LOW MARSH SUCCESSION ALONG AN OVER-WASH SALT MARSH CHRONOSEQUENCE

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A Dissertation presented to the Graduate Faculty of the University of Virginia in Candidacy for the Degree of Doctor of Philosophy

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May, 1998

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ABSTRACT

Young marshes of the Hog Island marsh chronosequence possessed well aerated sediment that was composed mainly of sand grains, and also showed high pore-water redox levels, but low sulfide, and ammonium concentrations. With age, these variables changed in a monotonic way, until the mature marsh, 150Y, demonstrated poorly oxidized sediments, composed mainly of fine grains, and low pore-water redox, with high nutrient levels. Distinct physico-chemical stages were described using correspondence analysis (CA). CA also showed that temporal stability in physico-chemical characteristics of these marshes generally increased with marsh age.

Spartina alterniflora end of season biomass was greatest in marshes of intermediate age and lowest in very young and old marshes.

Uca spp. composition changed with marsh age: young marshes were inhabited by *U. pugilator* and older marshes by *U. pugnax*. The density of the marsh periwinkle, *Littorina irrorata*, also showed age related changes that were related to *Spartina alterniflora* stem density patterns. Density of the ribbed mussel decreased with age, and the mud snail, *Ilyanassa obsoleta*, was confined solely to the two older marshes of the chronosequence.

Each community was best described by the composition of its snails. Young marshes were characterized by greater periwinkle (*Littorina irrorata*) densities, while older marshes contained more mud snails (*Ilyanassa obsoleta*) than periwinkles. Community inter-annual stability, like physico-chemical stability mentioned above, generally increased with marsh age.

A species-poor ecosystem, these low marshes of the Hog Island chronosequence, underwent succession that tended toward a climax ecosystem or attractor. The important aspects of this process were summarized by the variables on correspondence analysis vector one, entitled 'bio-aeration'. Factor scores of vector one generally proceeded from values associated with low levels of pore-water sulfide, ammonium, redox and high *Uca* spp. density in young marshes to the opposite variable values in 150Y, the mature marsh of the chronosequence. As was the case for physico-chemical stage and biological community, young marsh ecosystems showed much greater inter-annual instability than marshes older than about 21 years.

ACKNOWLEDGMENTS

Graduate degrees are awarded to individuals, but the effort involves a community. I wish to thank but some members of my graduate community.

Firstly, I wish to thank my committee, Bruce Hayden, Dave Smith, and Fred Diehl for their patience, insight, and support over the years. I would like to give special thanks to my advisor Jay Zieman for being as excited as I have been about the Hog Island marsh chronosequence, for the physical, and at times emotional support necessary to complete this work, and for keeping me thinking about the 'big picture'. For funding, I am indebted to the Virginia Coast Reserve of the Long Term Ecological Network, the Willian H. Bannon Foundation, and to my employer, Piedmont Virginia Community College. Thanks go to Randy Carlson, site manager of the VCR and especially to our boat driver, Jimmy Spitler whose rides to and from Hog Island, and logistic help in transporting gear and equipment were greatly appreciated.

Many other UVa Envi Sci faculty helped me in planning and carrying out my work: To the late Bill Odum for his unbounded enthusiasm, and to Linda Blum, Hank Shugart, Aaron Mills, Karen McGlathery, Peter Berg, John Porter, Pat Wiberg, Bob Dolan, and Shao Guofan for advice and counseling.

A grad student's day-to-day teachers in the field and lab are fellow grad students, and I was blessed with a wonderful 'field faculty'. Many thanks to Vaughan Turekian, Ishi Buffam, Trine Christiansen, Dave Richardson, Craig Layman, Eric Bricker, Dave Carleton, Claire Cosgrove, and Todd Dennis.

To my fellow Hog Islanders, I have only warmest memories. Many thanks to my 'field guide' to the south Hog marshes, Dave Osgood, who startled me with the notion that salt marshes 'develop'. To Kindra Loomis, many thanks for the help and enthusiasm in the field. Special thanks to Brian Silliman for sharing his unbounded motivation and enthusiasm for virtually all learning, and for making my field work so much fun. Most of all, I would like to thank my field partner of two seasons, Christy Tyler, a wonderful scientist, friend, and responsive audience to my 'magic tricks'.

Finally, eternal thanks to my family who supported me in my many trips to 'the Shore'. Thanks to my mother-in-law, Beth Tucker, who fed my body with her wonderful cakes, and my soul with her kindness and courage. I wish that my father-in-law, Robbie Tucker, could be here to witness the fruition of my labors. He would be proud. A most special appreciation to my wife, Mary Lee. I am grateful to have had a partner who understood my need to go away to do field work. She has always been an inspiration to live life to the fullest.

I am dedicating this dissertation to the memory of Antoinette Walsh Lord,

a mia madre

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CHAPTER ONE

INTRODUCTION TO SUCCESSION THEORY WITH SPECIAL REFERENCE TO COASTAL SALT MARSHES

1. Introduction to succession theory with special reference to coastal marshes

1.1 General succession theory

Although the term 'succession' was first used in 1806 by DeLuc (cited by Clements, 1916) to describe hydroseres in Germany, research into ecological succession is largely a 20th century enterprise, and one that has been dominated by ideas generated from terrestrial ecosystems, not wetlands.

The work of Cowles and especially Clements earlier this century laid the foundation for a theory of succession and provided ammunition for the controversy that would follow. Cowles (1899) studied the dynamics of sand dune communities at the southern end of Lake Michigan. He found that long-term trends were controlled mainly by large-scale climatic events that drastically altered dunes, but that community dynamics in the time between these events was auto-regulated by the biota. The Clementsian model (Clements, 1916) describes succession as an autogenic process during which each plant community, or seral stage, alters the local environment so that it is less harsh and more favorable to the next seral stage, but unfavorable to itself; Clements called this process 'facilitation'. Seral stages also pass through a predictable series (a sere) that terminates in a 'climax community'. The analogue that Clements envisioned for ecological succession was that of organismal growth and maturity to an adult stage (Clements, 1916). Gleason (1917) immediately took issue with Clements' symbolism. In his view, ecosystems do not show 'juvenile to adult' developmental tendencies. Rather succession depends on the sum of interactions between individual plants with the environment and each other. Gleason broadened the spectrum of allowable developmental paths to include successional reversals. He weakened Clements' notion of a fixed final stage of succession, calling it instead a 'tentative climax'.

Important enhancements in successional theory arose from mid-20th century efforts that were a reaction to the inflexibility of the Clements (1916) model. Clements (1936) himself was forced to concede that ecosystem development was not as predictable as he had once proposed. His reaction to criticism, however, was to obscure the notion of multiple climaxes with jargon. 'Sub-climax', 'pre-climax', and 'dis-climax' were all born from Clements' efforts to reconcile the reality of poly-climaxes with his original mono-climax theory. Whittaker (1953) recognized that climax communities were highly site-specific, and that many paths (seres) could lead to the same climax community, as well as different climaxes emerging from the same sere. Whittaker's climax was a system characterized by a steady-state with a self-maintaining population, a high level of complexity and species diversity, and maximum sustained utilization of environmental resources. He also included successional reversals in his model, calling these, 'deflected development' (Whittaker, 1953). One of the most provocative papers of this century on ecosystem development was the 1969 work of E.P. Odum entitled, 'The Strategy of Ecosystem Development', wherein he defined ecological succession as:

> 'an orderly process of community development, that is reasonably directional, and therefore, predictable. It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go.'

He goes on to suggest that the process culminates in a stable ecosystem, one which has come to be called the 'climax community'. To Odum, the major goal of succession is increased system homeostasis, that is maximal protection from environmental disturbance. In the process of becoming better buffered from the environment, ecosystems travel through a predictable series of changes that demonstrate increased organic matter storage, species diversity, spatial heterogeneity, stability, and nutrient conservation. Like Odum (1969), Vitousek and Reiners (1975) predicted that mature ecosystems are better able to sequester nutrients than younger ones. Connell and Slatyer (1977) represented the first major departure from facilitation as the only successional mechanism. Their facilitation was termed a Type I model of succession. The Type II model, their 'tolerance' model, proposed that a successional sere constitutes a predictable sequence of plant species based on different resource utilization patterns of individual species. Their 'inhibition' model (Type III) predicted that early colonizers garner all the space in a system and are displaced only if disturbance events provide gaps in which pioneer species could be replaced.

More recent efforts to unify successional theories only stress the divergence of views that 'seem to spring largely from an unachievable search for an ecological Shangri-La' (Miles, 1987). Bormann and Likens (1979), adhering to Margalef's dictum that 'biomass is the keeper of organization' (Margalef, 1968), focused on biomass changes during forest succession at Hubbard Brook Valley in the White Mountains of New Hampshire. They discovered a three-stage process of re-growth after clear-cutting within a second-growth northern hardwood forest. Biomass accumulates during the first or 'aggradation' phase, decreases slightly during the 'transition' phase, and finally fluctuates about a somewhat lower mean value during the 'steady state' phase. During this final phase, species composition and relative importance of species remain constant. In his 'resource-ratio hypothesis', Tilman (1985 and 1988) describes succession as a response of plant communities to a combination of increasing soil nutrients and decreasing light availability over time. Succession therefore involves a progression of plant strategies ranging from efficient nutrient sequestration in the early stages to greater light efficiency with ecosystem age. His model also allows for seral reversion and multiple climaxes (steady states). Most models have emphasized a steady state climax that maximizes stability and species diversity. Kaufman (1993 and 1995), however, proposed a climax model that maximizes the flexibility of ecosystems in the face of disturbance. Using Boolean networks of two variables, species number and degree of species interconnectedness, he found that computer models progress to a 'self-organized critical state' that is on the edge between predictable structure and unpredictability (chaos). At this position, ecosystems have the maximum number of achievable options in the face of disturbance. However, this flexibility comes at a price. Population dynamics at this critical state (a climax community) are described mathematically by power laws, meaning that the level of response to a disturbance has no relation to the magnitude of the disturbing force. That is, responses are non-linear, and even small scale disturbances can alter species composition significantly. The 'ecosystem as organism' view that Clements (1916) created has survived in the work of Aoki (1995) who estimated the changes in entropy in two lakes, one oligotrophic (Lake Biwa in Japan) and one eutrophic (Lake Mendota in Wisconsin, USA). Since lakes typically develop from oligotrophic to eutrophic over time, Aoki used these two situations as end-points of a developmental continuum. Aoki concluded that entropy production rises during the early phase, levels off in the intermediate phase (an assumption, since he had no intermediate aged lake), and then drops during the later phase of ecosystem development. He found a similar pattern of entropy changes in the human life span from fertilization to death, and concluded, like Clements (1916) that organismal development is a worthy model for ecosystem development.

1.2 Application of succession theory to coastal salt marshes

Theories about successional processes in coastal salt marshes have lagged behind those developed for terrestrial ecosystems. One reason for this discrepancy is historical. Clements himself (1936) classified coastal wetlands as 'serclimaxes', ephemeral pre-climax stages that are prevented from reaching maturity, the climax community, by frequent environmental disturbance. While it is true that coastal marshes, especially over-wash marshes, experience 'clock-resetting' disturbances of sometimes ferocious intensities, these marshes persist for thousands of years, and are, in ecological time, permanent features. Tansley (1941) agreed:

> It is true that I have never found evidence in the British Isles that salt marsh passes normally into 'land vegetation', but it is a perfectly legitimate and indeed inevitable inference that, if fresh water replaces salt water, fresh-water marsh or reed swamp will supervene, and that if the surface of the land rises above the ground water-level, terrestrial vegetation, culminating in the climatic climax, will be initiated....Meanwhile, salt-marsh vegetation *does* represent a climax 'in the conditions under which it exists'.

A second reason for this lack of successional theory in salt marshes is the monocultural nature of what I refer to as the low marsh, the region of a marsh nearest the water and dominated by *Spartina alterniflora*. Because succession has been described in almost all environments on the basis of changes in plant communities, how does one describe succession of a one-species plant community? Obviously, zoological and physico-chemical factors must be included in the description of low marsh seral stages, and this is relatively unfamiliar territory for botanists. A third reason is the understandable view that coastal and island systems are wholly at the mercy of allogenic forces, such as storms. While it is true that storms, especially 'north-easters' along the north

Atlantic coast can completely inundate back-barrier island marshes under meters of sand, evidence is accumulating that autogenic forces are important in structuring salt marshes between these catastrophic events. For instance, works by Bertness implicate ribbed mussels (Bertness, 1984) and fiddler crabs (Bertness, 1985) as important agents in determining *Spartina alterniflora* production in the low marsh. Finally, few salt marsh chronosequences whose marshes can be reliably aged, have been discovered in coastal areas where human influence has not also altered the landscape.

Despite the prejudices that have slanted successional research toward terrestrial systems, there are valid reasons for thinking that succession proceeds differently in coastal marshes than in forests and old fields. Tidal pulsing has no terrestrial counterpart; this subsidy (Odum, 1979) may alter the appearance of intertidal community succession. Secondly, coastal marshes exist in sediments that are low in oxygen and high in toxic compounds (Pomeroy and Wiegert,1981). The process of coastal marsh succession might therefore reflect strategies that minimize the effects of these compounds, rather than maximize nutrient uptake and light availability, strategies common to terrestrial plant communities (Tilman, 1985). Moreover, salinity stress, which is common in temperate to tropical intertidal ecosystems (Davy and Costa, 1992), demands osmotic energy ouptuts that are not demanded of most terrestrial plants.

The initial steps in salt marsh conversion, that is, the transition from mud or sand flat to marsh, has been described by a few authors. Davis (1910) compared the two leading marsh developmental types of his day. A 'Mudge-Davis' marsh is one that transgresses toward the upland due to a rising sea level and an accumulation of peat from high marsh plants. A 'Shaler' marsh accumulates sediment as *Spartina alterniflora* invades a mud flat and thereby induces deposition. 'Shaler' marshes build from low marsh to high marsh as accretion slowly raises the sediment surface. Once mean high water is reached, *Spartina alterniflora* is out-competed by other macrophytes and a different plant community begins - the high marsh. At the same time, a 'Shaler' marsh expands sea-ward, following the colonization trail of *Spartina alterniflora* as it also elevates sediment platform in that direction. Brookes-Knight (1934) realized that the two marsh types might be age-related. He proposed that young marshes are 'Shaler' type, that expand in all directions possessing a raised platform, usually resulting from *Spartina alterniflora* growth. Older marshes are 'Mudge-Davis' types that build up from 'Shaler' marshes, and extend their range upland, with the aid of rising sea level. Redfield's 1972 classic paper on marsh development in Barnstable Harbor, Massachusetts, took a combined 'Shaler-Mudge' approach. He observed predictable stages in development that began with colonization of mud flats by *Spartina alterniflora*, then proceeded through a panne marsh stage characterized by local bare areas. The next stage, the slough marsh stage looked somewhat like the previous stage, except for ridge formation around pannes. Finally, the slough marsh became elevated by local accretion to mean high water, where the high marsh now developed. Developmental time for a *Spartina* *alterniflora* marsh took only 5 years from mud flat colonization. Frey and Basan (1978) provided detailed predictions of changes to be expected during marsh succession. Because young marshes develop from colonized mud flats (sensu Shaler), they show a larger area of low marsh than high marsh. Plant zonation is simple, drainage is well developed, and sedimentation is rapid. A mature marsh has equal areas of low and high marsh, and *Spartina alterniflora* has formed into three height zones. Drainage is described as good, and deposition is slower than in young marshes. Old marshes have a majority of area in high marsh, a reduced area of tall form *Spartina alterniflora* in the low marsh, tidal channels are filled, and deposition is very slow.

