * TRE	5	20160	7	7.32	**0.000**
All	ELE * TRE	2	2659	1	2.41	0.094
All	EXP * ELE * TRE	7	11705	4	3.03	**0.006**
All	Error	122	67221	23		

Table A9. SNK-test on *C. fragile* performance on additional performance experiments along elevation gradient. SNK-test on *C. fragile* of seven growth experiments for treatments with more than two levels (elevation and experiment number). For treatments with only two levels significant differences can be deducted from **Table 6** and **Fig. 18-21**.

Exp	Elevation	n	%	Group	Exp	Elevation	n	%	Group
16	-0.5	2	-100	1	39	-1.26	8	-94.6	1
16	-0.7	4	-92.6	1	39	-0.86	8	-38.6	2
16	-2.1	2	-74.7	1	39	-0.46	8	-25.5	2
16	-1.1	3	-24.3	2	All	-1.1	37	-56.4	1
16	-0.9	4	-22.5	2	All	-0.3	53	-42	1 & 2
16	-1.7	4	-17.7	2	All	-0.7	53	-40.4	1 & 2
16	-1.9	4	-11.3	2	All	-1.9	6	-32.4	2
16	-1.5	4	-5.9	2	All	-1.5	8	-11.8	2
16	-1.3	4	-0.8	2	All	E41	18	-69.8	1
28	-0.45	6	-80.9	1	All	E28	24	-63.4	1
28	-0.65	6	-65.3	1	All	E40	12	-61	1
28	-0.85	6	-55.3	1	All	E39	24	-52.9	1
28	-1.05	6	-52.2	1	All	E16	31	-33.1	2
33	-1.26	8	-46.1	1	All	E38	24	-25	2
33	-0.86	8	-5.8	2	All	E33	24	-14.1	3
33	-0.46	8	9.5	2	38	-1.26	8	-71.4	1
38	-0.46	8	-1.9	2	38	-0.86	8	-1.6	2

Table A10. $r^2_{Pearson}$ correlation matrix comparing performances between species from seven additional performance experiments along elevation gradients. Significant *p*-values are in bold. Only *Fucus* vs. *Agardhiella* and *Fucus* vs. *Gracilaria* had negative $r_{Pearson}$, none of which were significant.

		Codium	*Fucus*	*Agardhiella*	*Gracilaria*	*Hypnea*	*Ulva*
Codium	r^2	0.10	0.24	0.13	0.24	0.17
	p	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	n	156	157	142	125	114
Fucus		r^2	0.01	0.01	0.01	0.00
		p	0.352	0.402	0.356	0.518
		n	157	142	124	113
Agardhiella			r^2	0.11	0.40	0.13
			p	**0.000**	**0.000**	**0.000**
			n	143	125	114
Gracilaria				r^2	0.10	0.15
				p	**0.001**	**0.000**
				n	113	113
Hypnea					r^2	0.21
					p	0.000
					n	114
Ulva						r^2
						p
						n

Table A11. Fragmentation, fluorescence yield, and reattachment for additional performance experiments conducted along an elevation gradient. Fragmentation and Yield were measured in E33, E38, E39, E40 and E41. and reattachment was further measured in E28. Note that the reattachment data under the 'Hyp'-column correspond to *Hypnea* reattaching to the cage structure (i.e. not attaching to itself).

Exp	Aga	Cod	Fuc	Gra	Hyp	Ulv	Aga	Cod	Fuc	Gra	Hyp	Ulv
			Fragments (mean)						**Yield (SD)**			
33	96	5	17	0	154	58	0.10	0.13	0.17	0.05	0.06	0.06
38	142	30	21	17	442	25	0.09	0.22	0.13	0.05	0.20	0.13
39	128	49	-5	47	235	94	0.11	0.30	0.25	0.13	0.17	0.25
40	11	0	10	75	367	0	0.25	0.17	0.26	0.09	0.04	0.14
41	0	0	6	31	250	0	0.31	0.26	0.22	0.22	0.14	0.35
			Fragments (n)						**Reattachment (mean)**			
28							0.00	0.00	0.00	0.00	0.00	0.00
33	24	22	24	24	24	24	0.21	0.62	0.00	1.21	0.75	0.71
38	24	23	24	24	24	24	0.13	0.04	0.17	0.50	0.25	0.33
39	24	21	21	12	23	12	0.09	0.00	0.00	0.50	0.22	0.08
40	9	6	10	12	3	12	0.00	0.00	0.00	0.17	0.00	0.00
41	5	10	18	16	2	16	0.00	0.00	0.00	0.13	0.00	0.00
			Fragments (SD)						**Reattachment (n)**			
28							3	20	23	23	7	24
33	216	21	38	0	211	106	24	22	24	24	24	24
38	186	88	51	64	159	90	24	23	24	24	24	24
39	229	155	34	98	194	175	23	21	21	12	23	12
40	33	0	32	176	115	0	9	6	10	12	3	12
41	0	0	24	125	354	0	5	10	18	16	2	16
			Yield (mean)						**Reattachment (SD)**			
28							0	0	0	0	0	0
33	0.69	0.77	0.66	0.69	0.71	0.78	1.02	0.90	0.00	2.08	1.87	3.47
38	0.74	0.70	0.74	0.72	0.63	0.83	0.45	0.21	0.48	0.66	0.68	0.92
39	0.75	0.67	0.66	0.76	0.72	0.68	0.42	0.00	0.00	0.80	0.60	0.29
40	0.45	0.51	0.50	0.57	0.66	0.71	0.00	0.00	0.00	0.58	0.00	0.00
41	0.48	0.36	0.62	0.41	0.54	0.49	0.00	0.00	0.00	0.50	0.00	0.00
			Yield (n)									
33	24	22	24	24	24	24						
38	24	23	24	24	24	24						
39	24	21	21	12	23	12						
40	9	6	10	12	3	12						
41	5	10	18	16	2	16						

Table A12. Light reduction in cages. Treatments in cages were based on sampling at 4 different time periods during a summer day 2002. Horizontal positioned cages were applied in Chapter 5, and vertical positioned cages in the additional performance experiments briefly described above.

Mesh type	**Control**	**None**	**White**	**Black**	**None**	**White**	**Black**
Cage Position		**Horizontal**	**Horizontal**	**Horizontal**	**Vertical**	**Vertical**	**Vertical**
PAR	1072	957	734	525	880	496	318
SD	703	631	508	448	595	316	226
n	50	10	10	10	5	5	5
% PAR reduction	0	11	32	51	18	54	70

Table A13. Rankings of current velocity, drift algae accumulations, sedimentation, drag on practice golf balls, accumulated sediments based on SNK-test ($p < 0.05$) following univariate ANOVA (from Chapter 6 experiments).

Variable	Treat1	Treat2	n	Log(x+1)	Group	Variable	n	Log(x+1)	Group
Current	Cov	Con	24	0.53	2	Drag	23	1.11	1
Current	Cov	Dri	24	0.49	2	Drag	24	1.16	1
Current	Cov	Sed	24	0.05	1	Drag	22	1.17	1
Current	Hyd	Cur	24	0.62	3	Drag	23	1.15	1
Current	Hyd	Pro	24	0.18	1	Drag	23	1.14	1
Current	Hyd	Wav	24	0.27	2	Drag	23	1.15	1
Drift	Cov	Con	60	1.47	1	Sediment	48	0.33	2
Drift	Cov	Dri	60	2.67	3	Sediment	48	0.20	1
Drift	Cov	Sed	60	2.05	2	Sediment	48	0.58	3
Drift	Hyd	Cur	60	1.93	1	Sediment	48	0.37	1
Drift	Hyd	Pro	60	2.14	2	Sediment	48	0.36	1
Drift	Hyd	Wav	60	2.12	2	Sediment	48	0.38	1
Drift	Tim	1	36	2.04	1&2	Sediment	36	0.67	4
Drift	Tim	2	36	1.94	1	Sediment	36	0.00	1
Drift	Tim	3	36	2.23	2	Sediment	36	0.47	3
Drift	Tim	4	36	2.18	1&2	Sediment	36	0.34	2
Drift	Tim	5	36	1.92	1				
Sedimentation	Cov	Con	12	0.96	2				
Sedimentation	Cov	Dri	12	0.84	1				
Sedimentation	Cov	Sed	12	1.00	2				
Sedimentation	Hyd	Cur	12	0.99	2				
Sedimentation	Hyd	Pro	12	0.89	1				
Sedimentation	Hyd	Wav	12	0.92	1&2				

Table A14. Rankings of Animal and Plant richness and abundance, and abundance of *C. fragile, C. virginia, G. verrucosa, A. subulata, U. curvata, Enteromorpha* sp. based on SNK-test ($p < 0.05$) following univariate ANOVA (Chapter 6 experiments).

Treat1	Treat2	n	Var	Log(x+1)	Group	Var	Log(x+1)	Group	Var	Log(x+1)	Group
Cov	Con	48	AniR	0.48	1	PlaR	0.75	3	Ulv	0.33	2
Cov	Dri	48	AniR	0.45	1	PlaR	0.62	2	Ulv	0.30	2
Cov	Sed	48	AniR	0.44	1	PlaR	0.47	1	Ulv	0.06	1
Hyd	Cur	48	AniR	0.47	1	PlaR	0.63	2	Ulv	0.25	2
Hyd	Pro	48	AniR	0.46	1	PlaR	0.63	2	Ulv	0.25	2
Hyd	Wav	48	AniR	0.43	1	PlaR	0.58	1	Ulv	0.18	1
Tim	1	36	AniR	0.48	2	PlaR	0.63	2	Ulv	0.07	1
Tim	2	36	AniR	0.37	1	PlaR	0.66	2	Ulv	0.16	2
Tim	3	36	AniR	0.47	2	PlaR	0.67	2	Ulv	0.46	3
Tim	4	36	AniR	0.50	2	PlaR	0.50	1	Ulv	0.22	2
Cov	Con	48	AniC	0.75	2	PlaC	1.38	3	Aga	0.29	2
Cov	Dri	48	AniC	0.43	1	PlaC	0.94	2	Aga	0.03	1
Cov	Sed	48	AniC	0.43	1	PlaC	0.40	1	Aga	0.01	1
Hyd	Cur	48	AniC	0.54	1	PlaC	1.02	2	Aga	0.08	1
Hyd	Pro	48	AniC	0.56	1	PlaC	0.89	1	Aga	0.25	2
Hyd	Wav	48	AniC	0.51	1	PlaC	0.81	1	Aga	0.01	1
Tim	1	36	AniC	0.54	1	PlaC	0.83	2	Aga	0.06	1
Tim	2	36	AniC	0.46	1	PlaC	1.120	4	Aga	0.13	1
Tim	3	36	AniC	0.44	1	PlaC	0.97	3	Aga	0.13	1
Tim	4	36	AniC	0.70	2	PlaC	0.70	1	Aga	0.13	1
Cov	Con	48	Cra	0.60	2	Cod	0.49	2	Ent	0.29	2
Cov	Dri	48	Cra	0.12	1	Cod	0.03	1	Ent	0.62	3
Cov	Sed	48	Cra	0.21	1	Cod	0.01	1	Ent	0.12	1
Hyd	Cur	48	Cra	0.26	1	Cod	0.14	1	Ent	0.41	2
Hyd	Pro	48	Cra	0.35	1	Cod	0.22	1	Ent	0.27	1
Hyd	Wav	48	Cra	0.32	1	Cod	0.16	1	Ent	0.36	2
Tim	1	36	Cra	0.25	1	Cod	0.12	1	Ent	0.35	2
Tim	2	36	Cra	0.34	1	Cod	0.15	1	Ent	0.68	3
Tim	3	36	Cra	0.30	1	Cod	0.23	1	Ent	0.29	2
Tim	4	36	Cra	0.35	1	Cod	0.19	1	Ent	0.06	1
Cov	Con	48	Gra	1.02	2						
Cov	Dri	48	Gra	0.24	1						
Cov	Sed	48	Gra	0.21	1						
Hyd	Cur	48	Gra	0.64	2						
Hyd	Pro	48	Gra	0.41	1						
Hyd	Wav	48	Gra	0.42	1						
Tim	1	36	Gra	0.39	1						
Tim	2	36	Gra	0.55	2						
Tim	3	36	Gra	0.55	2						
Tim	4	36	Gra	0.47	1&2						

Table A15. Secchi depth, Temperature, Salinity, Suspended Solids and Dissolved oxygen in Hog Island Bay. Data are mean values from nearly monthly sampling from 31-03-1999 to 17-10-2002 (data collected by Kathleen Overman, Phillips Smith and Jason Restein, as part of the VCR/LTER Water Quality Monitoring Program).

	Secchi (cm)	**n**	**SD**	**Max**	**Min**	**Salt (ppt)**	**n**	**SD**	**Max**	**Min**
CSm	90	35	33	150	38	31.3	33	1.4	33.1	27.9
GC	87	35	35	170	35	30.3	33	2.5	35.1	22.3
MI	99	35	29	158	55	31.7	33	1.4	35.0	28.0
NC	97	35	38	210	38	31.5	33	1.8	35.2	25.1
OH	99	34	36	167	20	30.6	32	2.3	36.0	24.0
PCh	70	35	23	119	29	27.9	33	4.7	36.3	15.8
PCm	77	35	27	169	25	29.2	33	3.7	35.3	19.0
QI	109	35	38	205	60	31.6	33	1.4	35.0	29.1
RB	90	35	32	167	30	31.0	33	1.8	35.1	25.7
SH	92	25	27	160	47	31.6	33	1.5	35.0	27.9
Tot		339	34	210	20	30.7	329	2.7	36.3	15.8
	T (C)	**n**	**SD**	**Max**	**Min**	**TSS (gDW/L)**	**n**	**SD**	**Max**	**Min**
CSm	16.4	36	7.5	29.0	4.0	0.270	30	0.567	2.558	0.027
GC	17.1	36	7.9	31.0	3.8	0.388	30	1.052	5.586	0.021
MI	16.4	36	7.6	30.0	4.7	0.239	29	0.434	1.828	0.025
NC	16.6	36	7.6	29.0	3.4	0.247	30	0.484	2.027	0.025
OH	18.3	35	7.6	32.0	4.6	0.215	30	0.416	1.927	0.019
PCh	17.5	36	7.8	31.0	3.6	0.323	30	0.754	3.822	0.022
PCm	17.2	36	7.9	30.5	3.3	0.277	30	0.453	1.684	0.023
QI	15.7	36	7.2	28.0	4.6	0.235	30	0.469	1.936	0.026
RB	16.9	36	7.9	30.5	4.7	0.307	30	0.752	3.788	0.025
SH	16.4	36	7.7	29.5	3.0	0.274	30	0.478	1.986	0.029
Tot	16.9	359	7.6	32.0	3.0	0.277	299	0.610	5.586	0.019
	DO (ml/L)	**n**	**SD**	**Max**	**Min**					
CSm	7.00	25	2.23	11.90	2.00					
GC	6.63	25	2.10	10.80	2.20					
MI	7.66	25	2.29	12.80	3.50					
NC	6.87	25	2.25	11.70	2.20					
OH	7.16	25	2.08	10.50	2.50					
PCh	6.38	25	2.47	12.20	2.10					
PCm	6.60	26	2.17	11.30	2.40					
QI	7.48	25	2.16	11.50	3.20					
RB	6.98	25	2.23	11.60	2.00					
SH	7.30	25	2.20	12.50	3.40					
Tot	7.01	251	2.21	12.80	2.00					

Appendix Figures

Fig. A1. Approximate geographic range of *C. fragile*. The introduction of ssp. *tomentosoides* in Chile is based on pers. com. Trowbridge (2004).

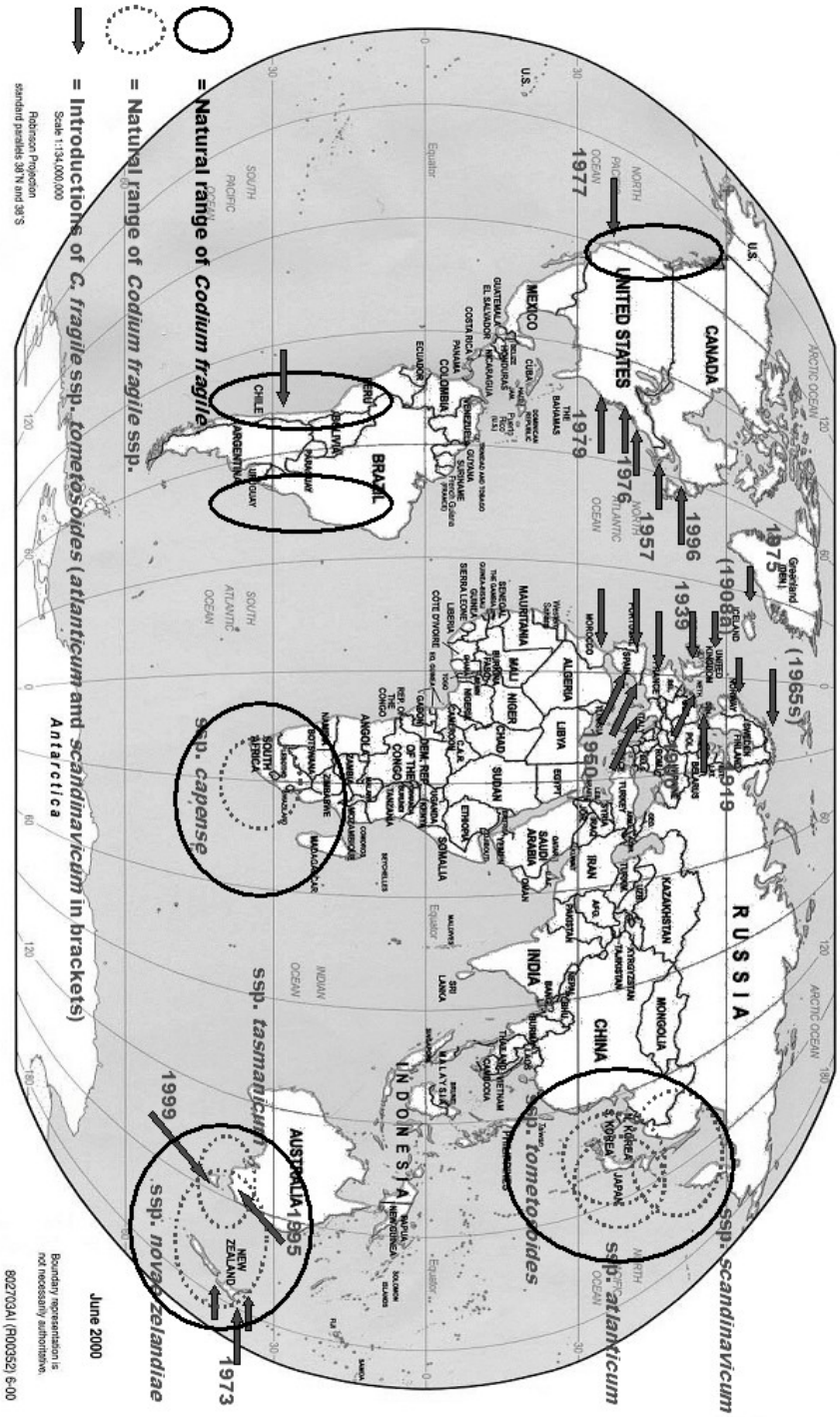


Fig. A2. Attachment survey. Counts of attachment types for separate species (top figure) and for all species pooled (bottom figure).

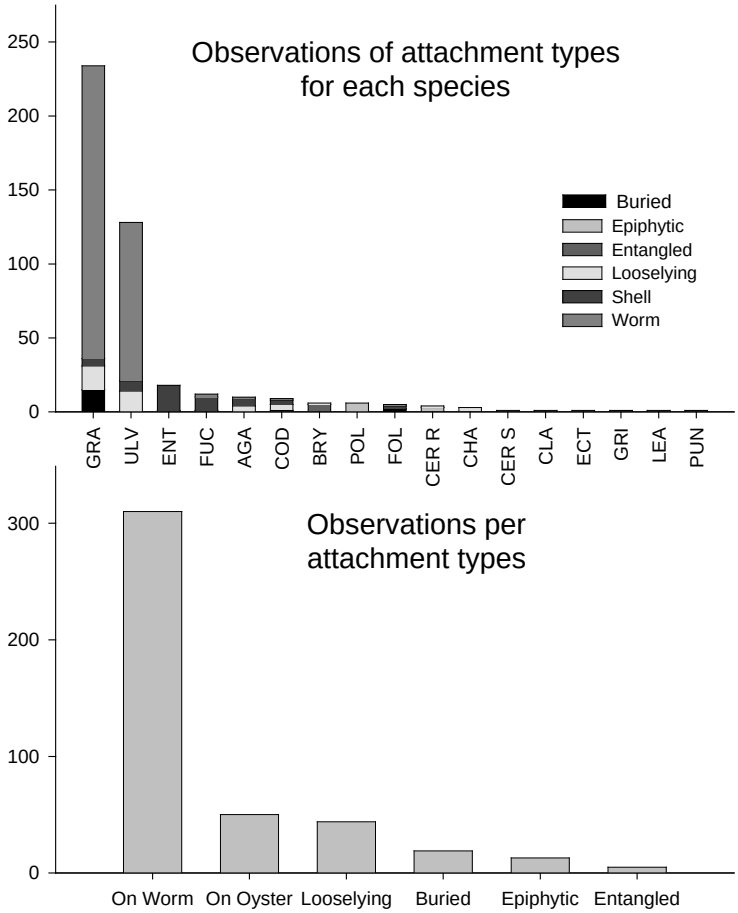


Fig. A3. *G. verrucosa* dominance and *D. cuprea* tube caps. Top photo: A typical intertidal mudflat dominated by scattered *G. verrucosa* clumps. Bottom photo: A close-up of the *G. verrucosa* clumps. Each hummock is a *D. cuprea* tube cap with incorporated *G. verrucosa*.

Fig. A4. Algae incorporated into *D. cuprea* tube caps. Top photo: *G. verrucosa* and *U. curvata* incorporated into a tube cap (natural incorporation). Bottom photo. An example of a *C. fragile* fragment incorporated into a tube cap (from a single-species cage in the Preference experiment, Chapter 4).

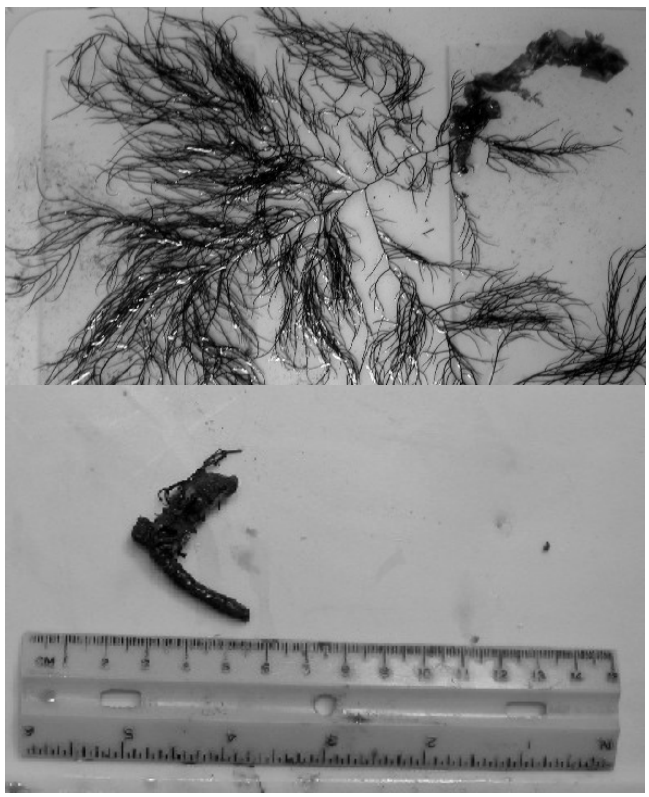
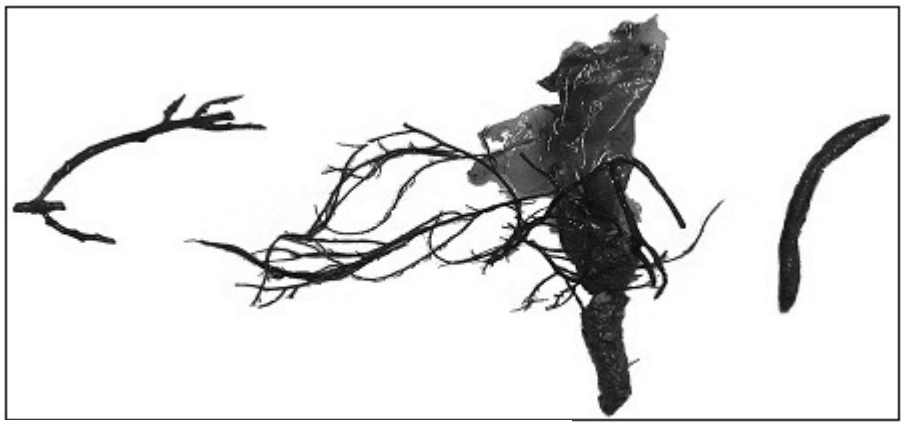


Fig. A5. *D. cuprea* preference experiment. Top photo: Example from an all-species addition cage where *G. verrucosa*, *G. foliifera*, and *U. curvata* were incorporated, but *C. fragile* (right) and *A. subulata* (left) were not. Graph A: Initial biomass used in cages, Graph B: Biomass changes of algae in cages. Error bars are 95% confidence limits.