Two works emphasize differences in patterns of marsh development based on marsh geomorphology. Orson and Howes (1992) studied cores from Waquoit Bay, Massachusetts, and concluded that marshes that are open to estuaries show a relatively slow, gradual change in plant communities. Moreover, competition is important in determining plant community structure. In marshes that are somewhat closed to the adjacent estuary, succession is rapid, punctuated, and driven by physical forces that affect hydrology and pore-water salinity. Using aerial photographs and topographic maps, DeLeeuw et. al. (1993) showed that current marsh topography is dictated by sediment accretion (a la Shaler) in estuarine marshes, but by the buried antecedent over-wash sand surface in island marshes.

It might seem that succession in multi-species marsh plant communities (usually in the high marsh) should be predictable, since environmental gradients in these marshes are so steep and zonation, is therefore, well-defined. Walker has suggested otherwise:

> In a system which has often been considered one of the most unvarying in plant ecology, the variety of courses actually taken is remarkable and demands that, even in situations free from allochthonous influences, predictions be made only in terms of probability (Walker, 1970).

Using permanent plots for 30 years, Roozen and Westhoff (1985) described four different successional outcomes for marshes in the Netherlands. Plant communities at higher elevations showed a more pronounced tendency toward poly-climax outcomes than did low marsh communities. Beeftink (1979), who studied different Netherlands marshes for about 15 years, came to conclude that the same climax can be achieved through a variety of seres. Through pollen analysis, radiometric procedures, and macrofossil techniques, Clark and Patterson (1985) traced 1000 years of marsh history for a Long Island salt marsh. Their record shows a series of discontinuous plant communities with little gradation between them.

Does biology play a role in succession of multi-plant salt marsh communities? Working in a Rhode Island marsh, Shumway and Bertness (1994) have found evidence for plant cooperation in the colonization of small bare patches (secondary succession), and plant competition in the colonization of large patches. Davy and Costa (1992) reviewed work done mainly in Latin American salt marshes, and concluded that biological forces are important in development in benign areas - high marsh and older marshes. Physical forces dominate in areas of higher plant stress, that is, at lower elevations and in young marshes.

Because the low marsh is monospecific, a complete description of low marsh succession must transcend plant community variables (because these are invariant with time) and include physico-chemical factors. Using this approach, several authors have verified some of Odum's strategies for ecosystem development (Odum, 1969). Childers, et al. (1993) monitored nutrient fluxes to and from three South Carolina marshes along a spatial gradient in geologic age. Only relative ages were known for these marshes. The young marsh imported most nutrient species, and exported organic and total suspended solids, while the older marsh exported ammonium, dissolved organic carbon, and some suspended solids, both organic and total. Dame and Gardner (1993), working at North Inlet, South Carolina found similarly that their young marsh was a net nutrient importer from the adjacent estuary and the older marsh a nutrient exporter. Osgood, Santos and Zieman (1995) described an exception to this age-related pattern of nutrient flux. The Virginia barrier island sand flat that they studied registered a higher level of nutrient standing stock than a nearby 14-16 year old island salt marsh. The sand flat was underlain by a buried mud flat that may have been the source of upwelling nutrients that confounded the picture.

Osgood and Zieman (1993) described differences in pore-water physico-chemical variables in two sets of mid-Atlantic *Spartina alterniflora* back-barrier marshes of different ages: young marshes were 10-13 years old, and the older marshes were known to be more than 100 years old. Sediment showed an accumulation of organic matter and small grained particles (silt and clay) with age. Pore-water trends with age included increasing ammonium and phosphate stocks, and decreasing oxidation-reduction potential. In addition, they estimated that it takes 10-13 years for pore-water chemistry to reach values associated with a mature marsh.

Table 1.1 presents a summary of succession research presented in this section.

TABLE 1. 1 Summary of succession research mentioned in the introduction.

Authors	Ecosystem type	Age-related characteristics		Other aspects of succession
		young system	mature system	
Clements (1916)	theoretical	harsh conditions	benign climax	1. predictable 2. monoclimax expected
Whittaker (1953)	theoretical	low species diversity, complexity	high species diversity, complexity	1. site-specific climax 2. seral reversals
Odum (1969)	theoretical	1. allogenic forces important	1. autogenic forces important	predictable sequence of seral stages
Vitousek and Reiners (1975)		2. system a nutrient importer	2. system a nutrient exporter	
Connell and Slatyer (1977)	theoretical			1. Type I succession: facilitation 2. Type II succession: tolerance 3. Type III succession: inhibition
Bormann and Likens (1979)	northern hardwood forest	1. low biomass 2. rapid species turnover	1. peak biomass at intermediate age, then falling to steady state 2. stable species composition	
Tilman (1985)	theoretical	N-limited system	light-limited system	reversal of seral stages and polyclimaxes

Table 1.1 cont'd

Authors	Ecosystem type	Age-related characteristics		Other aspects of succession
		young system	mature system	
Kaufman (1993)	theoretical		system goes to self-organized critical state	seres unpredictable
Davis (1910)	salt marsh in general	low elevation	higher elevation	*Spartina alterniflora* traps sediment, raising marsh surface
Brookes-Knight (1934)	salt marsh in general	'Shaler' marsh (extension by accretion)	'Mudge-Davis' marsh (extension upland)	succession an auto-ecological process of sediment trapping
Redfield (1972)	salt marsh in general	bare areas predominate	*Spartina alterniflora* spread uniformly	1. predictable stages 2. 5 yr to maturity
Frey and Basan (1978)	salt marsh in general	1. large low marsh 2. high drainage 3. rapid sediment 4. simple zonation	1. large high marsh 2. low drainage 3. slow sediment 4. complex zonation	
Roozen and Westhoff (1985)	multi-species salt marsh			increased tendency toward polyclimax at higher elevations
Beeftink (1979)	salt marsh			different seres, same climax

Table 1.1 continued

Authors	Ecosystem type	Age-related characteristics		Other aspects of succession
		young system	mature system	
Clark and Patterson (1985)	multi-species salt marsh			seral stages discontinuous, unpredictable
Davy and Costa (1992)	multi-species salt marsh	allogenic forces important	autogenic forces important	1. increasing autogenic importance with elevation 2. reduced allogenic importance with elevation
Childers, et. al. (1993) Dame and Gardner (1993)	*Spartina alterniflora* marsh	system a nutrient importer	system a nutrient exporter	
Osgood and Zieman (1993)	*Spartina alterniflora* marsh	1. low sediment organic content 2. high sediment sand content 3. low pore-water nutrients	1. high sediment organic content 2. high sediment sand content 3. high pore-water nutrients	takes 10-13 yrs for pore-water to develop

1.3 Significance

1.3.1 Theories of over-wash marsh succession

Is the Clementsian model adequate in describing succession in highly disturbed systems such as over-wash marshes (Figure 1.1)? Note the linear path to the climax community, and the greater tendency at all seral stages to 'advance' toward the climax rather than to 'revert' to earlier stages. Although each seral stage has a particular tendency toward self-maintenance (that accounts for the longevity of that stage), the system marches inexorably toward the climax community. This model is perhaps more representative of terrestrial ecosystems such as forests that experience physical disturbances much less frequently than highly dynamic coastal systems (Hayden, et al., 1991). Low disturbance frequency allows the forest sufficient time to develop in a somewhat predictable pattern, although even this predictability is mythical (H.H. Shugart, personal communication).

Perhaps a more realistic view of over-wash marsh succession is shown in Figure 1.2. Over-wash events, which are common occurrences on barrier islands (Godfrey and Godfrey, 1976) are creators, destroyers, and spreaders of back-barrier marshes. The sand supplied by an over-wash event acts as the platform on which an emerging salt marsh is built, and existing marshes spread by the same mechanism (Godfrey and Godfrey, 1976). Moreover, existing marshes are probably 'detoxified' by the cleansing action of over-wash storms (J. Zieman,

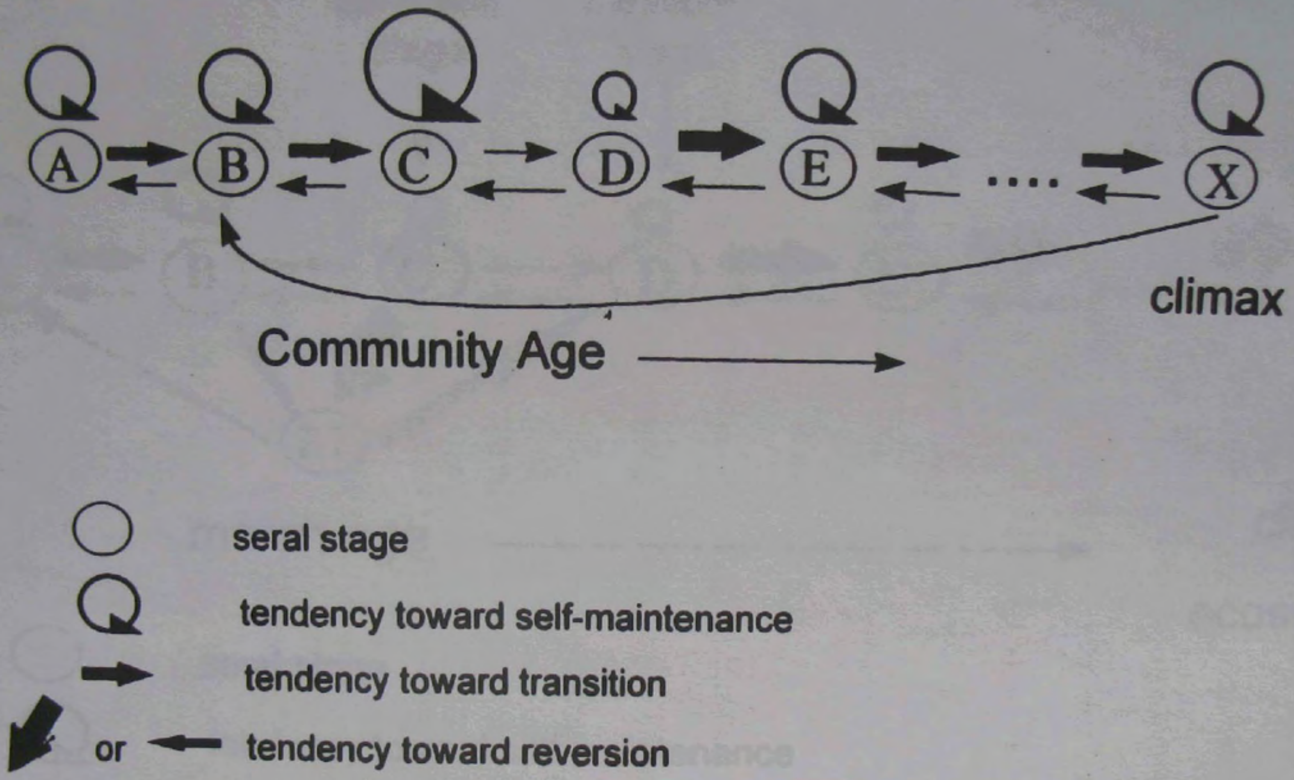


Figure 1. 1 Clementsian succession.

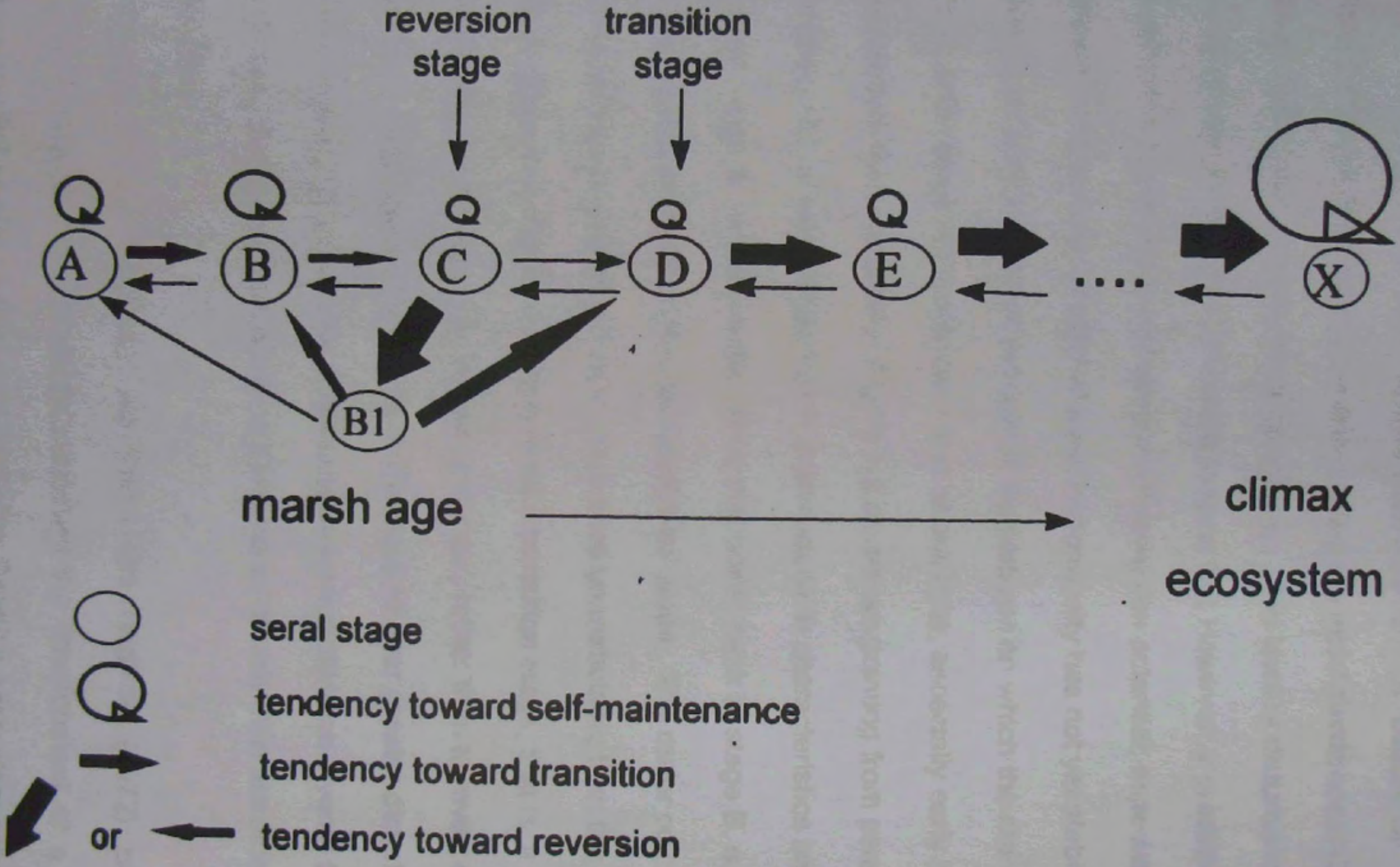


Figure 1. 2 Succession in highly disturbed ecosystems. The developmental trajectories are more numerous in this model than in Clements' because of the greater potential for disturbance that alters successional pathways.

personal communication). Severe over-wash storms, caused by hurricanes, or more likely by north-easters along the mid-Atlantic coast (Dolan and Davis, 1992), can bury marshes completely. This level of disturbance causes complete reversion of the marsh to sand flat. However, a gradation of over-wash severity results in a continuum of reversion potential, especially in the early stages of development when the plant community has not yet stabilized the sediment sufficiently to prevent erosion of the platform on which the marsh exists. Therefore, seral stage reversion can occur at any time, especially early in a sere. Such reversions are portrayed in Figure 1.2 as arrows pointing from seral stage C to either stage B1, a seral stage that is intermediate in characteristics between stage B and stage C, or the smaller arrow that points back to stage B, suggesting a complete reversion backward in developmental stage. The major point is that an over-wash marsh sequence looks much more unpredictable than the terrestrial one. Seral stage D in Figure 1.2 represents a transition stage, that is, a seral stage whose tendency is to jump toward a 'climax', rather than to revert or even maintain itself. Reversion beyond this stage requires ever greater disturbance intensities. Figure 1.2 also implies that seral stage variety is an inverse function of age. Young marshes of the same age are more variable than are older, same-aged marshes.

Over-wash marshes may not follow the Redfield (1972) pattern of development (Figure 1.3). Redfield observed the development of a lagoonal marsh system that emerged from mud flats after *Spartina alterniflora* colonization

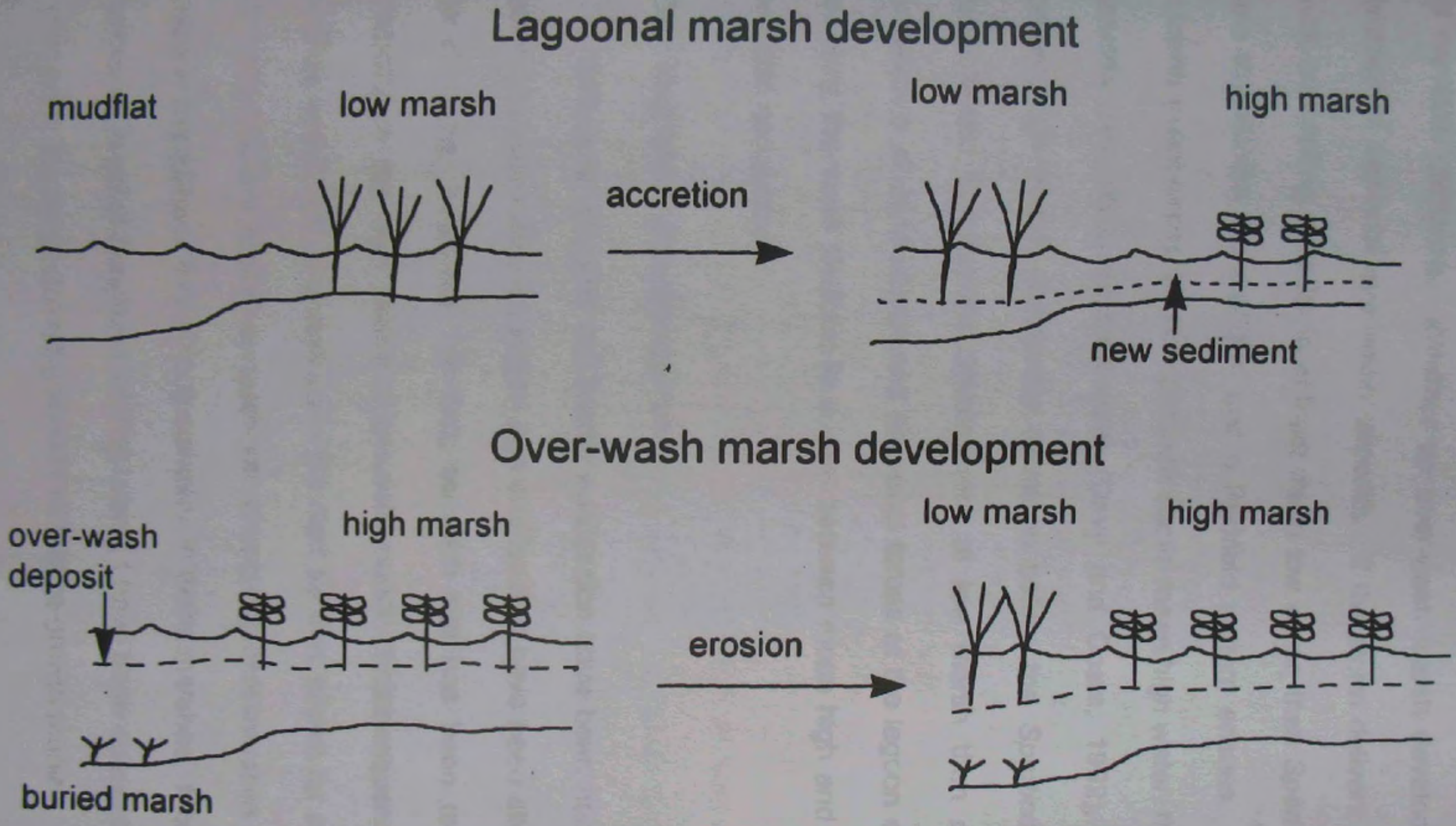


Figure 1. 3 Theory of over-wash marsh development.

of elevated platforms. Whether an over-wash marsh develops this way is a function of depth of over-wash deposits. If the storm delivers enough sand to raise an existing mud flat to at least mean low water, then *Spartina alterniflora* is able to colonize the platform and a Redfield pattern ensues. If, however, an extreme event raises the new platform above mean high water, the upper limits of *Spartina alterniflora* establishment (Davy and Costa, 1992), then the multi-species high marsh community develops before the *Spartina alterniflora* low marsh does. Subsequent development of low marsh then depends on the combination of depositional and erosional forces at the lagoon end of the marsh that bring the sand platform to a level between mean high and mean low water (personal conclusion)

1.3.2 Hog Island chronosequence

Efforts to describe salt marsh succession have been hampered partly by inadequate information on marsh age at sites that have been allowed to develop free of human influence. In fact, no such site has been reported until the discovery of the Hog Island over-wash marsh chronosequence. This unique situation, which will be described in the next section, allows for a 'space for time' substitution where spatial comparisons among adjacent marshes translates into a temporal description, that is, to succession in these marshes. Moreover, by using a series of aerial photographs of Hog Island, I have been able determine to within a few years, the absolute ages of each strip of re-growth marsh.

1.3.3 A multivariate approach to successional state change

Efforts to describe salt marsh succession either have used univariate statistical methods applied to both biological and physical variables, or multivariate methods applied to plant community data only. What has been needed is a broader approach where multivariate analyses are applied to a set of physico-chemical and biological variables from the same marshes. The most significant combinations of all variables measured then constitute sets of new 'latent variables' or vectors (called axes using correspondence analysis, or CA, in this study). Having defined a successional 'stage' or seral stage using these vectors, the actual number of such stages in a chronosequence can be determined statistically. Then the rate and direction of stage change, among other things can be estimated. In this study, I define a physico-chemical stage, or PC-stage, as a subset of chronosequence marshes that has a significantly different mean factor score than another subset of these marshes. I consider the PC-stage to be a seral stage (minus the weight of biological variables that operate in that seral stage). Thus, adding biological vectors to the physico-chemical vectors determined in this chapter will constitute a more complete description of a seral stage. Biological vectors will be added in Chapter 3, a separate CA will be run on those variables alone (which will be used to define a biological stage or community), and then a final CA will be run on the entire data set in Chapter 4, and seral stage will be defined and analyzed.

1.3.4 Man-made marshes

This study has important consequences for the intentional creation and maintenance of salt marshes on over-wash deposits. Within planted marshes, macrophytes are planted or set as seed (Seneca, et al, 1976) at requisite elevations along the gradient, spaced appropriately (Broome, et al, 1986) then left to natural processes. Although some planted *S. alterniflora* marshes look typical, they lack normal marsh fauna (Cammen, 1976 and Zedler, 1988), and therefore are not functioning, and perhaps are not models of naturally developing salt marshes. Understanding what combinations of physico-chemical and biological variables drive salt marsh succession from stage to stage is of obvious utility, and would be a major contribution of this work.

1.4 Objectives

1. *To describe the successional changes in low marsh plant and epifaunal invertebrate communities within over-wash marshes of five different ages.*

2. *To describe the successional changes in low marsh pore-water physico-chemical variables within ovewash marshes of five different ages.*

3. *To determine approximate time to maturity for each variable in objectives 1. and 2.*

4. *To compare the patterns of biological and physico-chemical succession in each of the three Spartina alterniflora height zones (tall, medium, and short) of the low marsh.*

5. *To determine the relative importance of biological and physico-chemical factors in driving low marsh succession.*

6. *To define low marsh seral stagse using correspondence analysis, and to determine the rate of seral stage changes during succession in each of the three Spartina alterniflora height zones.*

1.5 Organization

In Chapter One, I briefly outlined the historical views of ecosystem succession in general, and the application of traditional succession theory to over-wash salt marshes. I suggested ways in which such marshes may differ in their successional patterns from terrestrial systems and briefly introduced the unique opportunity that the Hog Island marsh chronosequence presents. I also described the type of statistical analysis that will allow me to define seral stage, and briefly discussed the usefulness of the information from this work to man-made marshes.

Chapter Two is a more detailed introduction to the Hog Island chronosequence via its recent history as chronicled by aerial photographs. I also introduce my data collection scheme, and describe the results of two field season's data on substrate physico-chemical comparisons among the five different aged marshes along the chronosequence. General variable trends and relative time to maturity (using the 150+ yr old mature marsh of the chronosequenceas a reference) for each variable is reported for each of the three *Spartina alterniflora* height zones and compared to literature values. Multivariate analysis is performed on these physico-chemical data in order to reduce the variable set to a few important variables that describe physico-chemical seral stage. Biological variables are not considered in this chapter, hence it is an attempt to describe overwash marsh succession in physical terms only.

Chapter Three describes biological comparisons among the five marshes along the chronosequence. *Spartina alterniflora* variables compared include plant stem densities, plant heights, flowering percent, and end of season biomass using data collected over two field seasons. The density, areal biomass, and individual biomass of the following epifaunal macro-invertebrate species are also reported in this chapter: *Uca* spp., *Littorina irrorata, Ilyanassa obsoleta*, and *Geukensia demissa*. Factors that structure this invertebrate community are discussed, as are developmental trends in species composition and relative species contributions to community biomass. Multivariate analysis is applied to these data to define biological stage in the absence of the physical variables analyzed in Chapter Two. In addition, the temporal patterns of biological trends noted in this Chapter are compared with temporal trends of physical variables described in Chapter Two.

Chapter Four explores a multivariate approach to describing ecosystem scale succession in the low marshes of the Hog Island chronosequence. Correspondence analysis (CA) is used to reduce the combined physical and biological data that I have collected over two field seasons to those combinations of variables that explain the maximum amount of the variation in the data. I use this technique to define seral stage and determine the number of stages that exist among the five different aged marshes that I studied. Having defined seral stage, I then use CA factor scores to describe the directions of seral stage change in low marsh succession along this marsh age series, as well as successional rate. The relative importance of physical and biological factors in determining patterns of succession is inferred by comparing the amount of data variation that is explained by each variable. Finally, patterns of succession are compared for each *Spartina alterniflora* height zone, and the emerging patterns are discussed in light of traditional succession theory and the theory of over-wash marsh succession that I proposed in Chapter One.

CHAPTER TWO

LOW MARSH SEDIMENT AND PORE-WATER CHANGES ALONG AN OVER-WASH SALT MARSH CHRONOSEQUENCE

2. Low marsh physico-chemical succession along an over-wash salt marsh chronosequence

2.1 *Introduction*

Although ideas regarding ecological succession originated in the late 19th and early 20th centuries (Cowles, 1899 and Clements, 1916, 1936), application of these concepts to coastal marshes has had to await a shift in our view of these ecosystems. But for the rare admission of their permanence:

> '.... Salt marsh vegetation *does* represent a climax (community) in the conditions under which it exists....' (Tansley, 1941, his emphasis),

salt marshes have been considered ephemeral systems, simply seral stages in the process of becoming a true terrestrial climax community. Compounding this reluctance to apply succession theory to salt marshes is the monocultural nature of mid-Atlantic low marshes, an area that consists exclusively of *Spartina alterniflora*. Traditional descriptions of succession have been based on changes in plant communities over time. Indeed, the very names of seral stages originate from the dominant plants of that stage. Does succession or a process similar to it occur in monocultural plant communities?

Another argument for supporting the traditional view that succession is inapplicable to salt marshes is the understandable view that coastal intertidal systems are primarily at the mercy of allogenic forces, such as storms. While it is true that 'north-easters' along the north Atlantic coast can, for instance, completely inundate back-barrier island marshes under meters of sand (Fitch, 1991), evidence is accumulating that autogenic forces are also important in structuring salt marshes in the intervals between these infrequent catastrophic events. For instance, work by Bertness implicates ribbed mussels (Bertness, 1984) and fiddler crabs (Bertness, 1985) as important agents in determining *Spartina alterniflora* production in the low marsh. Finally, no salt marsh chronosequences whose marshes could be aged accurately, have been reported in coastal areas that are relatively free of anthropogenic disturbance.

There are valid reasons to think that succession proceeds differently in coastal marshes than in forests and old fields. For instance, the chemical and biological subsidy that accompanies tidal pulsing to coastal wetlands has no terrestrial counterpart (Odum, 1979). Secondly, coastal marshes exist in sediments that are low in oxygen and high in toxic compounds (Pomeroy and Wiegert,1981). The process of coastal marsh succession might therefore reflect plant strategies that minimize the effects of increasing substrate hypoxia and toxicity with age, rather than maximize nutrient uptake and light availability, strategies that are common to succession in terrestrial plant communities (Tilman, 1985). Moreover, salinity stress, which is characteristic of temperate to tropical intertidal ecosystems (Davy and Costa, 1992), demands osmotic-related energy outputs that are not required of most terrestrial plants. The demands of such a harsh environment on the plant community reduces the energy available for reproduction and expansion of the community, and may limit the range of available developmental pathways.

Several authors have reported predictable age-related changes in substrate variables in *Spartina alterniflora* marshes. Childers, et al. (1993) monitored nutrient fluxes to and from three South Carolina marshes along a spatial gradient of geologic age. Only relative ages were known for these marshes. The young marsh imported most nutrient species, and exported organic and total suspended solids, while the older marsh exported ammonium, dissolved organic carbon, and some suspended solids, both organic and total. Dame and Gardner (1993), working at North Inlet, South Carolina found similarly that their young marsh was a net nutrient importer from the adjacent estuary and the older marsh a nutrient exporter. Osgood, Santos and Zieman (1995) described an interesting exception to this age-related pattern of nutrient flux. The Virginia barrier island sand flat that they studied registered a higher level of nutrient standing stock than a nearby 14-16 year old island salt marsh. However, the sand flat was underlain by a mud flat that was the hypothesized source of upwelling nutrients that confounded the predicted pattern . Osgood and Zieman (1993) described differences in pore-water physico-chemical variables in mid-Atlantic *Spartina alterniflora* back-barrier marshes of different ages: young marshes were 10-13 years old, and the older marshes were probably more than 100 years old. Sediment showed an accumulation of organic matter and finer grained particles (silt and clay) with age. Pore-water trends with age included increasing ammonium and phosphate stocks, and decreasing oxidation-reduction potential. In addition, they estimated that it takes 10-13 years for pore-water chemistry to reach values associated with a mature marsh. Tyler (1997) likewise found increases in finer sediment particles and organic matter, as well as pore-water nutrients, and sulfide along creek-banks within marshes of varying age.