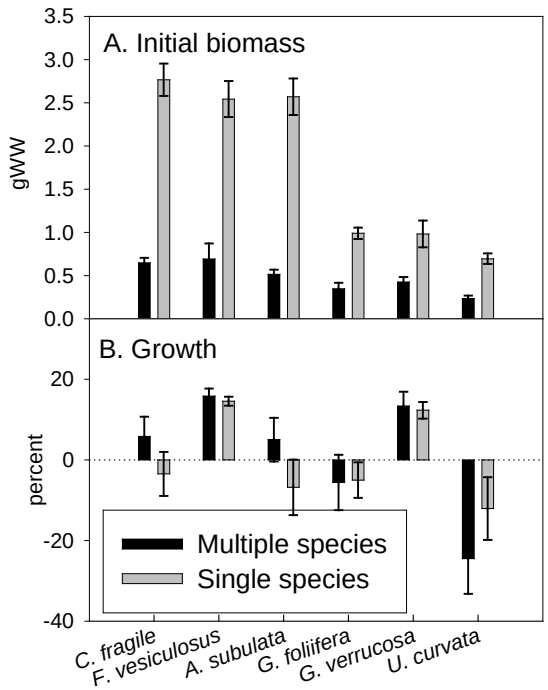


Fig. A6. *C. fragile* morphology and fragmentation. Top photo: *C. fragile* morphology in June (ruler 20 cm). Bottom photo: *C. fragile* morphology in November. Note the elongation of tissue and numerous indentions (arrows) from where fragmentation and breakage occur in biomechanical pull tests.

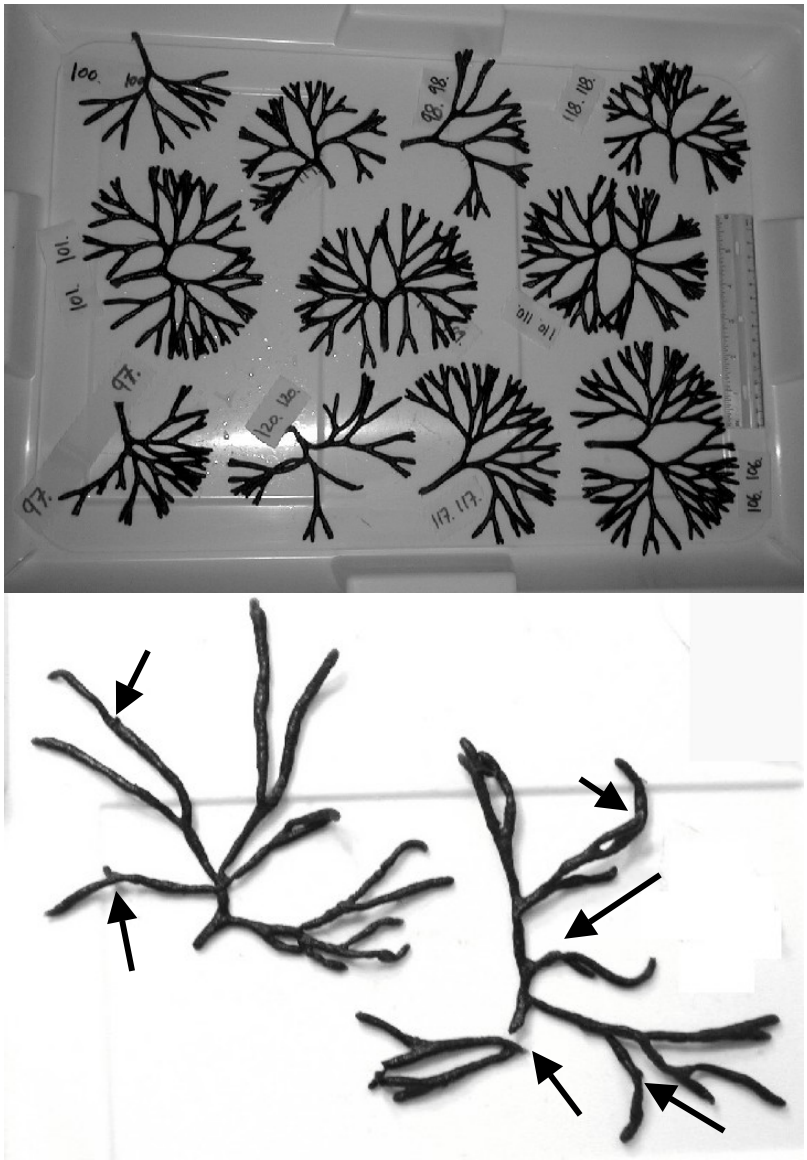


Fig. A7. Methodologies of performance experiments. Top photo: Twist tie wrapping of (from left to right) flagging tape marker, *F. vesiculosus*, *C. fragile*, *G. verrucosa* and *A. subulata* used for open plot incubation. Bottom photo. Typical set-op of closed cage experiment (Shoal 1 site, ± nutrient spikes, 4 replicates, 6 species per cage, and random allocation of fragments, treatments and cages to the float-structure). The cages fill with water and float ca. 20 cm below the surface.

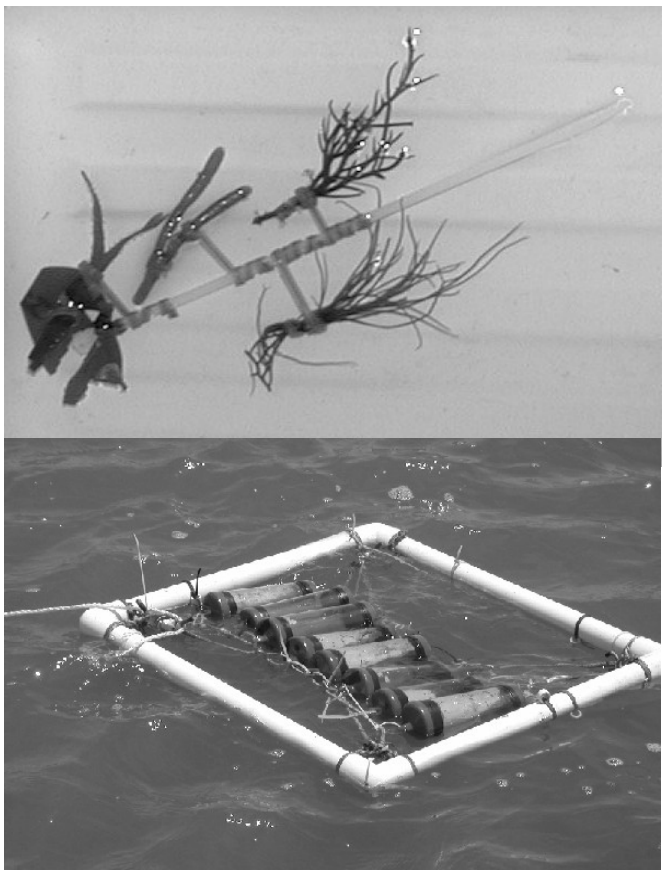


Fig. A8. Interaction plots of species, caging, distance from mainland, twist-tie wrapping and experimental design versus algal performance. The four graphs correspond to the significant interactions that was not depicted in Figure 5.1-5.5. Cf. Chapter 5 for descriptions of experimental designs and abbreviation. Note that species with large S:V ratio have small variation in cages but large variation in open plots (Exp. 37).

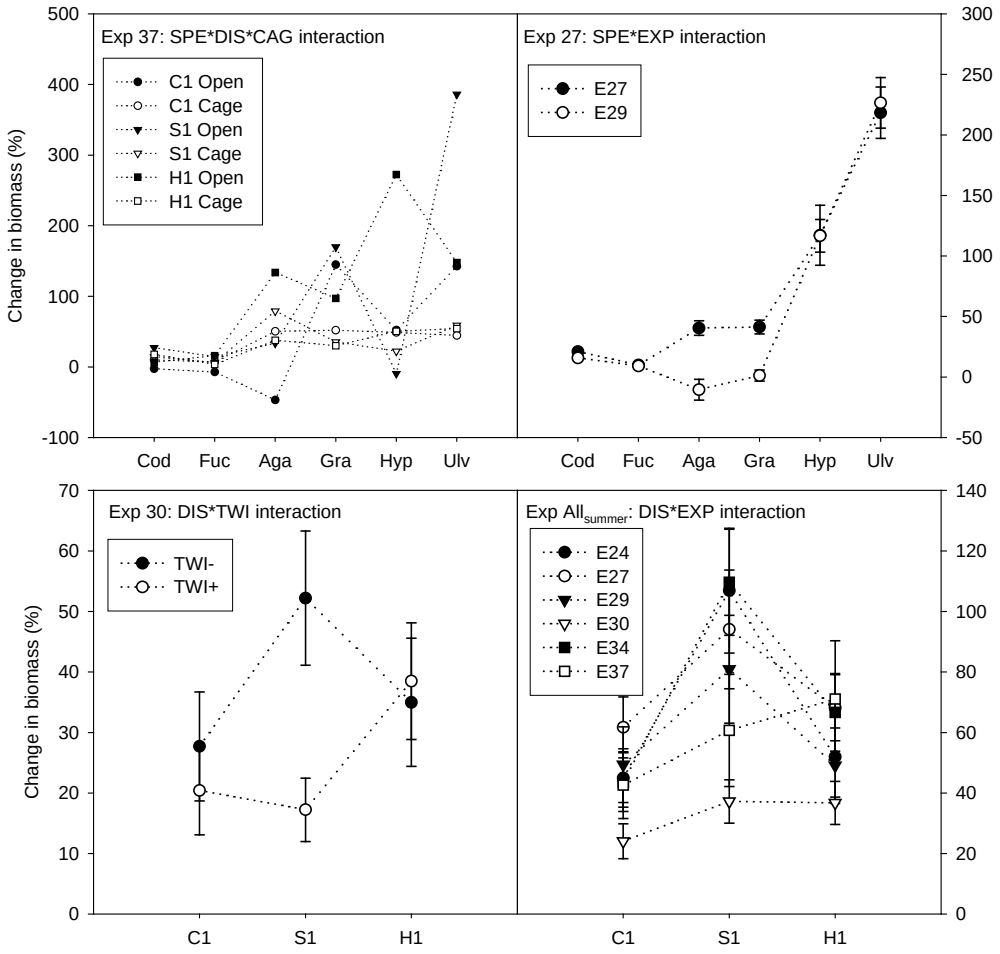


Fig. A9. Interaction plots of tissue fragmentation along the distance gradient. 100% fragmentation correspond to a fragment that during incubation broke into two pieces. n = 4, except for Eall (n = 16). Error bars are standard errors.

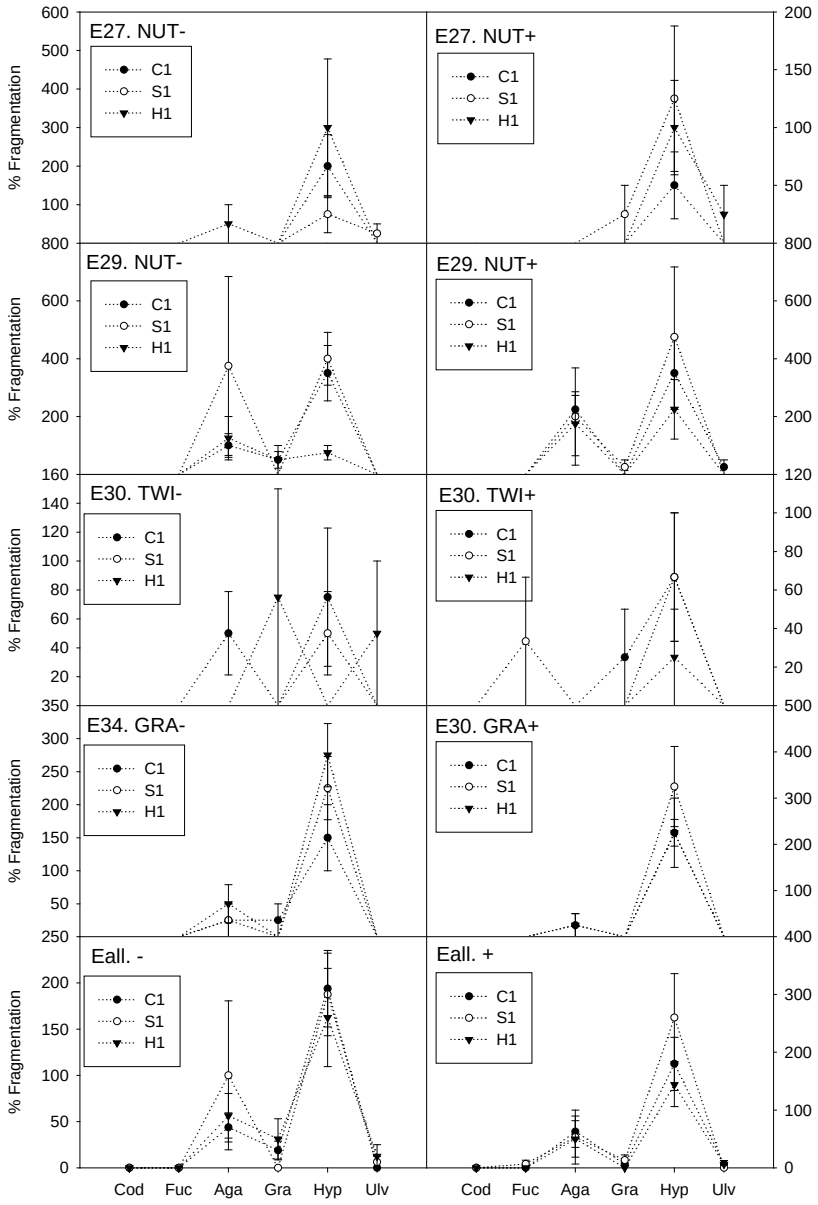


Fig. A10. Interaction plots of fluorescence yield along the distance from mainland gradient. Yield was measured with a Mini-Pam on moist-fragments after experimental incubation (default setting, ca. 9 mm distance, 30 degree angle). Fragments were exposed to dim laboratory light for at least 1 hour prior to measurements (ca. 5-10 $\mu Em^{-2}s^{-1}$). n = 4, except Eall (n = 20), and E19 (n = 4-8). Error bars are standard errors.

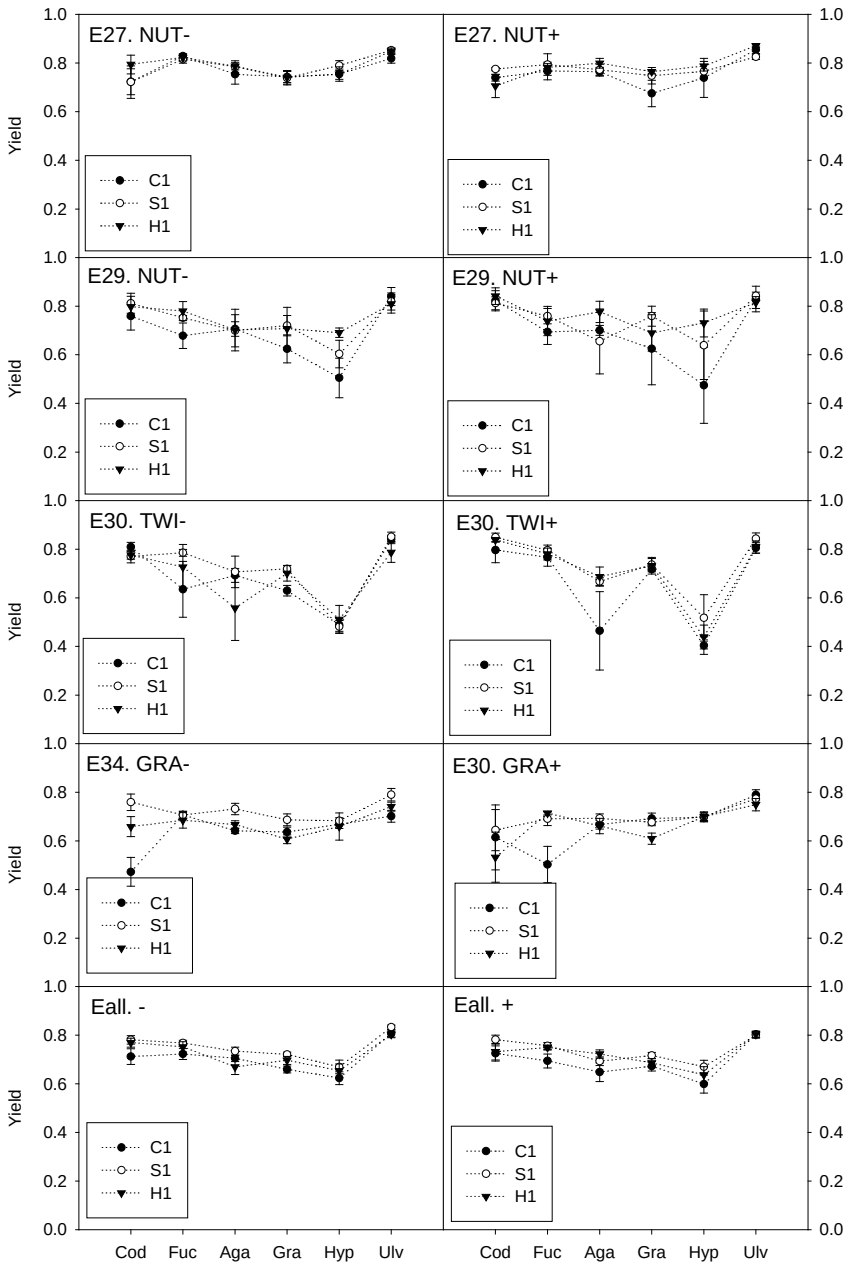


Fig. A11. Interaction plots of fluorescence yield along the distance gradient (continued from Fig. 14). n = 4, except Eall (n = 20), and E19 (n = 4-8). Error bars are standard errors.

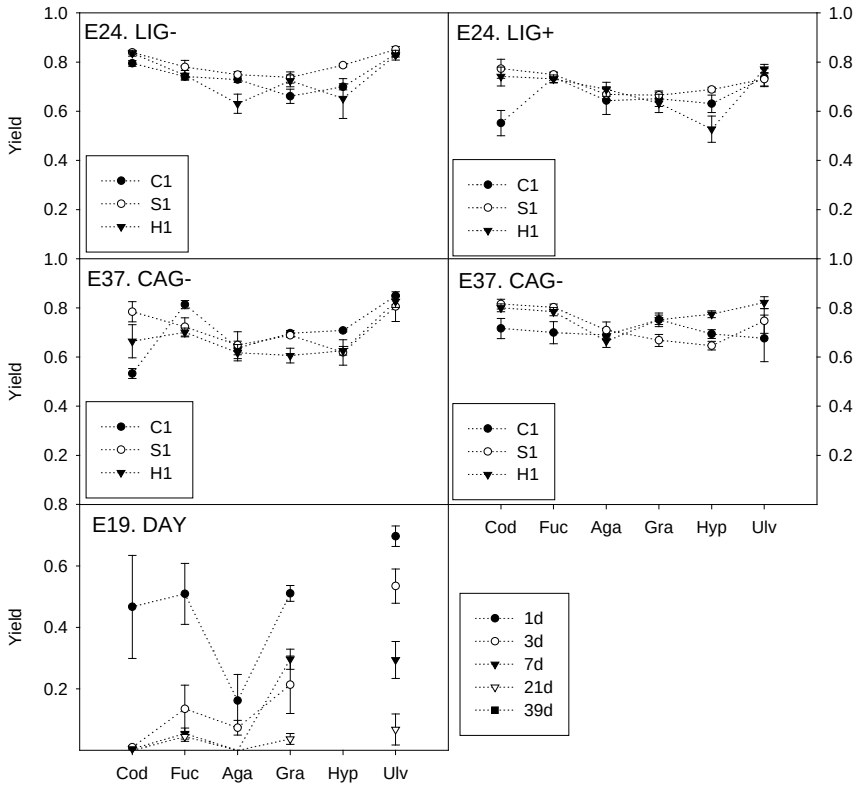


Fig. A12. Reattachment of *C. fragile* and *H. musciformis*. Top photo: *C. fragile* reattached onto *U. curvata*. These reattachments were observed after 2 weeks of incubation in an outdoor aquarium in November 2002 (no stirring or aeration). The small *C. fragile* fragment is ca. 2 cm long. Bottom photo. Close-up of entanglement of a *H. musciformis* apical hook to a mesh structure. A secondary attachment structure is typically produced following the entanglement.

Fig. A13. Interaction plots of reattachment of *H. musciformis* along the distance from mainland gradient. Number of produced reattachment structures versus different substrates (algal species and cage/mesh structure) within an enclosed cage. n = 4, except Eall (n = 20). Error bars are standard errors.

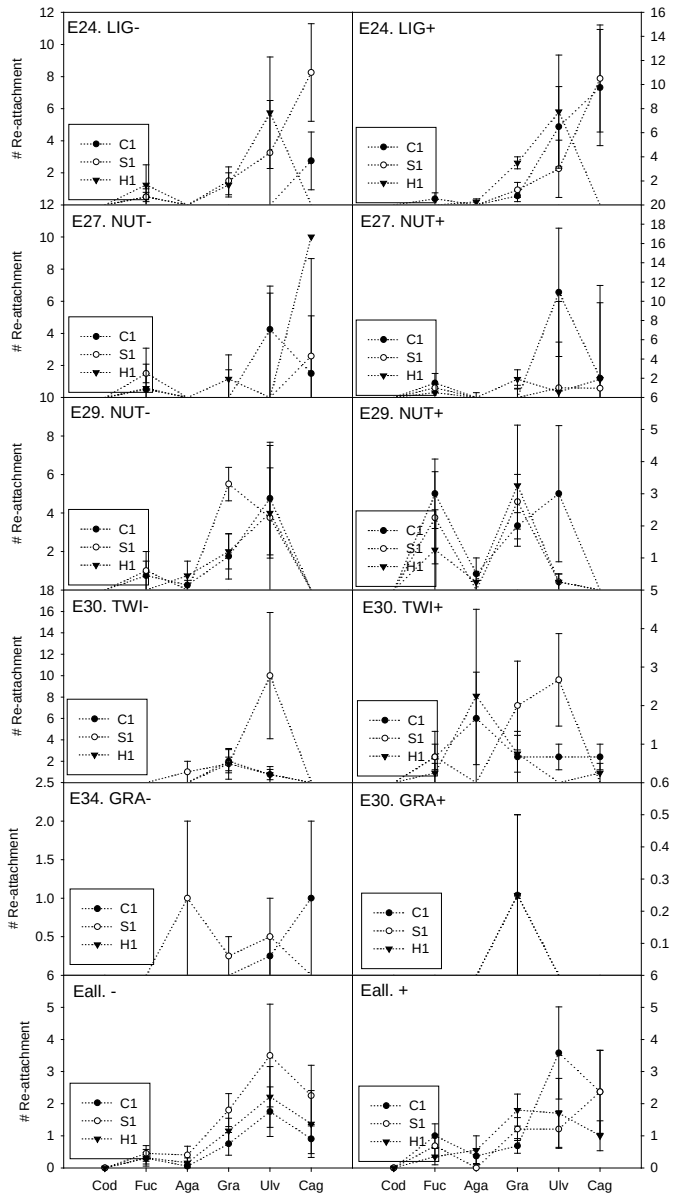


Fig. A14. Interaction plots of biomass performance patterns for additional experiments (E) along an elevation gradient (I). Confer Chapter 5 for general information of methodology. n = 2-6,. Error bars are standard errors.

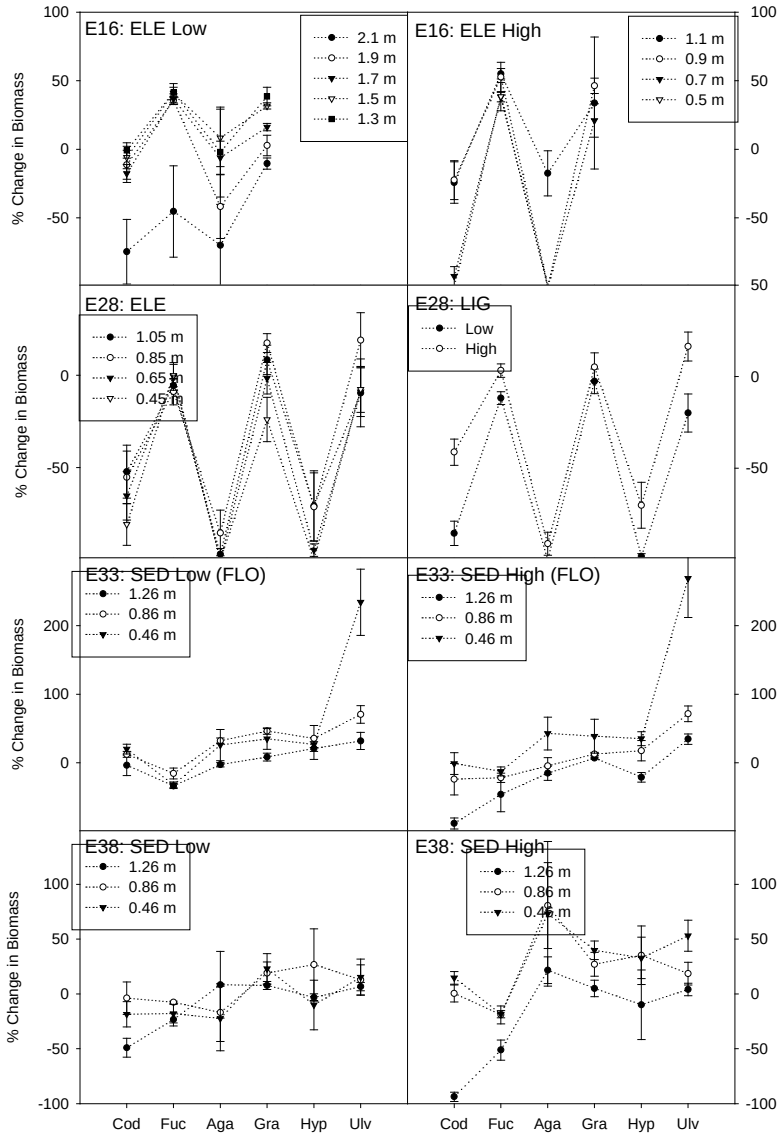


Fig. A15. Interaction plots of biomass performance patterns for additional experiments (E) along an elevation gradient (II). Different interactions are emphasized compared to Fig. A14. Confer Chapter 5 for general information of methodology. n = 2-6,. Error bars are standard errors.