In this study, I describe a back-barrier over-wash marsh chronosequence on Hog Island, Virginia and illustrate the vegetative history of these fringing marshes since 1962. I then report the results from sediment and pore-water data collected between 1995-1996 within marshes of five different ages along this chronosequence. Results are discussed especially in light of the work of Osgood and Zieman in end-member marshes (young vs. old) along this chronosequence and at nearby back-barrier and lagoonal marshes (Osgood and Zieman,1993 and 1993a, and Osgood, Santos, and Zieman, 1995), as well as Tyler (1997) whose work included physico-chemical measurements taken at creek-banks along the Hog Island chronosequence marshes. The results discussed herein constitute an important supplement to their work by supplying details of over-wash marsh succession in the very early and intermediate stages of development, and by considering pore-water and sediment development for each of the three *Spartina alterniflora* height zones that constitute these low marshes.

In addition, most efforts to describe salt marsh succession have either used univariate statistical methods applied to both biological and physical variables, or multivariate methods applied to biological community data only.

Because of the monocultural nature of the low marsh, what is needed is a broader approach where multivariate analyses are applied to a set of physico-chemical and biological variables from the same marshes. The most significant combinations of all variables measured then constitute sets of new 'meta-variables' or vectors. Correspondence analysis (CA) is the multivariate method I will use, and the 'meta-variables' or vectors are called axes. Having defined each seral stage using these vectors, the actual number of seral stages in a chronosequence can be determined statistically, and direction of seral stage change, among other things, can be estimated. In this Chapter, I define a physico-chemical stage or, or PC-stage, as a subset of chronosequence marshes that has a significantly different mean CA factor score than another subset of chronosequence marshes. I consider the PC-state to be a seral stage, minus the influence of biological variables that operate in that stage. Thus, adding biological vectors to the physico-chemical vectors determined in this chapter would constitute a more complete description of a seral stage. Biological vectors will be added in the next chapter. Subsequently, a separate CA will be run on those variables alone, which will be used to define a biological stage (community). A final CA will be run on the entire data set in Chapter 4, and seral stages of this chronosequence will be defined and their evolution characterized.

2.2 Methods

2.2.1 Study site

This work was carried out on Hog Island of the Virginia Coast Reserve of the Long Term Ecological Research network. Hog Island is a mid-Atlantic barrier island located approximately 10 km from the Eastern Shore of Virginia (Figure 2.1). Barrier islands are highly dynamic landscapes whose surfaces are frequently re-worked by storms (Hayden, et. al., 1991). Back-barrier marshes, especially over-wash marshes that form along over-wash fans of past storms are vulnerable to subsequent storm activity. Such marshes are often affected by over-wash transport of sand and water during north-easters until the island grows sufficiently wide to protect these marshes.

Back-barrier marshes of Hog Island are of two types. The marshes of the northern portion of the island are older and wider, and well protected by forest development from northeast storms; these are referred to as back-barrier lagoonal marshes, since these marshes have extended into Hog Island Bay, and probably spread over lagoonal, not over-wash sediments. Because maps of this region from 1853 show existing mature salt marshes, I have estimated the age of these marshes conservatively at 150+ years. It is likely that they are much older than that. The southern third of the island is over-wash plain whose marshes are narrower in width (fringing marshes) and vulnerable to severe north-easters. The Ash Wednesday north-easter of March 5, 1962, buried part of the existing mature marsh under 1.5 m of sand (Fitch, 1991), and transported enough sand south of this over-wash fan to extend the southern tip of the island approximately one km and raise the existing mud flats in Hog Island Bay to within marsh-growing elevation. Using a series of aerial photographs that begin in 1974, I have documented the re-growth of the mature unburied marsh southward, and the spectacular expansion of new marsh from the southern end of the island northward (Figure 2.2 and Figure 2.3). I have also determined the ages of five different marshes along this chronosequence. Figures 2.2 and 2.3 show the placement of the 1 yr marsh or plot (hereafter designated as 1Y), the 6 yr marsh (6Y), the 13 yr marsh (13Y), the 21 yr marsh (21Y), and the 150+ yr marsh (150Y) that was not buried in the 1962 storm. These ages were assigned by the year that a particular section of marsh first appeared on an aerial photograph. It is important to note that the actual ages of these marshes are dependent on the time interval between aerial photos that were used. For instance, 13Y is actually between 7 years and 13 years old. Throughout this study, however, I refer to each marsh by the maximum age possible for that marsh as determined by aerial photograph interval, and relative to the year 1995. This fact becomes most important in considering marsh 150Y which was actually anywhere between 22 years old and 150 years old in 1995. Although marsh growth can result in a mosaic of overlapping ages in one area, this pattern occurred only at the southern tip of Hog Island, not in the region in which I worked. Aerial photographs show a continuous and linear growth pattern from south to north,

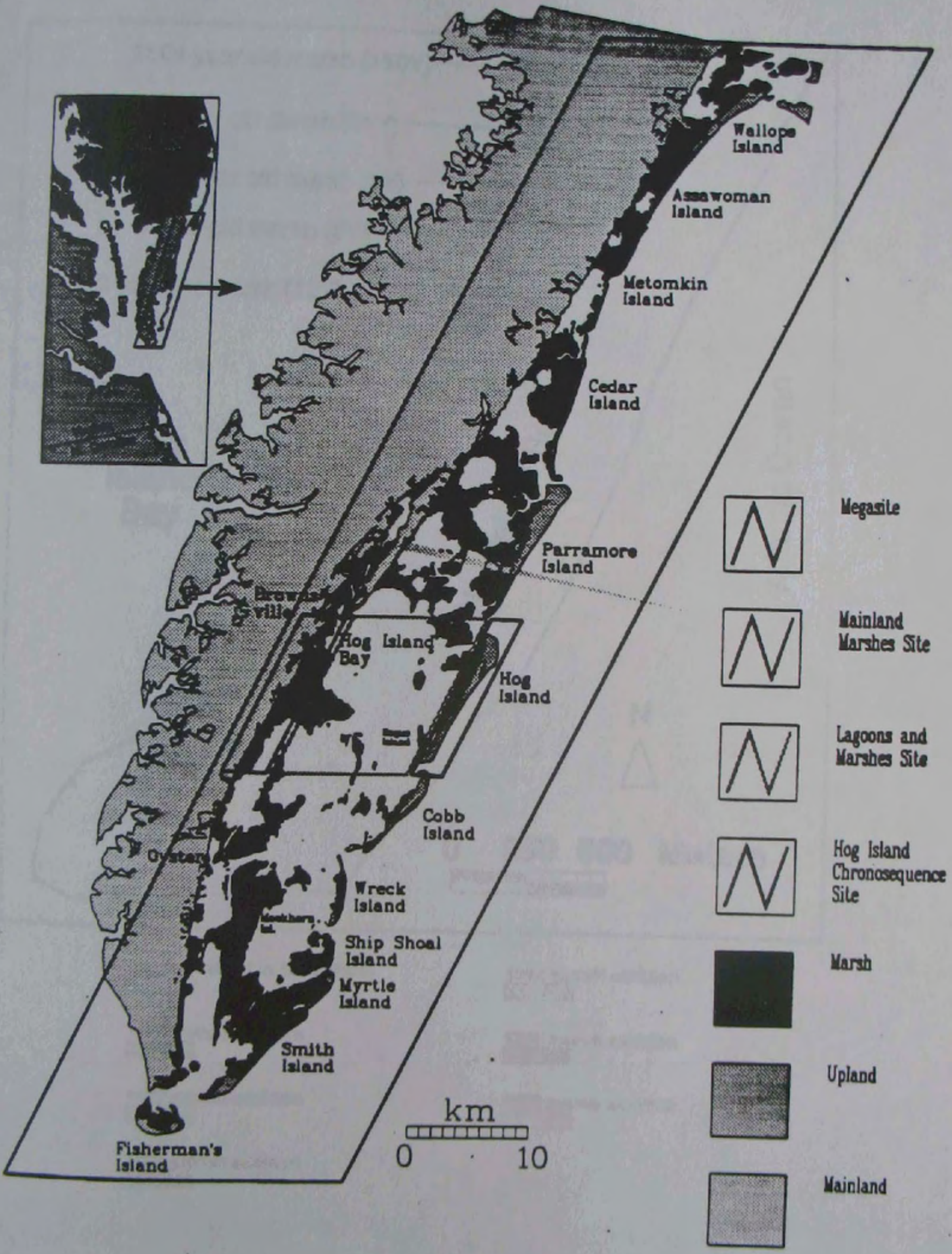


Figure 2. 1 The Virginia Coast Reserve and Hog Island.

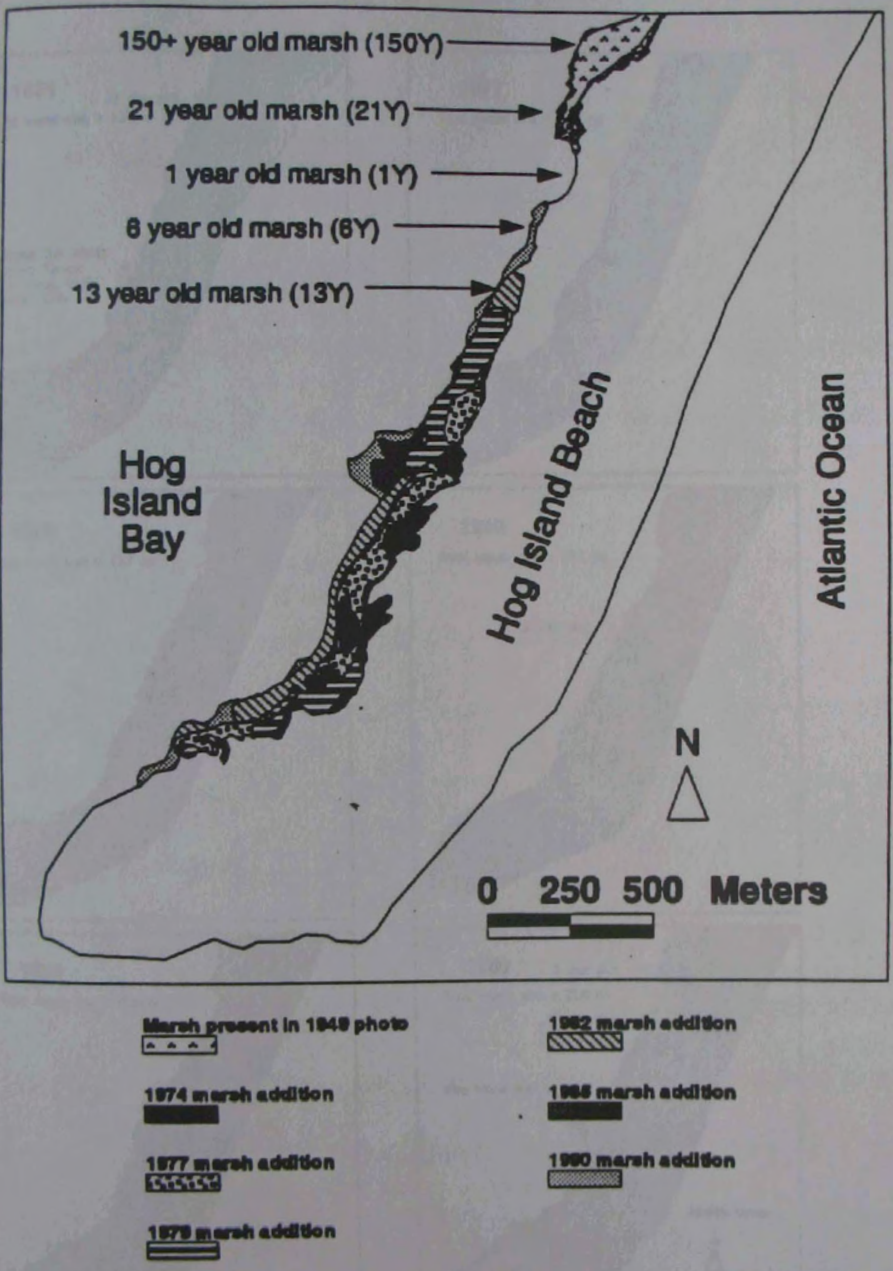


Figure 2. 2 Over-lay of different aged marshes along the Hog Island chronosequence.

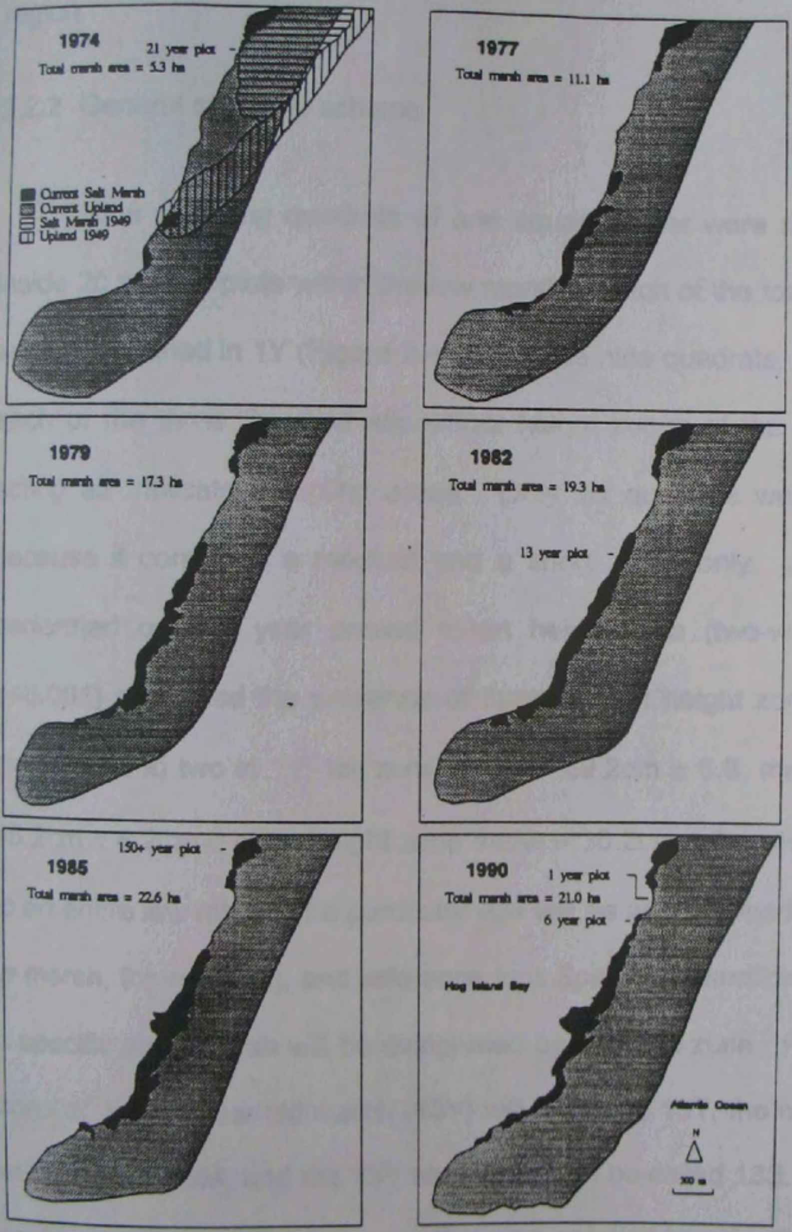


Figure 2. 3 Hog Island marsh growth following the 1962 Ash Wednesday storm.

leading to uniformity in marsh age at any spot along the chronosequence in this region.