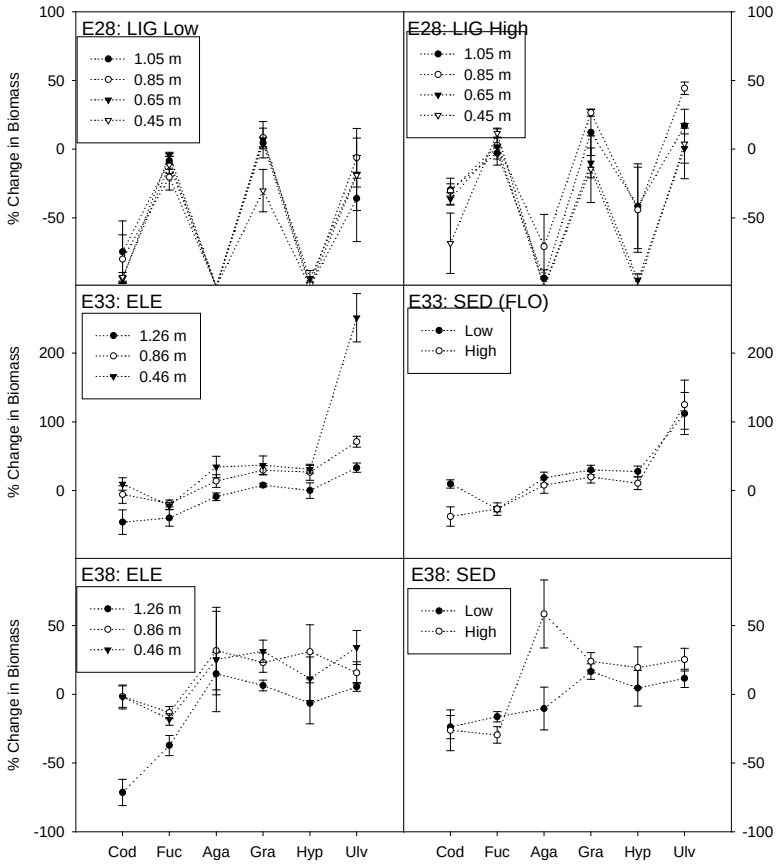


Fig. A16. Interaction plots of biomass performance patterns for additional experiments (E) along an elevation gradient (III). Confer Chapter 5 for general information of methodology and experimental designs. n = 2-6,. Error bars are standard errors.

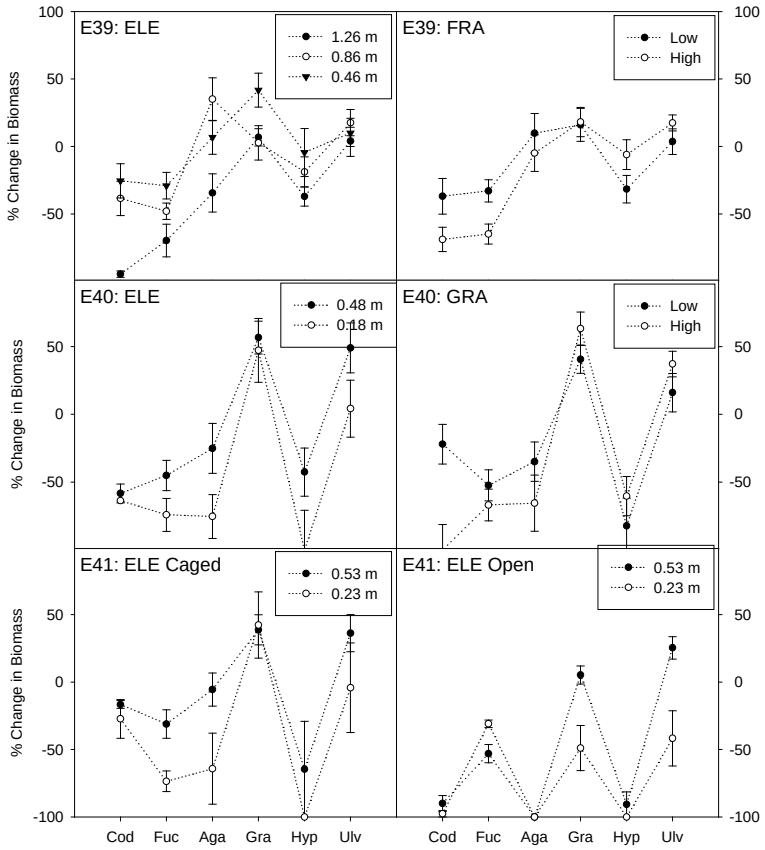


Fig. A17. Interaction plots of biomass performance patterns for additional experiments (E) along an elevation gradient (IV). Confer Chapter 5 for general information of methodology and experimental designs. n = 2-6. Error bars are standard errors.

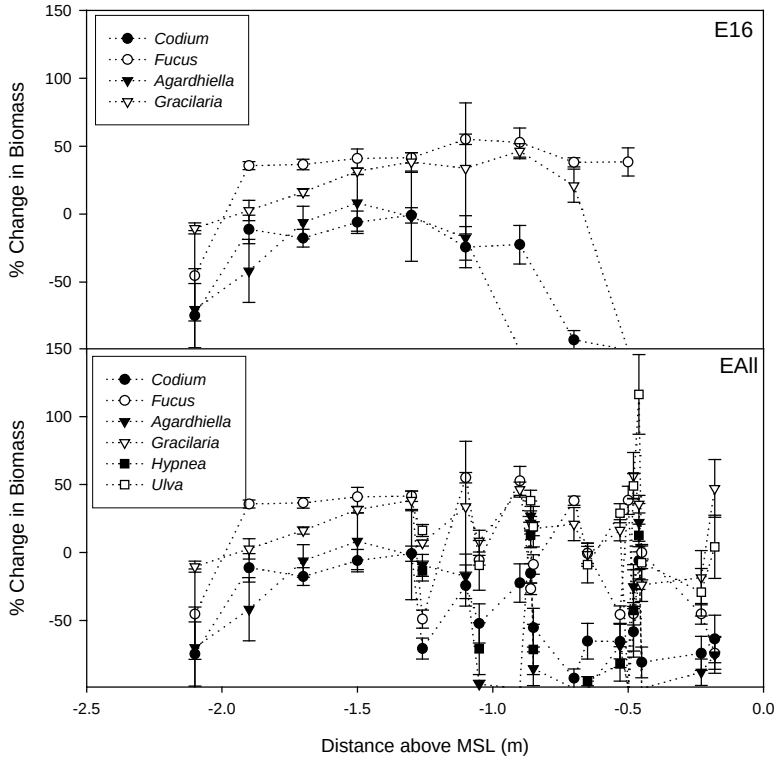


Fig. A18. Oyster reefs at mid-lagoon sites. Top photo: Typical wavy conditions in front of oyster reefs under moderate winds from west, north-west or south-west. Note the drift algal front that wave and currents push along the intertidal margin. Bottom photo: The wave-protected site behind the oyster reefs. Note the dominance of *C. fragile* at ca. 0.8 m below MSL (attached to unconsolidated and partly buried oyster shells, August 2001).

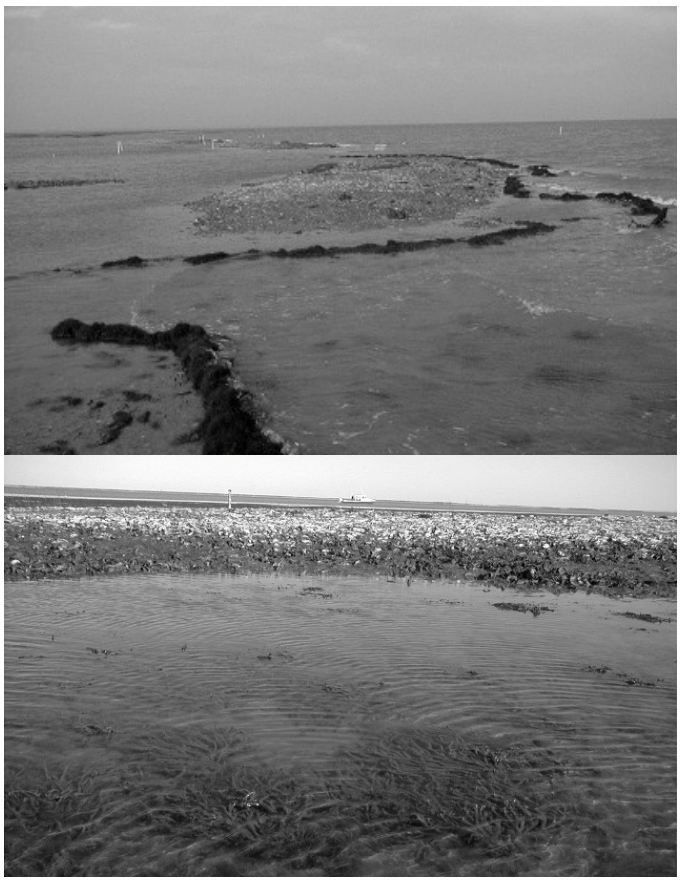


Fig. A19. Elevation map a mid-lagoon Shoal 1 site showing topography around oyster reefs. The oyster reefs are the dark and scattered areas from ca. 0.0 to 0.5 m below MSL (cf. Fig. A18). Each black dot correspond to the position of a set of three treatments: An open control plot, a sediment-trap cage and a drift-algal trap cage. Within each plot/cage four recruitment bricks were incubated (sub-replicates, cf. Chapter 6 for further design description).

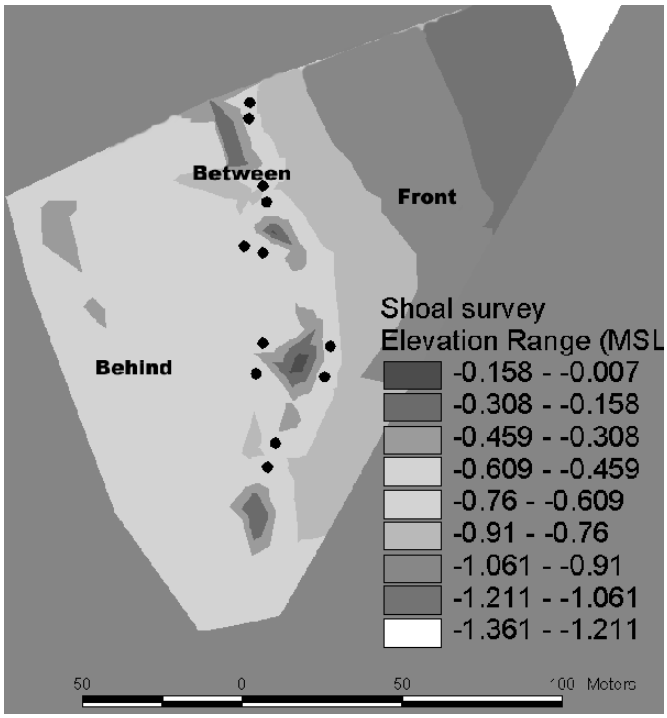


Fig. A20. Control recruitment bricks around oyster reefs. The top-photo show a typical open plot brick behind the oyster reefs in April 2002. Note numerous cm-long *C. fragile* recruits (arrows), relatively large cover of *A. subulata*, and scattered *Punctaria petalonia*. The bottom photo show the same brick changed into a *C. fragile* monoculture in late August 2004.