2.2.2 General sampling scheme

Nine sampling quadrats of one square meter were randomly established inside 20 m wide plots within the low marsh of each of the four older marshes; six were established in 1Y (Figure 2.4). Of these nine quadrats, three were placed in each of the three *Spartina alterniflora* height zones of the four older marshes, acting as triplicate sampling areas. Only six quadrats were placed within 1Y because it contained a medium and a short zone only. Analysis of variance performed on two year pooled mean height data (two-way ANOVA, Tukey, $p<0.001$) confirmed the presence of three distinct height zones in the four older marshes, and two in 1Y: tall zone mean = 69.2cm ± 6.8, medium height zone = 45.2cm ± 4.2, and short height zone mean = 30.2cm ± 2.4. Hereafter, references to an entire low marsh of a particular age will be as described above (1Y for the 1 yr marsh, for instance), and reference to a *Spartina alterniflora* height zone within a specific aged marsh will be designated by age and zone. For example, the tall zone of the 13 year old marsh (13Y) will be called 13T, the medium zone of 13Y will be called 13M, and the 13Y short zone will be called 13S. Each quadrat was equipped with a suction lysimeter that was installed to a depth of 10 cm, and was

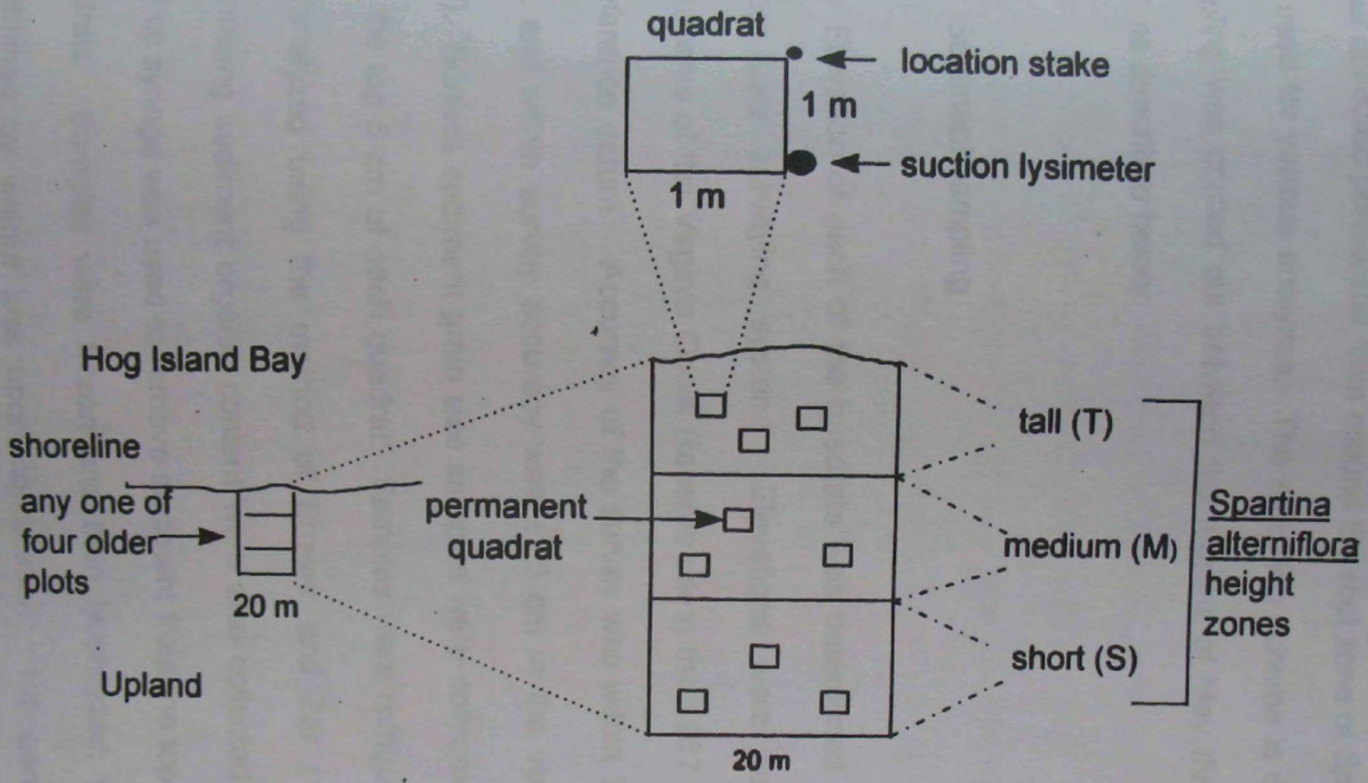


Figure 2. 4 General sampling scheme.

back-filled with native sediment (Chambers and Odum, 1990). The lysimeter or 'sipper collected pore-water from around the root zone of *Spartina alterniflora* that was used for various analyses. The sampling scheme is outlined in Figure 2.4. Sampling was carried out between the months of May through October, 1995-1996, as described below.

2.2.3 Sediment sampling

Elevation of each of the quadrats was determined using a Pentax Total Station laser surveying system. Elevations were tied to three existing benchmarks of the Virginia Coast Reserve using the 1967 USGS reduction level as reference datum. Accuracy of the survey was within 3 to 4 cm of the 1967 level, and within survey accuracy was ±1.5 cm in the vertical direction (Tyler, 1997). Surface sediment grain size samples were collected in September, 1995 from the top 5 cm of each quadrat. Samples were refrigerated, dried at 50 °C, and analyzed using the method of Brower and Zar (1984). Samples for determining sediment organic content were also collected in September, 1995. A 60 cc syringe was used to remove sediment from the top 10 cm of each of the quadrats. Samples were frozen and then lyophilyzed. Organic content was determined by weight loss upon combustion. Nitrogen was determined in sediment samples that were collected in October, 1995. A 5 cc syringe corer was used to withdraw sediment from the top 3 cm of each quadrat. Each sample was frozen and then lyophilyzed. Large pieces of shell, rock and plant material were removed and then samples were ground with mortar and pestle. Samples were analyzed using a Carlo Erba NA 1500 Elemental Analyzer. Sediment total phosphorous samples were collected in October, 1995, using 5 cc syringe corers to remove the top 3 cm of sediment from each quadrat. The samples were frozen, and then freeze-dried. A hot acid extraction method was followed by colorimetric analysis of soluble phosphate (Chambers and Fourqurean, 1991). This method does not identify various fractions of inorganic phosphate, and is probably an underestimate of total inorganic phosphate (Osgood, 1996).

2.2.4 Pore-water sampling

Pore-water temperature, pH, and redox samples were collected monthly from May through October, 1995 and 1996. Nitrogen gas was first blown into each lysimeter to purge it of standing water and to maintain anoxic conditions. A slight vacuum was applied using a hand pump, and then water was allowed to re-fill the lysimeter before sampling. Samples were removed by syringe, and transferred to an anaerobic chamber (appr. 10 ml capacity) in the field. Temperature, pH and oxidation-reduction potential were then measured immediately using a Jennco Electronics model 6009 meter. Salinity was also measured immediately after collection in the field using a temperaturecompensated salinity refractometer. Platinum potentials were converted to oxidation-reduction potentials by adding +199mV to each measured potential (Osgood, 1996).

Pore-water nutrient samples were collected from lysimeters during June, August and October of 1995-1996. Before extracting samples, each lysimeter was purged with nitrogen and allowed to re-fill with pore-water as described above. Ammonium and phosphate samples were collected from lysimeters in syringes and transferred through 0.45 micron membrane filters to test tubes containing 6N HCl. Samples were kept on ice until they were prepared for reading, within 6 hours of collection. Nitrogen gas was then bubbled into the samples for approximately 5 minutes to remove H_2S. Ammonium sample pH was readjusted with 6N NaOH, and samples were measured colorimetrically using the method of Parsons (1984). Phosphate samples were also read colorimetrically using an ammonium molybdate method (Lagera, 1986)

Sulfide samples were transferred unfiltered into test tubes containing zinc acetate. Samples were iced, transported to the lab, and read colorimetrically within 6 hours after collection using the method of Cline (1969) as modified by Otte and Morris (1994).

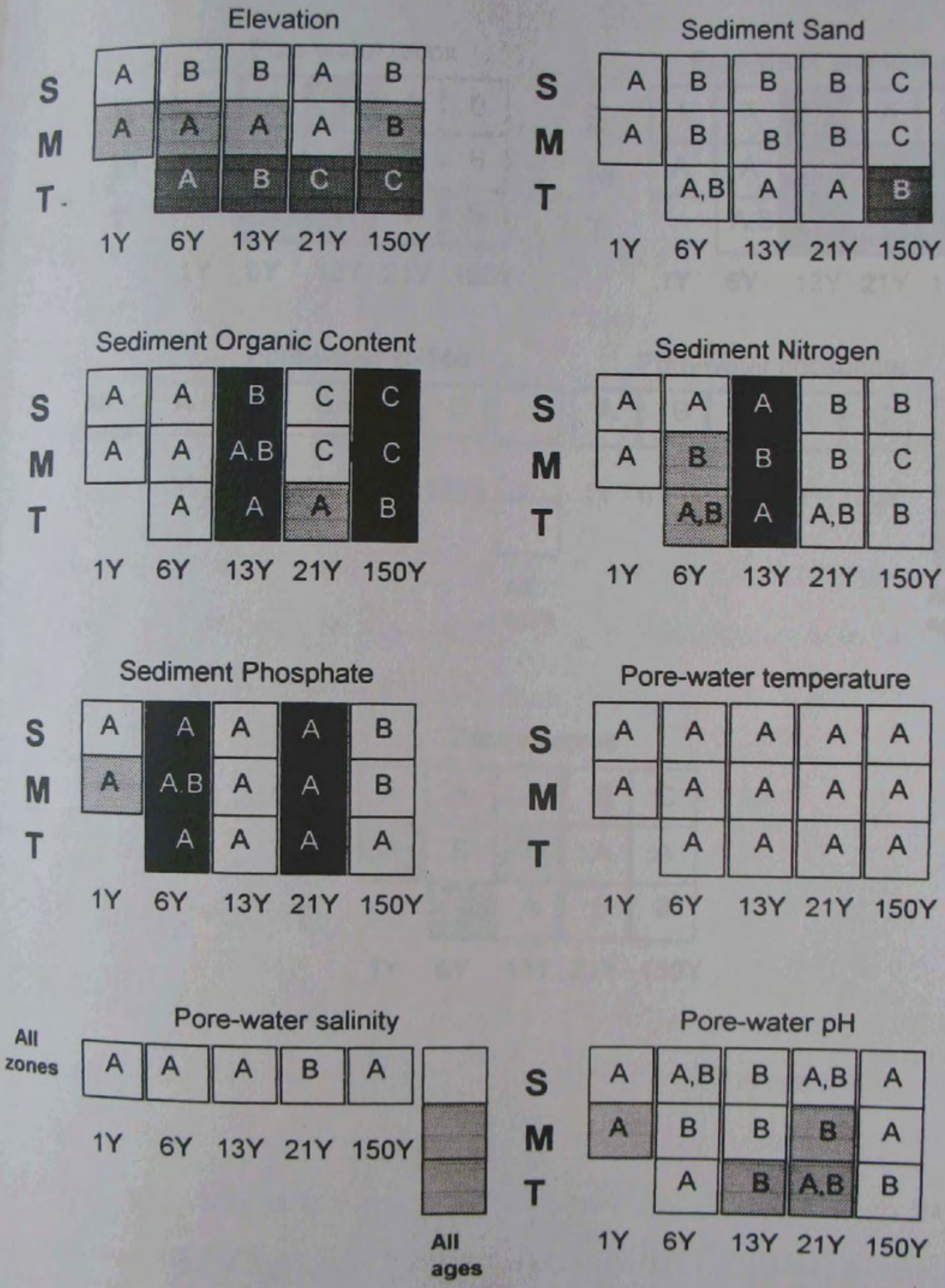
Pore-water nitrate-nitrite samples were collected during the months of June, August and October, 1995. Samples were collected from lysimeters as described above, and a colorimetric method (Jones, 1984) was used to analyze the samples. The mean value obtained for the 1995 season was less than the detection ability of the analysis system (2 μm/L). Hence, nitrate-nitrite samples were not collected in 1996, and no values are reported herein.

2.2.5 Data analysis

Data that were used for ANOVA either exhibited homogeneity of variance and were used as recorded or were transformed using square root and logarithm transformations. Tukey's post-hoc test was used in all multiple comparisons of means found significantly different by two-way ANOVA. Data that could not be transformed were analyzed by Kruskal-Wallis ANOVA (K-W ANOVA) on ranks, a non-parametric test); Student-Newman-Keuls (SNK) post-hoc test was performed on these data. All variations about the mean shown in graphs and tables are standard errors of the mean. Analysis of variance was performed using SigmaStat software, and all regression analyses were performed using Microsoft Excel software. Correspondence analysis was performed using Statistica software.

2.3 *Results*

Figure 2.5 summarizes the age and zonal groupings of each of the sediment and pore-water variables of chronosequences marshes. Age groupings



Elevation

	1Y	6Y	13Y	21Y	150Y
S	A	B	B	A	B
M	A	A	A	A	B
T		A	B	C	C

Sediment Sand

	1Y	6Y	13Y	21Y	150Y
S	A	B	B	B	C
M	A	B	B	B	C
T		A,B	A	A	B

Sediment Organic Content

	1Y	6Y	13Y	21Y	150Y
S	A	A	B	C	C
M	A	A	A.B	C	C
T		A	A	A	B

Sediment Nitrogen

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	B	B
M	A	B	B	B	C
T		A,B	A	A,B	B

Sediment Phosphate

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	A	B
M	A	A.B	A	A	B
T		A	A	A	A

Pore-water temperature

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	A	A
M	A	A	A	A	A
T		A	A	A	A

Pore-water salinity

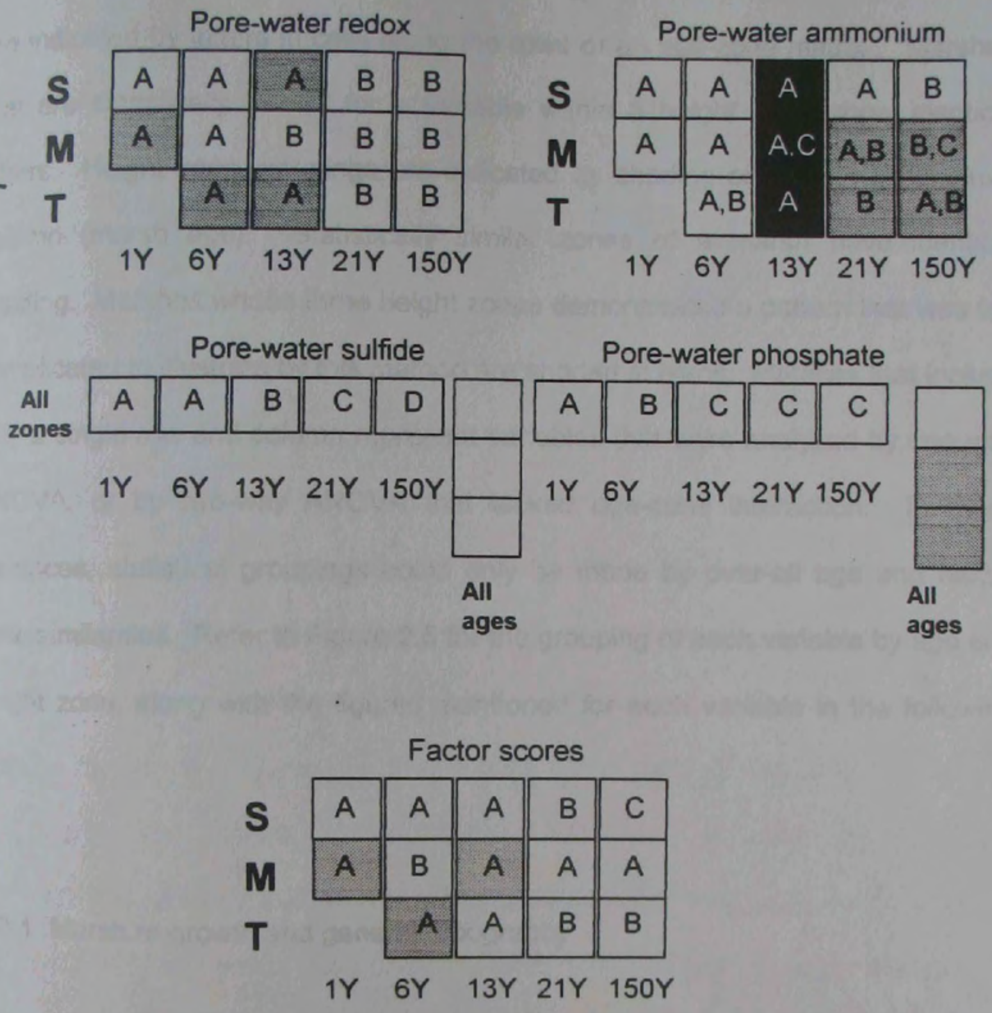
	1Y	6Y	13Y	21Y	150Y
All zones	A	A	A	B	A

All ages

Pore-water pH

	1Y	6Y	13Y	21Y	150Y
S	A	A,B	B	A,B	A
M	A	B	B	B	A
T		A	B	A,B	B

Figure 2. 5 Matrices showing the statistical grouping of each variable by marsh age and height zone. Age grouping is indicated by letters along the rows, and height zones are grouped within a marsh by shading. Marshes whose height zone grouping pattern was too complex to illustrate this way are shaded in black. Matrices that composed of a single row and column were analyzed by one-way ANOVA , and only whole-marsh or zone comparisons could be made.



Pore-water redox

	1Y	6Y	13Y	21Y	150Y
S	A	A	▨ A	B	B
M	▨ A	A	B	B	B
T		▨ A	▨ A	B	B

Pore-water ammonium

	1Y	6Y	13Y	21Y	150Y
S	A	A	■ A	A	B
M	A	A	■ A,C	▨ A,B	▨ B,C
T		A,B	■ A	▨ B	▨ A,B

Pore-water sulfide

	1Y	6Y	13Y	21Y	150Y
All zones	A	A	B	C	D

All ages

Pore-water phosphate

1Y	6Y	13Y	21Y	150Y
A	B	C	C	C

All ages

Factor scores

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	B	C
M	▨ A	B	▨ A	A	A
T		▨ A	A	B	B

Figure 2.5 continued

are indicated by letters in cells along the rows of an age-zone matrix . Marshes that are statistically similar for a variable within a height zone show identical letters. Height zone groupings are indicated by shading of cells in a particular column (marsh age). Statistically similar zones of a marsh have identical shading. Marshes whose three height zones demonstrated a pattern that was too complicated to illustrate by this method are shaded in black. Matrices that include only a single row and column represent variables that were analyzed by one-way ANOVA, or by two-way ANOVA that lacked age-zone interaction. In these instances, statistical groupings could only be made by over-all age and height zone similarities. Refer to Figure 2.5 for the grouping of each variable by age and height zone, along with the figures mentioned for each variable in the following text.

2.3.1 Marsh re-growth and general topography

Southern Hog Island is a highly dynamic landscape (Hayden et. al., 1991). Figure 2.3 shows the position of the upland and back-barrier marshes of southern Hog Island as they existed in 1949 and in 1974, the year of the first aerial photograph available after the Ash Wednesday storm. In the years between 1949 and 1974 (Figure 2.3), the southern end of the island underwent dramatic change as it extended southward a kilometer and doubled in width. By 1974, the mature marsh (150Y) which was not buried had spread less than 100 m or so south of its pre-storm location, while new marsh began to appear as patches along the southwestern coastline. Figure 2.3 shows these patches of fringing marsh doubling in area from 1974 to 1977(5.3 ha to 11.1 ha). They again doubled in area from 1977 to 1985 (11.1 ha to 22.6 ha) as they grew in a mostly northerly direction. Marsh area was lost between 1985 and 1990 (22.6 ha to 21.0 ha)

An age-related decline in mean elevation is evident in Figure 2.6, but it is unclear if this trend is developmental because it is not known how much over-wash sand was deposited onto each of the marshes. The horizontal axes on all bar graphs, labeled marsh age, are only approximate time scales, with the interval between 21Y and 150Y being the least accurate. Elevations of the samping quadrats ranged from -38.3 cm (with respect to mean sea level) in 21T to +64.3 cm in 1S (Figure 2.6). The lowest marsh over-all was 150Y (mean = +3.1 cm) and the highest was 1Y (mean = +49.9 cm). Elevation increased as expected from tall to medium to short *Spartina alterniflora* height zones only in 21Y and 150Y. Moreover, marsh surface was much bumpier in the three younger marshes (personal observation), and within two of them, 6Y and 13Y, the medium zone was at a higher mean elevation than the short zone.

2.3.2 Sediment variables

Figure 2.7 displays the percentage of sand, silt and clay in the surface sediments of the chronosequence marshes by height zone. All three zones showed a decrease of sand and an increase of silt and clay with age. The highest percentage of sand in surface sediments was in 1S (92.3%) and the least was in 150S (21.3%). Three marsh groups were separated by ANOVA using sand content as the dependent variable (two-way ANOVA, Tukey, p<0.001): 1Y had significantly more sand than the group consisting of 6Y, 13Y and 21Y, which had significantly more sand than 150Y (Figure 2.8). Marshes 1Y, 6Y 13Y and 21Y showed uniformity of sand content across the height zones, while 150T had significantly more sand than the other category of 150M-150S (p<0.001). Thus, there was a zonal differentiation in surface sand content with age. The time that it took to reach maturity, that is to possess as low a content of sand as that of 150Y, varied by height zone. It took only 6 years for the tall zone to reach maturity, while it took as much as 150 years for both the medium and short zones to reach it.

Sediment organic content generally increased with marsh age (Figure 2.9), from an overall low of 0.51% in 1Y to a maximum in 150Y of 9.2%. Moreover, whole marshes showed age groupings: 1Y, 6Y, and 13Y possessed significantly less organic matter than 21Y and 150Y (two-way ANOVA, Tukey, p<0.001). The tall zone overall showed the maximum concentration of organic matter with 6.4%; medium zone overall had 4.2% and the short zone overall measured 3.8%. Thus, overall medium and short zones constituted a single 'organic matter zone' that showed significantly less organic matter than the tall zone (p<0.001). However, the younger marshes (1Y and 6Y) demonstrated a uniformity of organic concentration in all zones, while the older marshes (13Y, 21Y and 150Y)

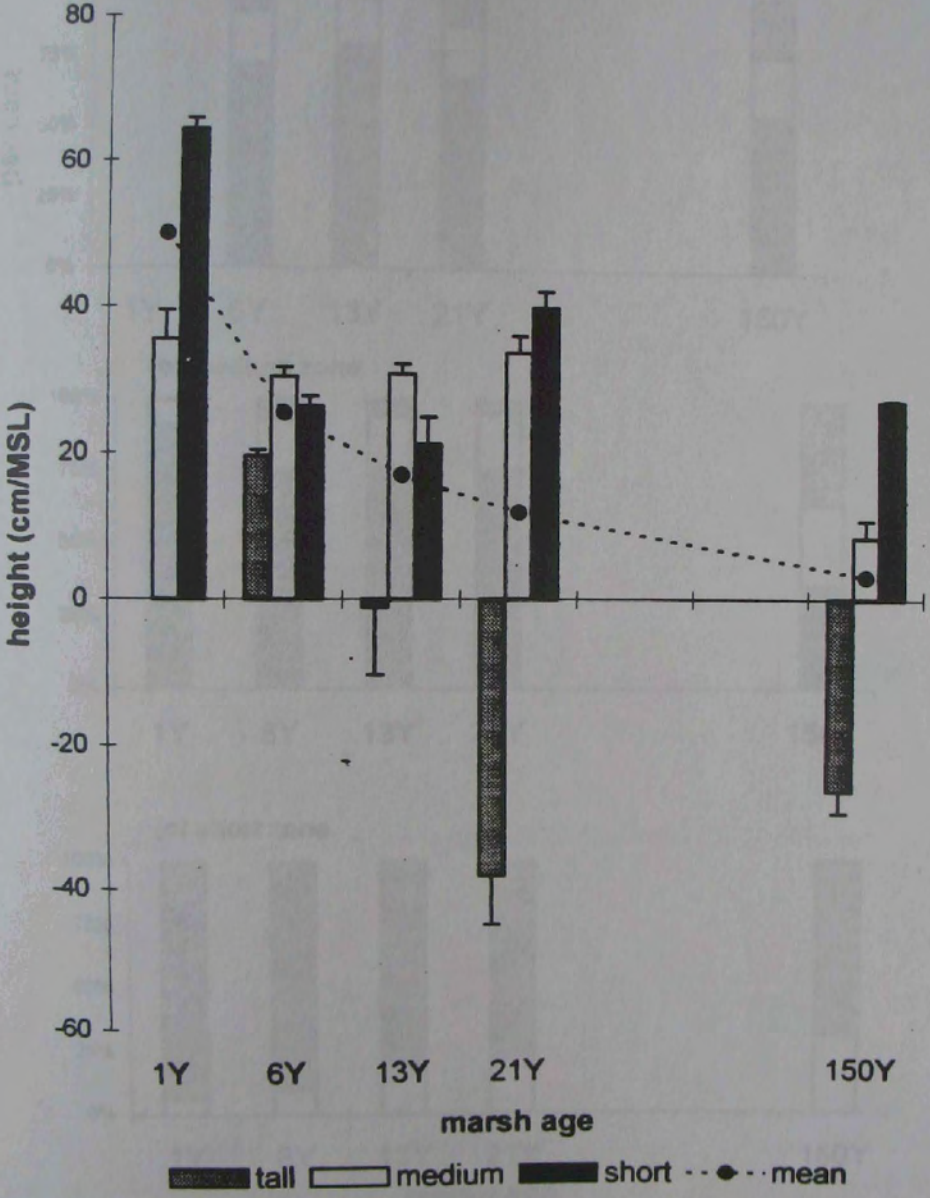
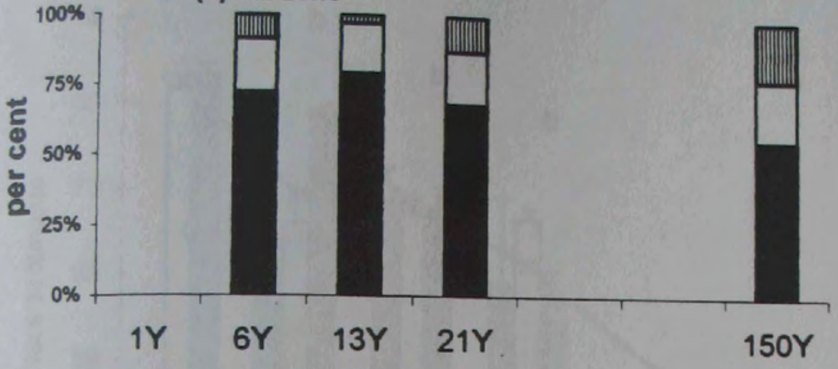
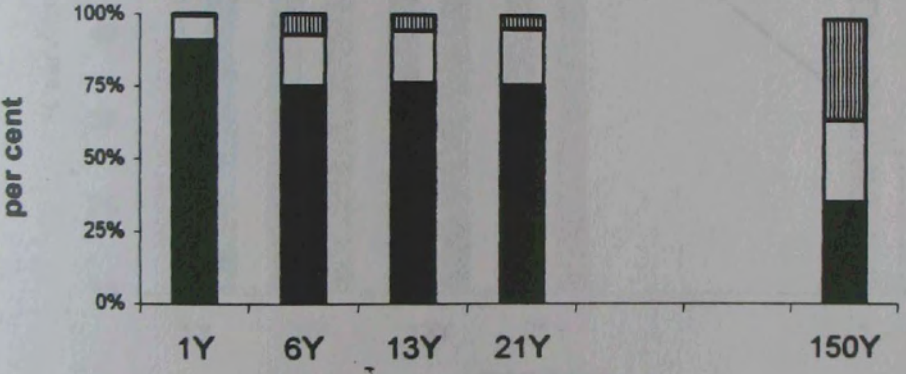


Figure 2. 6 Marsh surface elevation by marsh age and height zone.

(a) tall zone



(b) medium zone



(c) short zone

Figure 2. 7 Percentage of sand, silt and clay in surface sediments by marsh age and height zone for (a) the tall zone, (b) the medium zone and at the short zone.

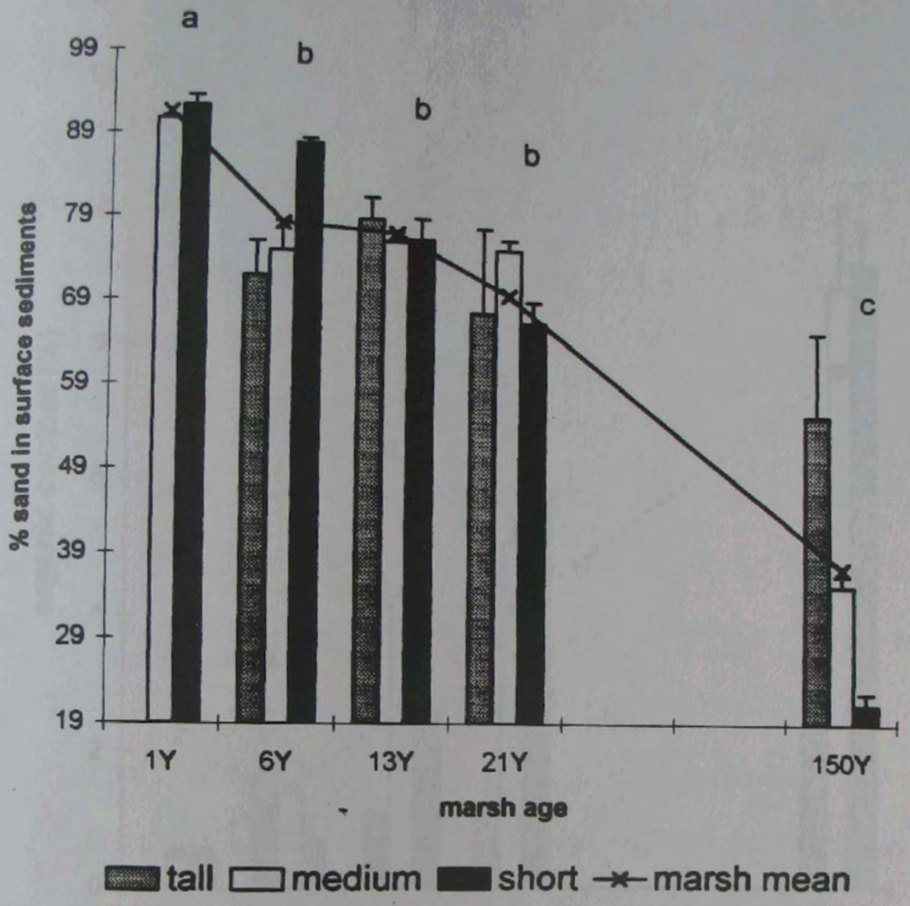


Figure 2. 8 Percentage of sand in surface sediments by marsh age and height zone, with whole marsh mean. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars.