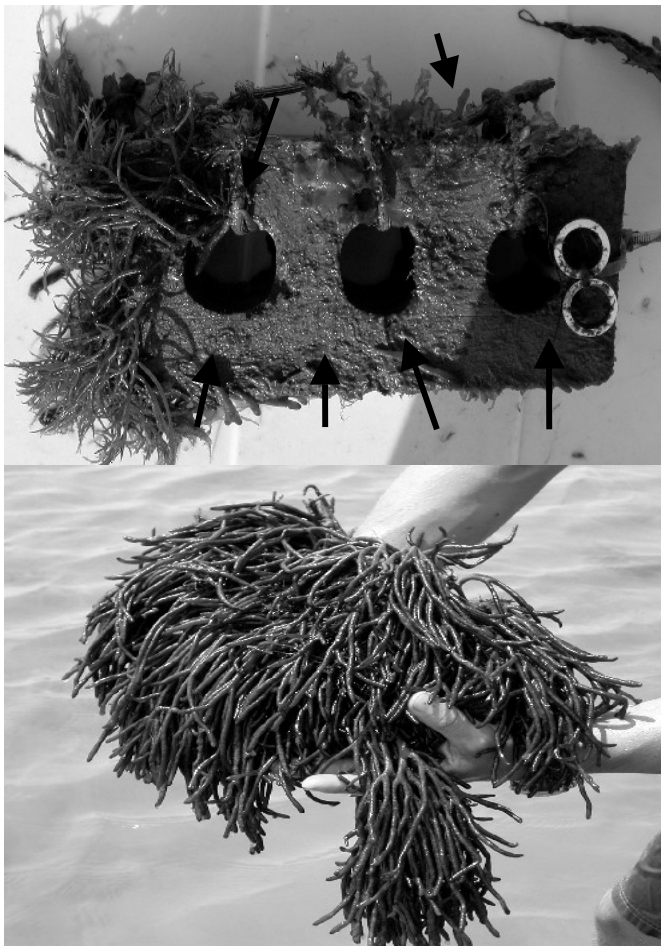


Fig A21. Interaction plots of plant richness, animal richness, plant cover, animal cover, and cover of the six most abundant taxa recruited onto bricks around oyster reefs. The figures are similar to the figures presented in Ch. 6, but with the time factor pooled (± SE, n = 16).

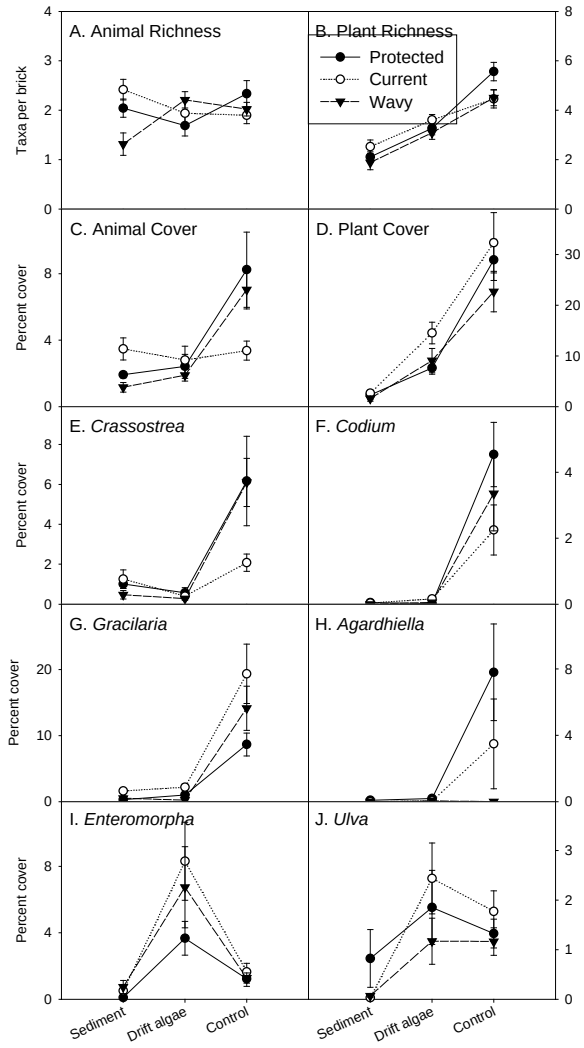


Fig. A22. Abundance of sessile oyster reef associated organisms at different sampling times at the mid-lagoon site (corresponding to experimental data presented in Chapter 6, but pooling the Cover and Hydrodynamic factors, n = 36).

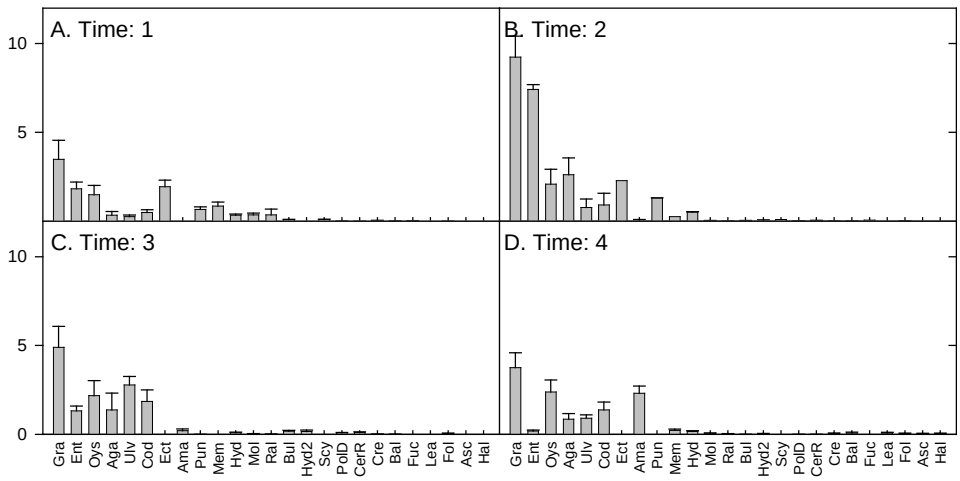


Fig. A23. Abundance of sessile oyster-reef associated organisms recruited onto bricks at different elevation levels at the mid-lagoon site (S1). Error bars are standard errors.

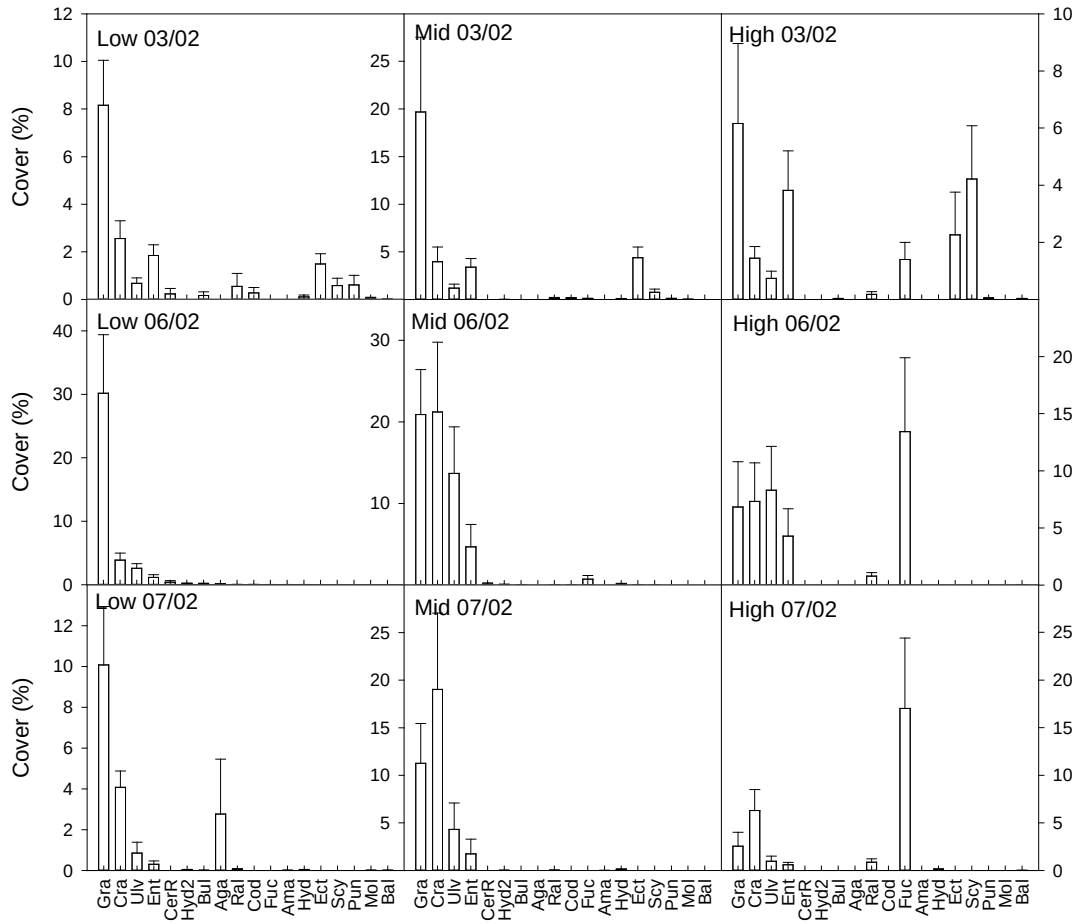


Fig. A24. Abundance of sessile oyster-reef associated organisms at recruited onto bricks at different positions along the distance from mainland gradient (C1, S1, H1). Error bars are standard errors.

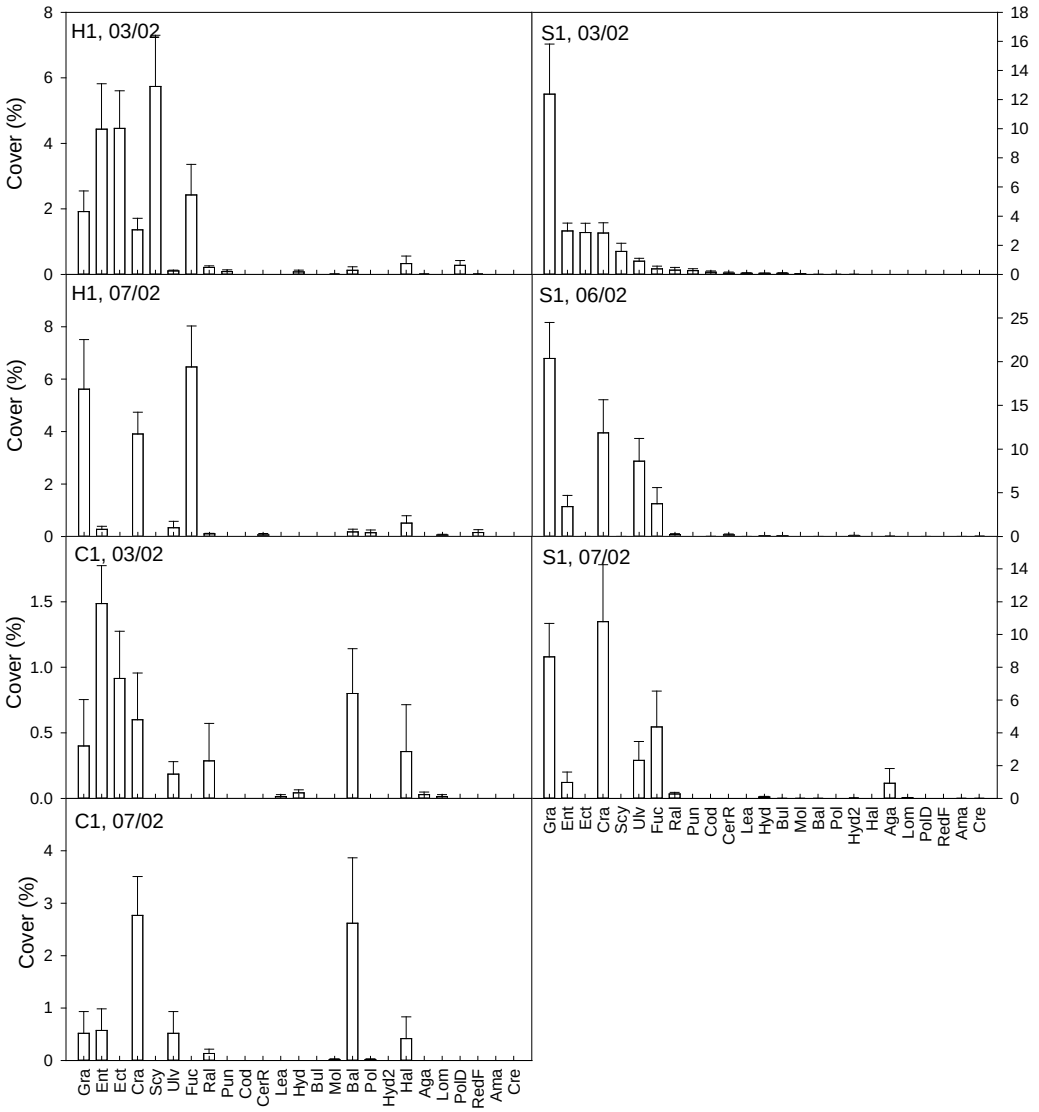


Fig. A25. Abundance of sessile oyster-reef associated organisms. Recruitment bricks were incubated at S1 and transplanted to C1, S1, and H1. Error bars are standard errors.