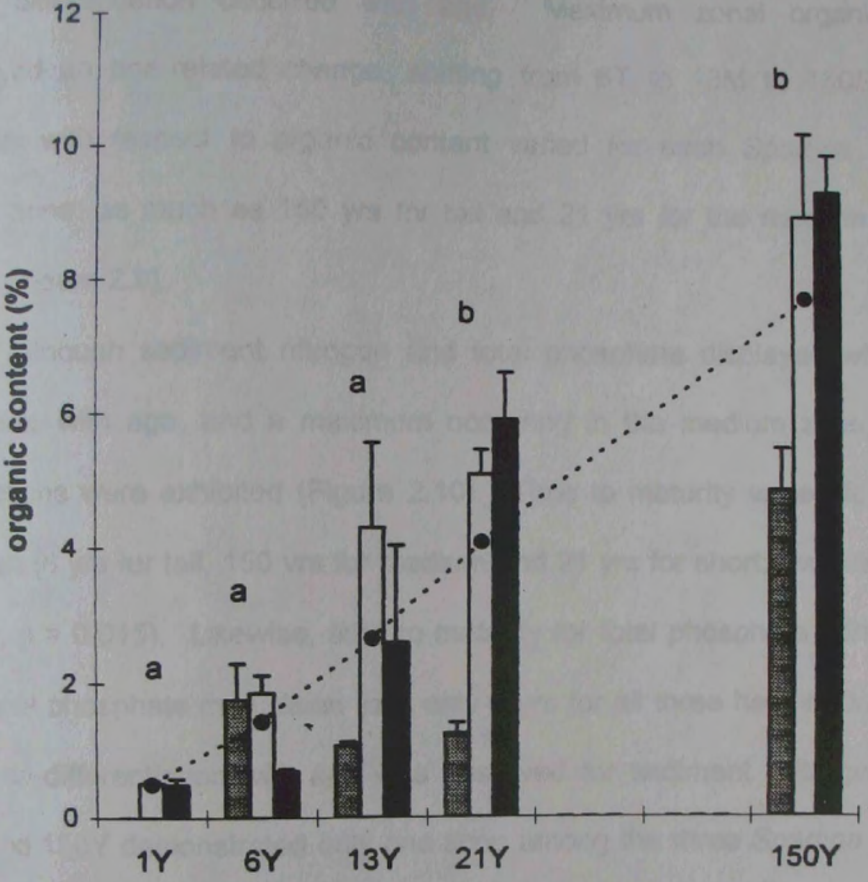


Figure 2. 9 Sediment organic content by marsh age and height zone. Marsh-wide mean is shown. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars.

displayed the two-zone pattern mentioned above, suggesting that some zonal differentiation occurred with age. Maximum zonal organic content displayed an age-related change, shifting from 6T to 13M to 150S. Time to maturity with respect to organic content varied for each *Spartina alterniflora* height zone: as much as 150 yrs for tall and 21 yrs for the medium and short zones (Figure 2.9).

Although sediment nitrogen and total phosphate displayed whole-marsh increases with age, and a maximum occurring in the medium zone, zone-age interactions were exhibited (Figure 2.10). Time to maturity varied for sediment nitrogen (6 yrs for tall, 150 yrs for medium and 21 yrs for short; two-way ANOVA, Tukey, $p = 0.015$). Likewise, time to maturity for total phosphate varied zonally; sediment phosphate maturation took only 6 yrs for all three height zones. Some zonal de-differentiation with age was observed for sediment nitrogen, as both 21Y and 150Y demonstrated only one zone among the three *Spartina alterniflora* height zones (two-way ANOVA, Tukey, $p<0.05$).

2.3.3 Pore-water variables

Pore-water temperature (Figure 2.11) showed no relationship with either marsh age or height zone (K-W ANOVA, SNK, $p = 0.60$). Minimum seasonal temperatures were found in September (18.0 °C) and maximum temperatures in

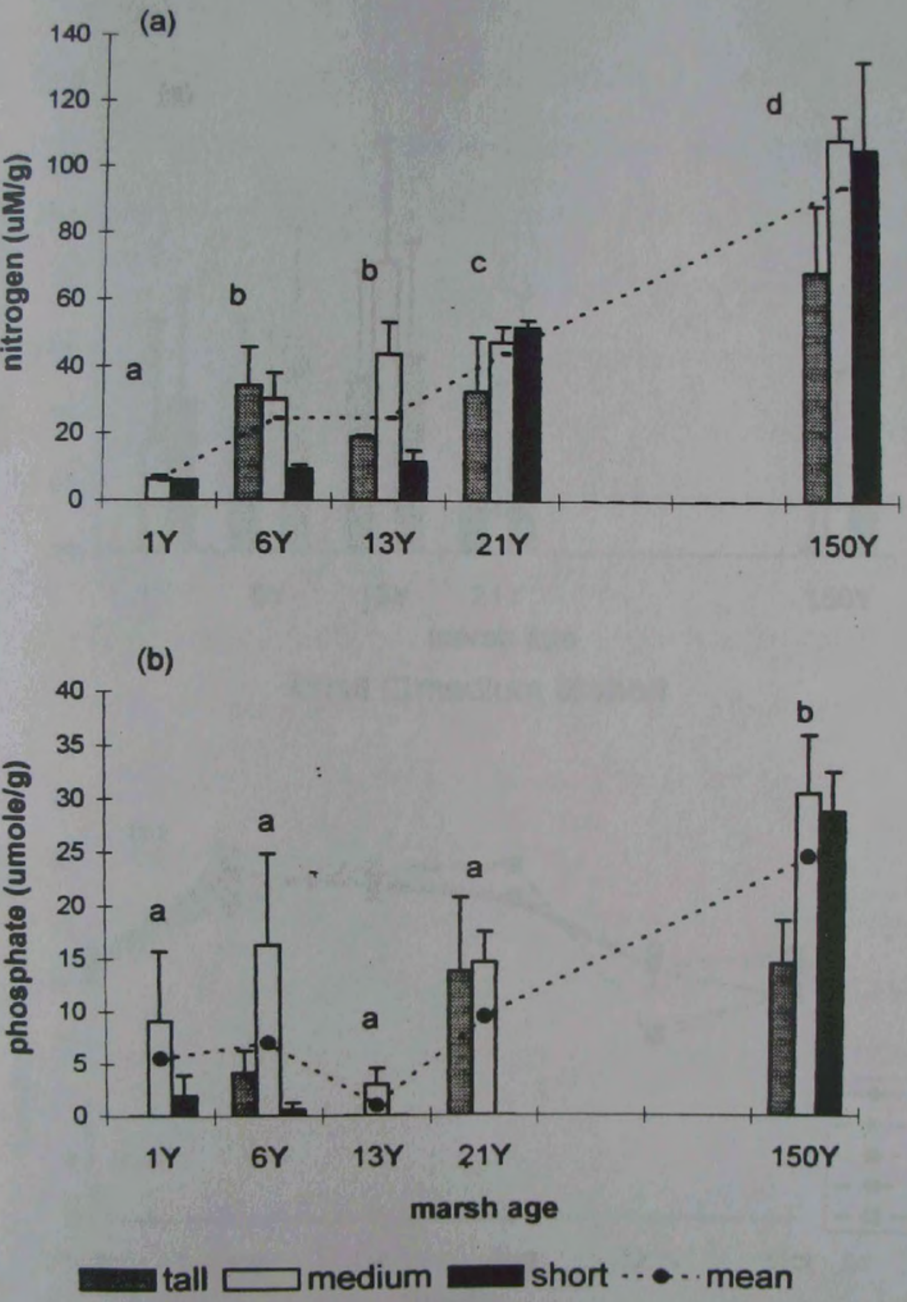


Figure 2. 10 (a) Sediment nitrogen and (b) total phosphate by marsh age and height zone. Marsh-wide mean is shown. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars.

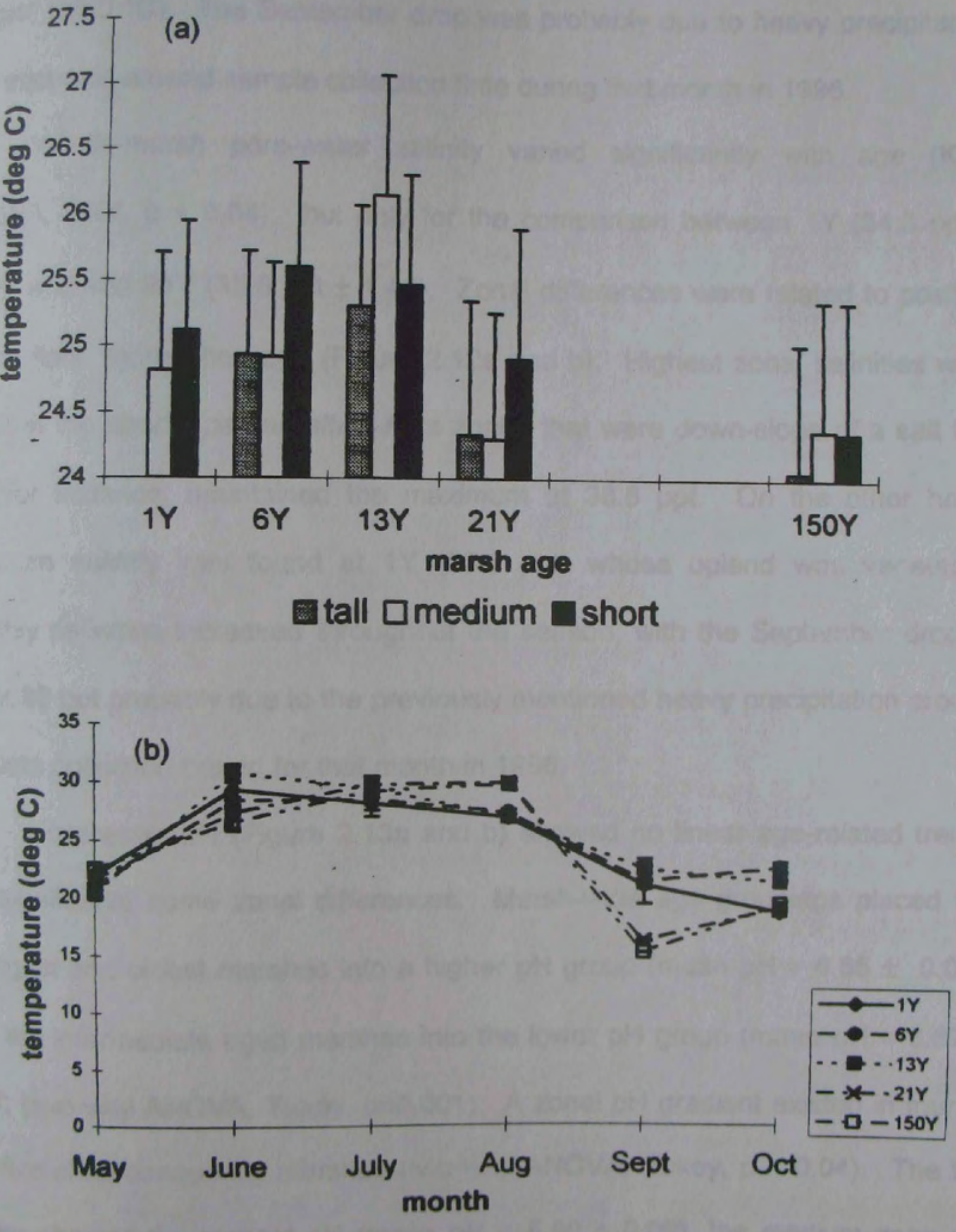


Figure 2. 11 (a) Pore-water temperature by marsh age and height zone and (b) monthly marsh-wide pore-water temperature.

August (30.0 °C). The September drop was probably due to heavy precipitation that occurred around sample collection time during that month in 1996.

Whole-marsh pore-water salinity varied significantly with age (K-W ANOVA, SNK, p = 0.04), but only for the comparison between 1Y (34.3 ppt ± 0.63) and and 21Y (35.8 ppt ± 1.43). Zonal differences were related to position of salt flats, rather than age (Figure 2.12a and b). Highest zonal salinities were found in the short *Spartina alterniflora* zones that were down-slope of a salt flat; 21S for instance, maintained the maximum at 38.6 ppt. On the other hand, minimum salinity was found at 1Y (33.6 ppt) whose upland was vegetated. Monthly salinities increased throughout the season, with the September drop to about 33 ppt probably due to the previously mentioned heavy precipitation around the data collection period for that month in 1996.

Pore-water pH (Figure 2.13a and b) showed no linear age-related trends but manifested some zonal differences. Marsh-wide age groupings placed the youngest and oldest marshes into a higher pH group (mean pH = 6.85 ± 0.02), and the intermediate aged marshes into the lower pH group (mean pH = 6.67 ± 0.07; (two-way ANOVA, Tukey, p<0.001). A zonal pH gradient existed in four of the five chronosequence marshes (two-way ANOVA, Tukey, p = 0.04). The tall zones showed the highest pH (mean pH = 6.80 ± 0.06), the medium zone pH mean was intermediate (mean pH = 6.77 ± 0.05), and the short zone mean was the lowest (mean pH = 6.72 ± 0.07). Time to maturity for each zone varied from one year for the short and medium zones to 13 years for the tall zone.

As expected, pore-water oxidation-reduction potential (redox) decreased with marsh age for all three height zones, from a maximum at 6S (101 mV ± 12) to a minimum of -63mV ± 9 at 150S (Figure 2.14a and b). Marshes 21Y and 150Y displayed significantly lower redox potential than the three younger marshes (-44mV ± 9 vs. +51mV ± 21, two-way ANOVA, Tukey, $p<0.001$). Age-zone interactions, however, showed a complicated pattern. Younger marshes demonstrated a variety of pairings of zones, but by 21Y, and continuing into 150Y, there existed a uniform redox zone within the three *Spartina alterniflora* height zones (two-way ANOVA, Tukey, $p<0.001$). Time to maturity showed the following zonal pattern: 21 yrs for tall, 13 yrs for medium and 150 yrs for short. Monthly marsh-wide redox values were at maximum in October (mean = 90.0mV) and lowest in July (mean =-5.0mV), and marshes 21Y and 150Y demonstrated consistently lower values throughout most of the season (Figure 2.14b).