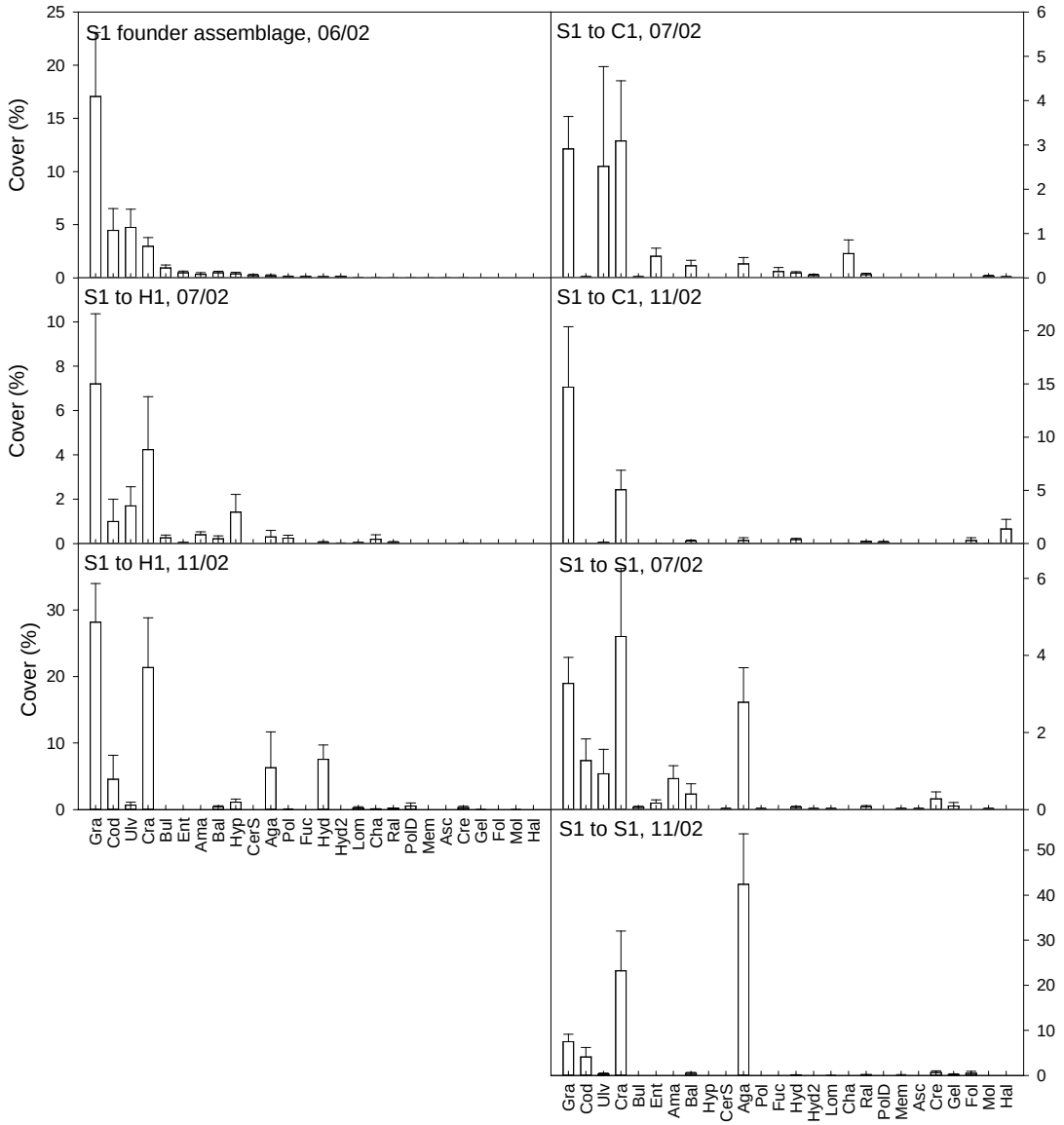


Fig. A26. Location of sample stations from the VCR/LTER WQ (Water Quality) Monitoring Program. Baseline map produced by K. Overman.

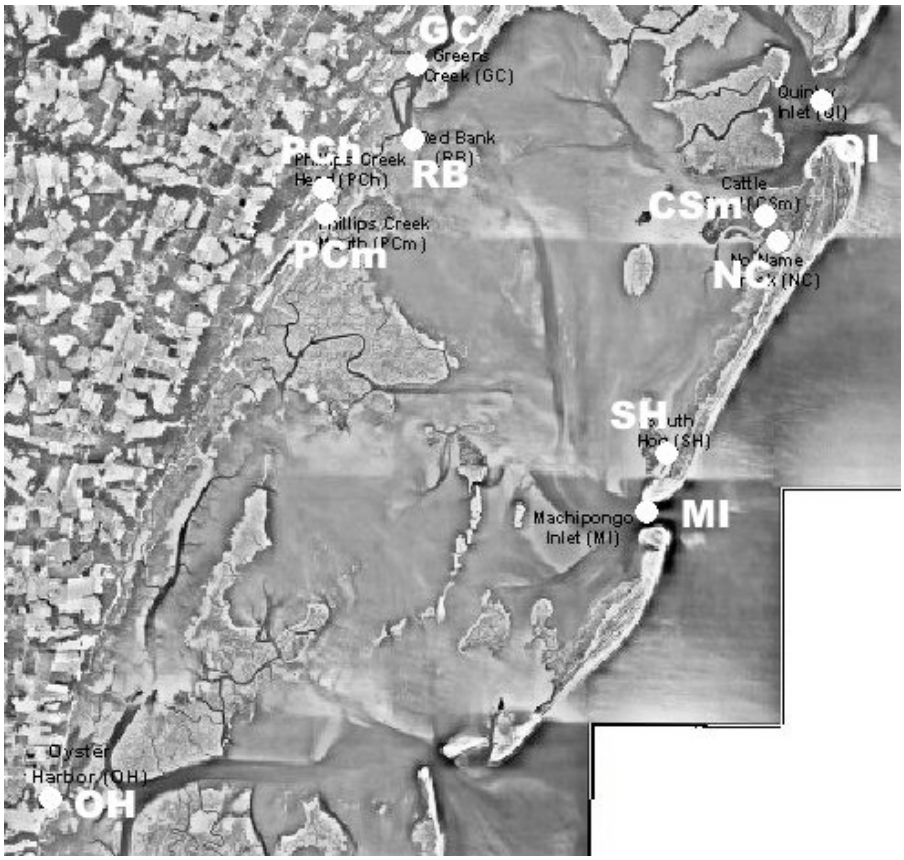


Fig. A27. Temporal development in total suspended solids from individual VCR/LTER WQ-sampling stations.

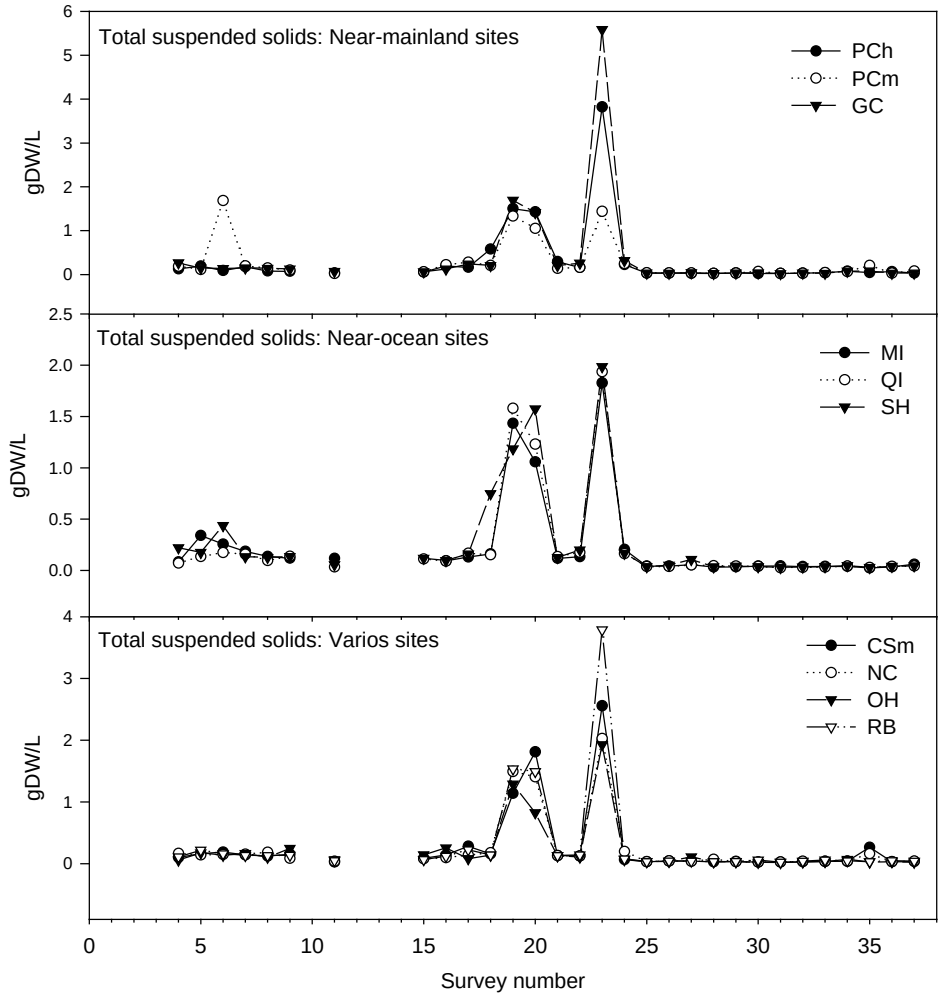


Fig. A28. Temporal development in temperature from individual VCR/LTER WQ-sampling stations.

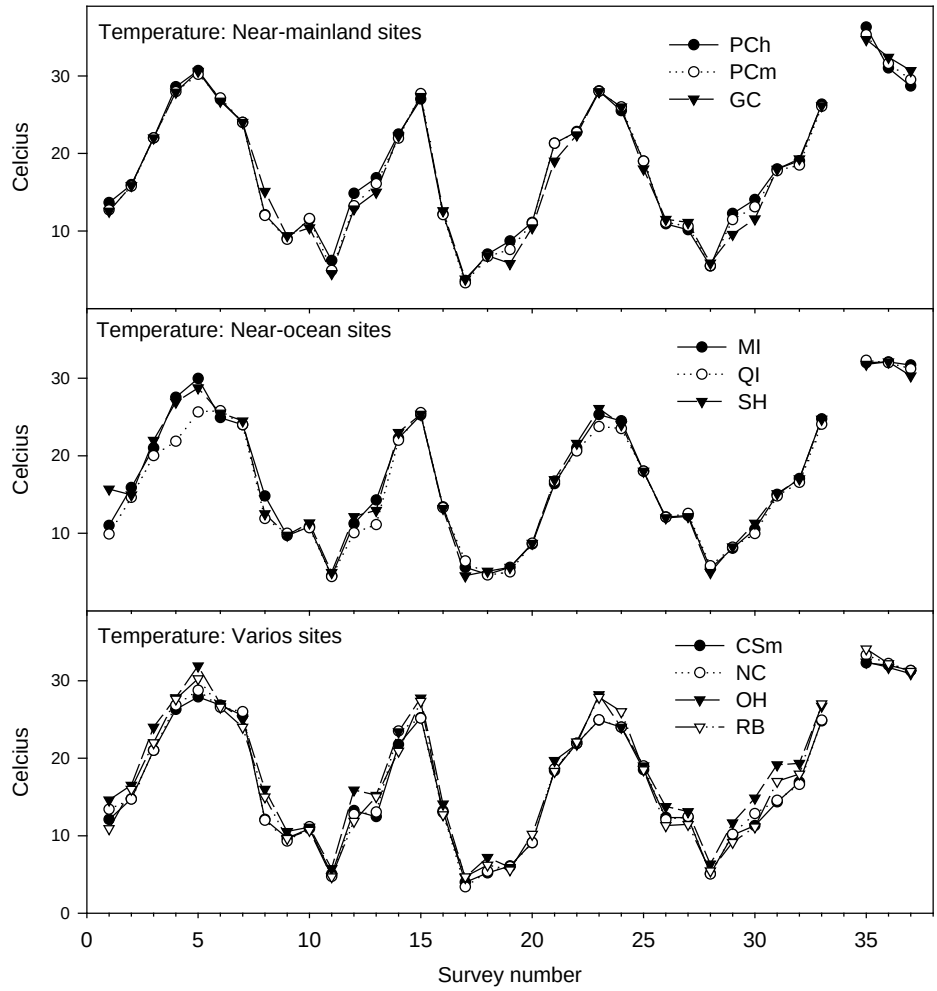


Fig. A29. Temporal development in secchi depth from individual VCR/LTER WQ-sampling stations. Secchi-depths are slighly under-estimated because a few observations were omitted due to shallow waters (i.e. data points where secchi depth > depth were omitted from the graph).

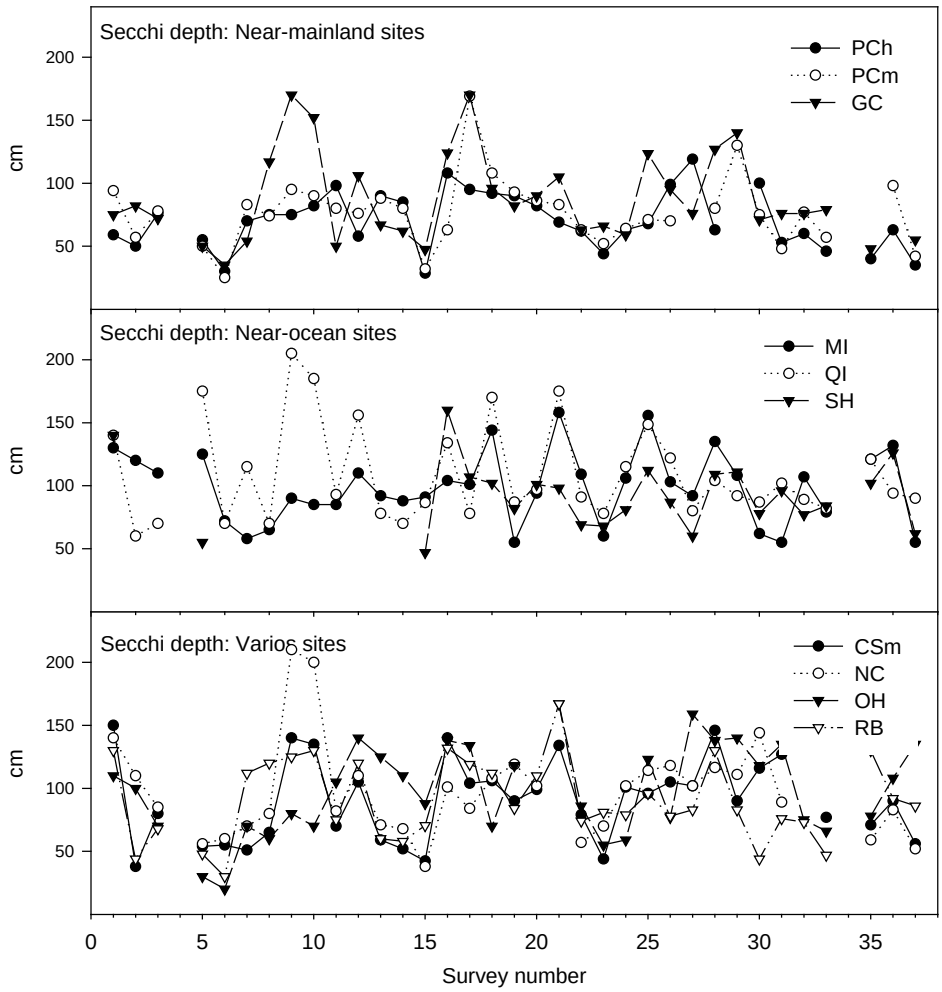


Fig. A30. Temporal development in salinity from individual VCR/LTER WQ-sampling stations.

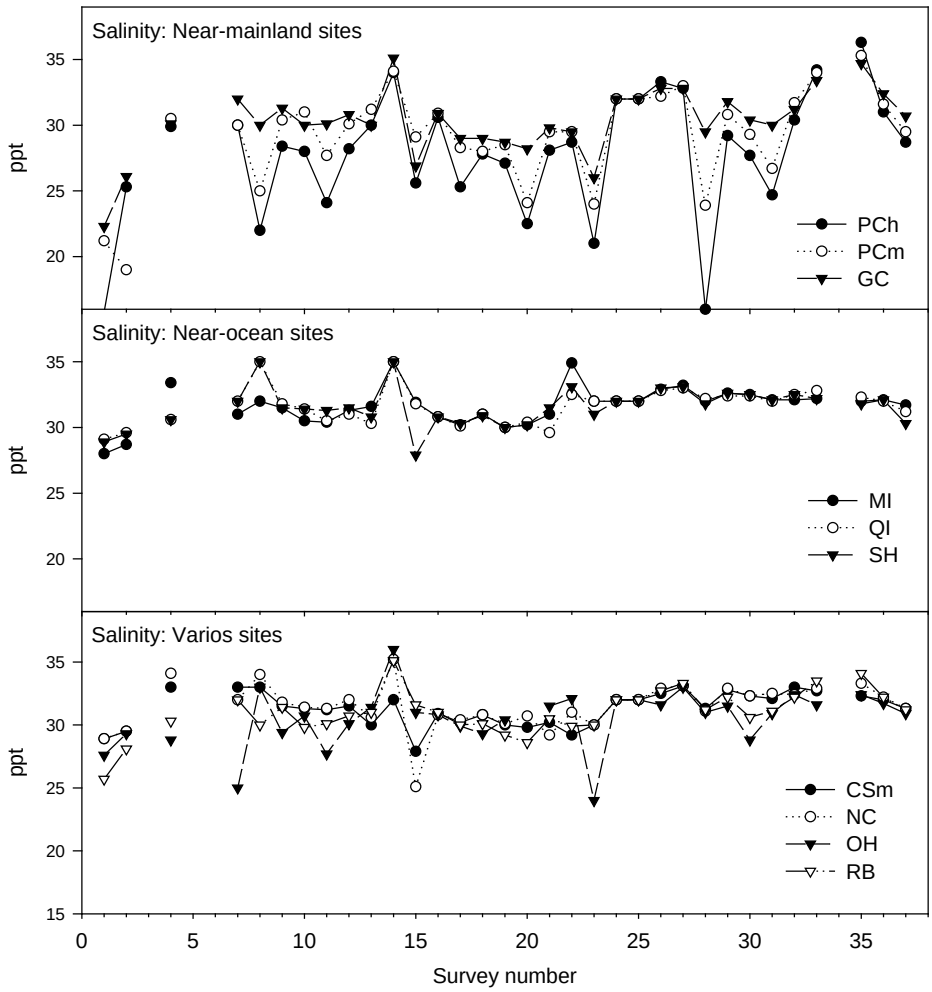


Fig. A31. Temporal development in dissolved oxygen from individual VCR/LTER WQ-sampling stations.

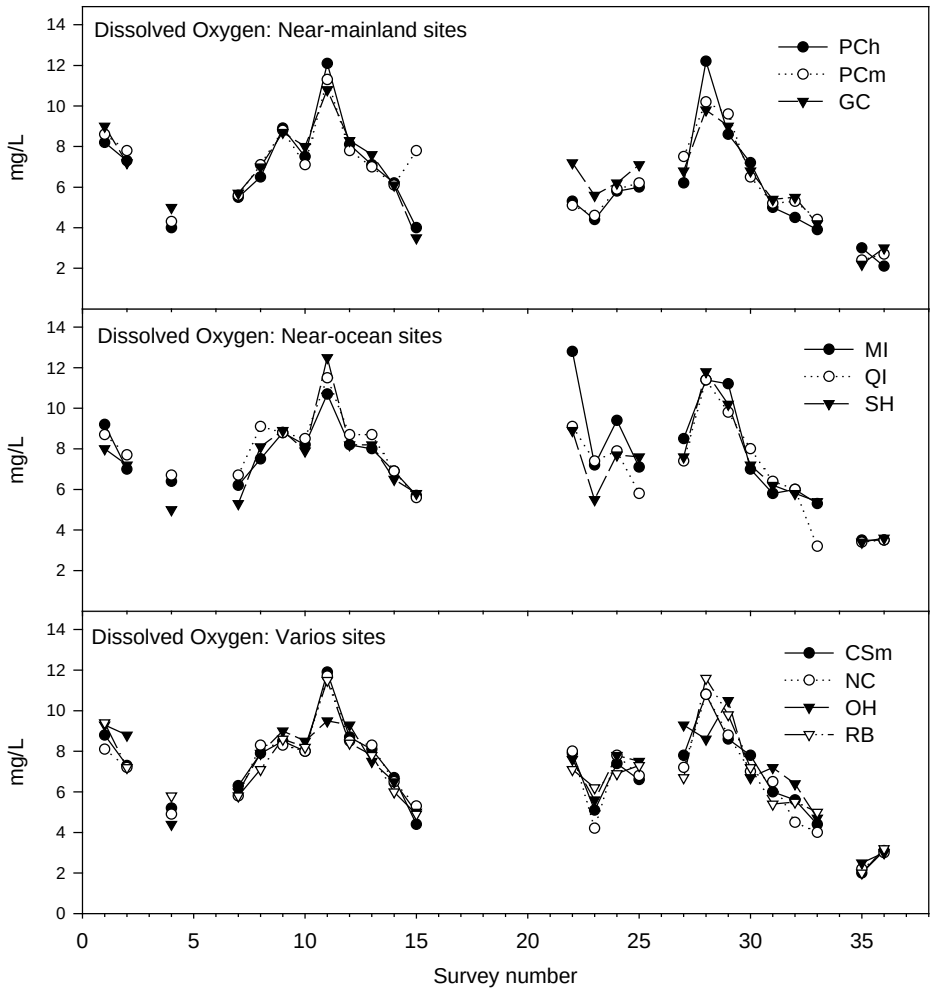
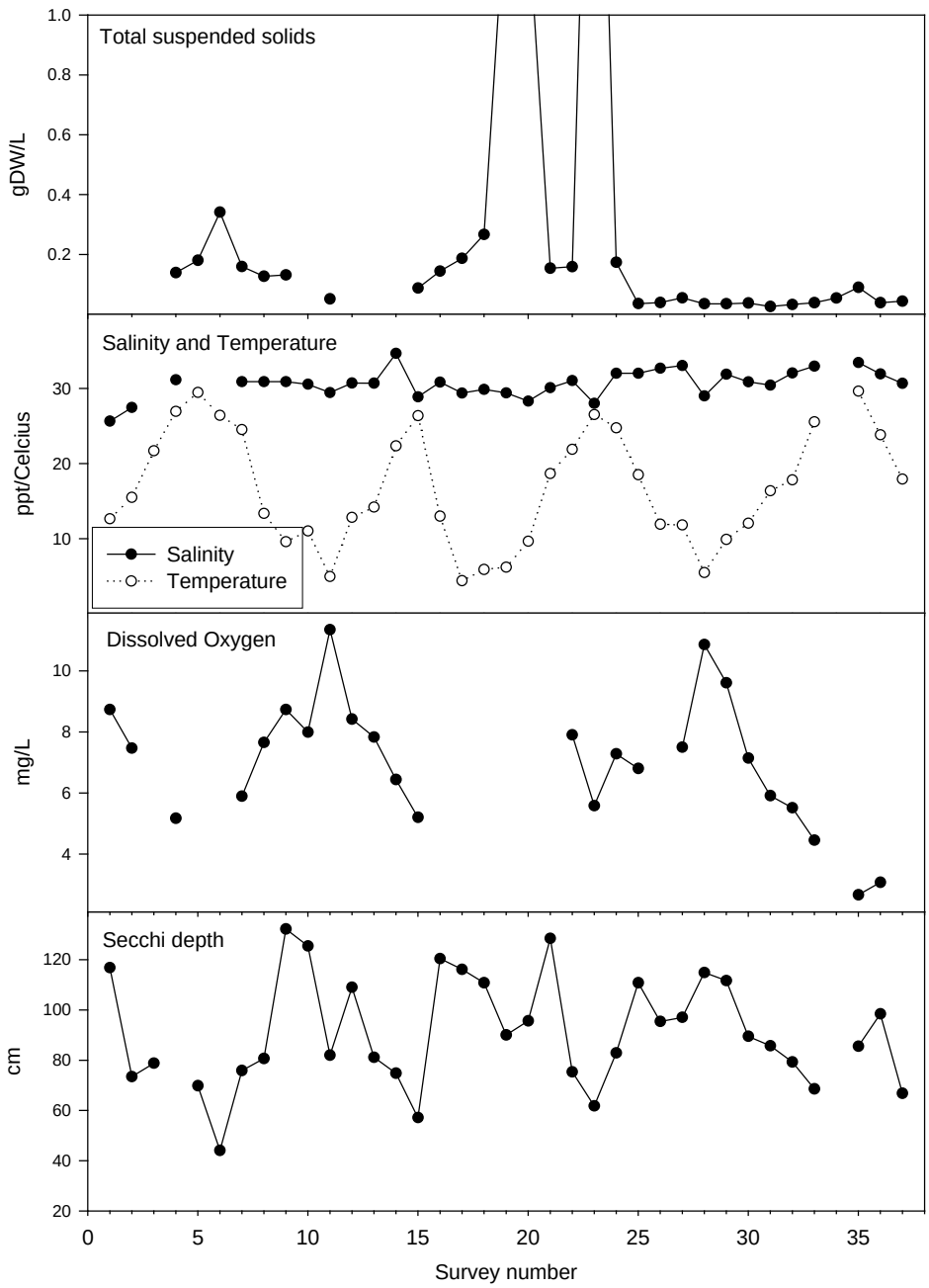


Fig. A32. Temporal development in total suspended solids, temperature, salinity, dissolved oxygen and secchi depth pooled from 10 VCR/LTER WQ-sampling stations.



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