Pore-water ammonium and sulfide exhibited some similarities in spatial and temporal patterns (Figure 2.15 and 2.16). For instance, both species generally increased with age on a marsh-wide basis. Ammonium increased from 9.7μM ± 0.7 in 1Y to 65.9μM ± 35 in 150Y and sulfide increased from 68.2μM ± 50 in 1Y to 787.1μM ± 270 in 150Y. Moreover, highest zonal maxima occurred in 150S for both species (136.0μM ± 37 for ammonium and 1318.3μM ± 166 for

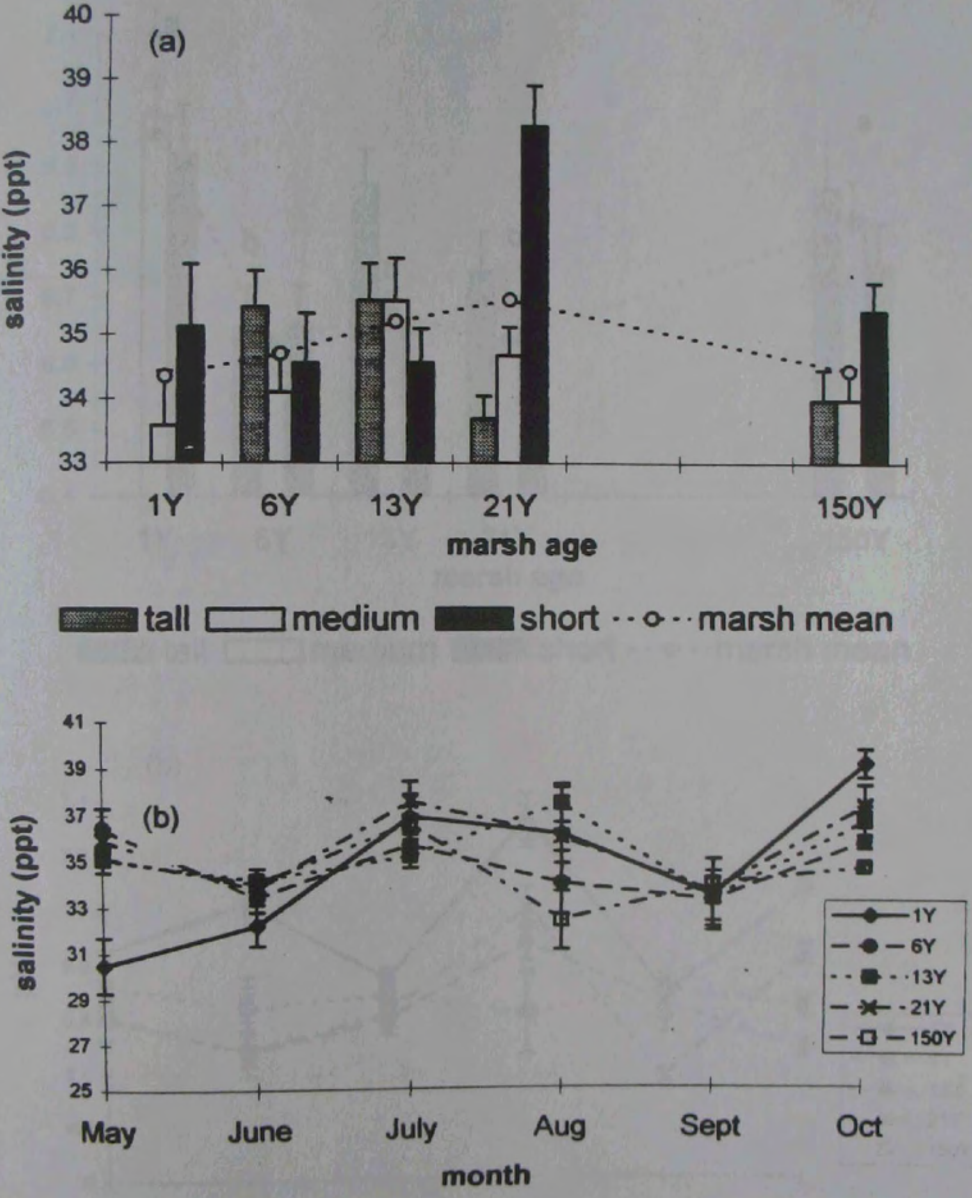


Figure 2. 12 (a) Pore-water salinity by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-ware salinity.

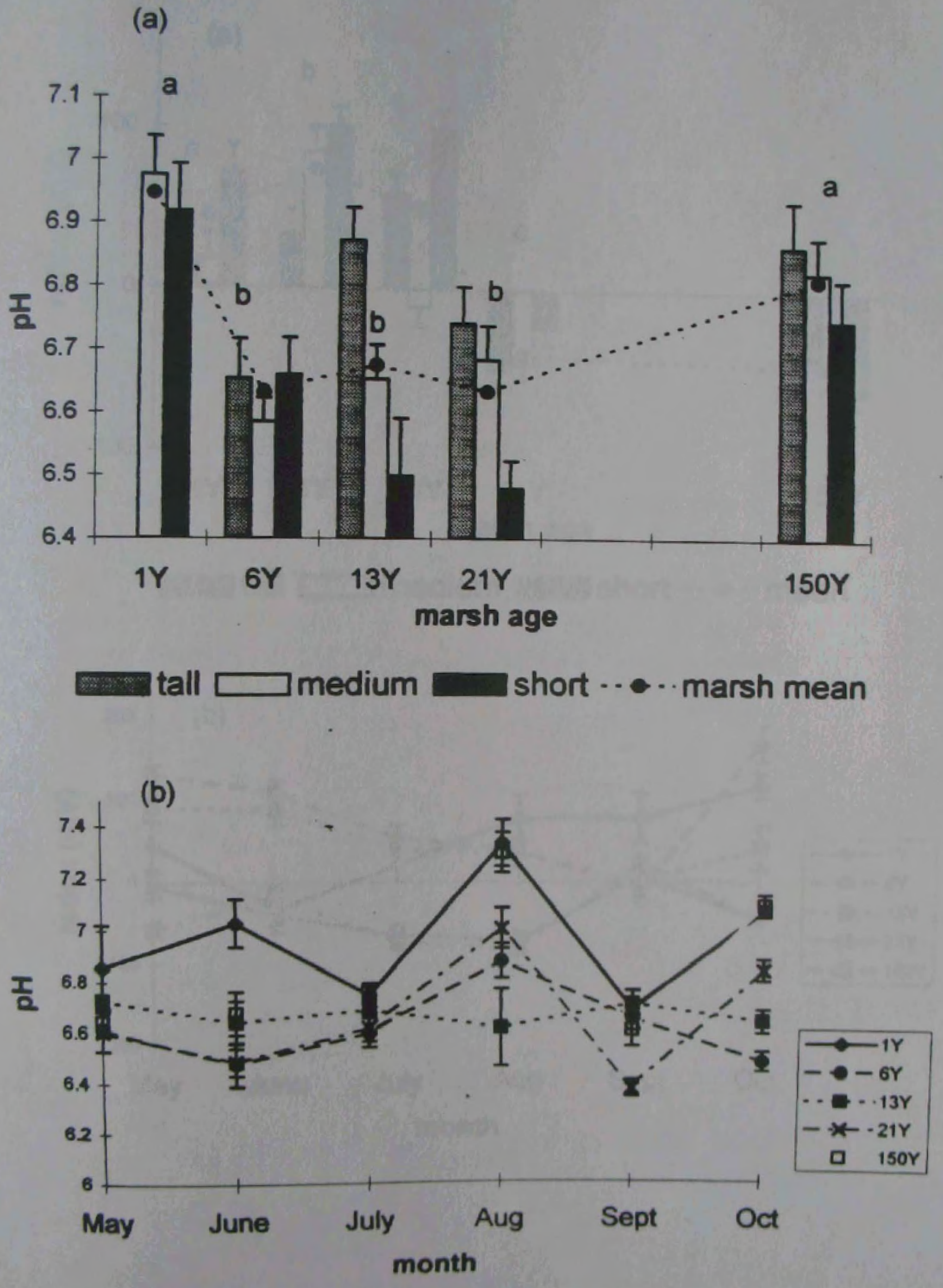


Figure 2. 13 (a) Pore-water pH by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-water pH.

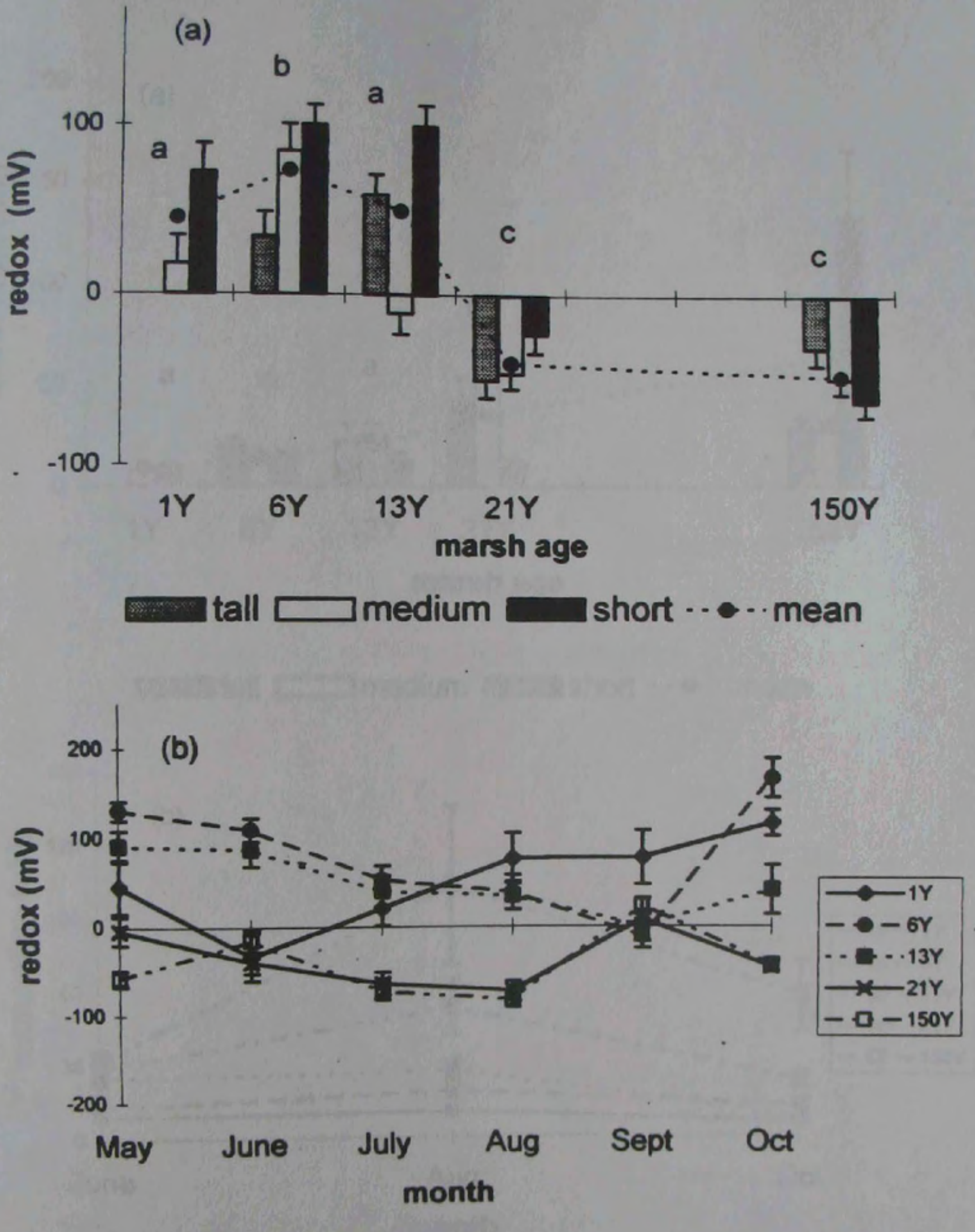


Figure 2. 14 (a) Pore-water oxidation-reduction potential by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-water redox.

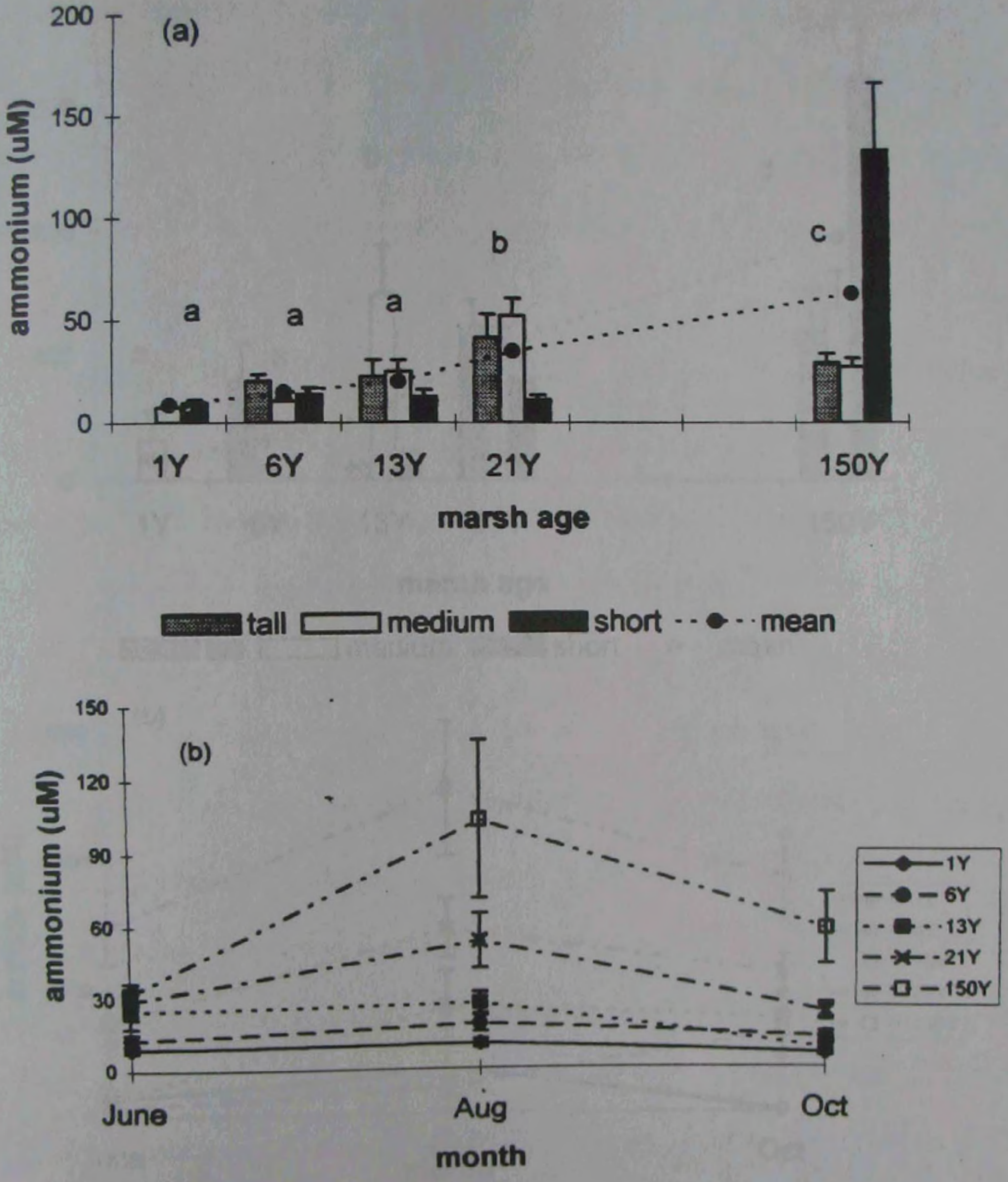


Figure 2. 15 (a) Pore-water ammonium concentration by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-water ammonium concentration.

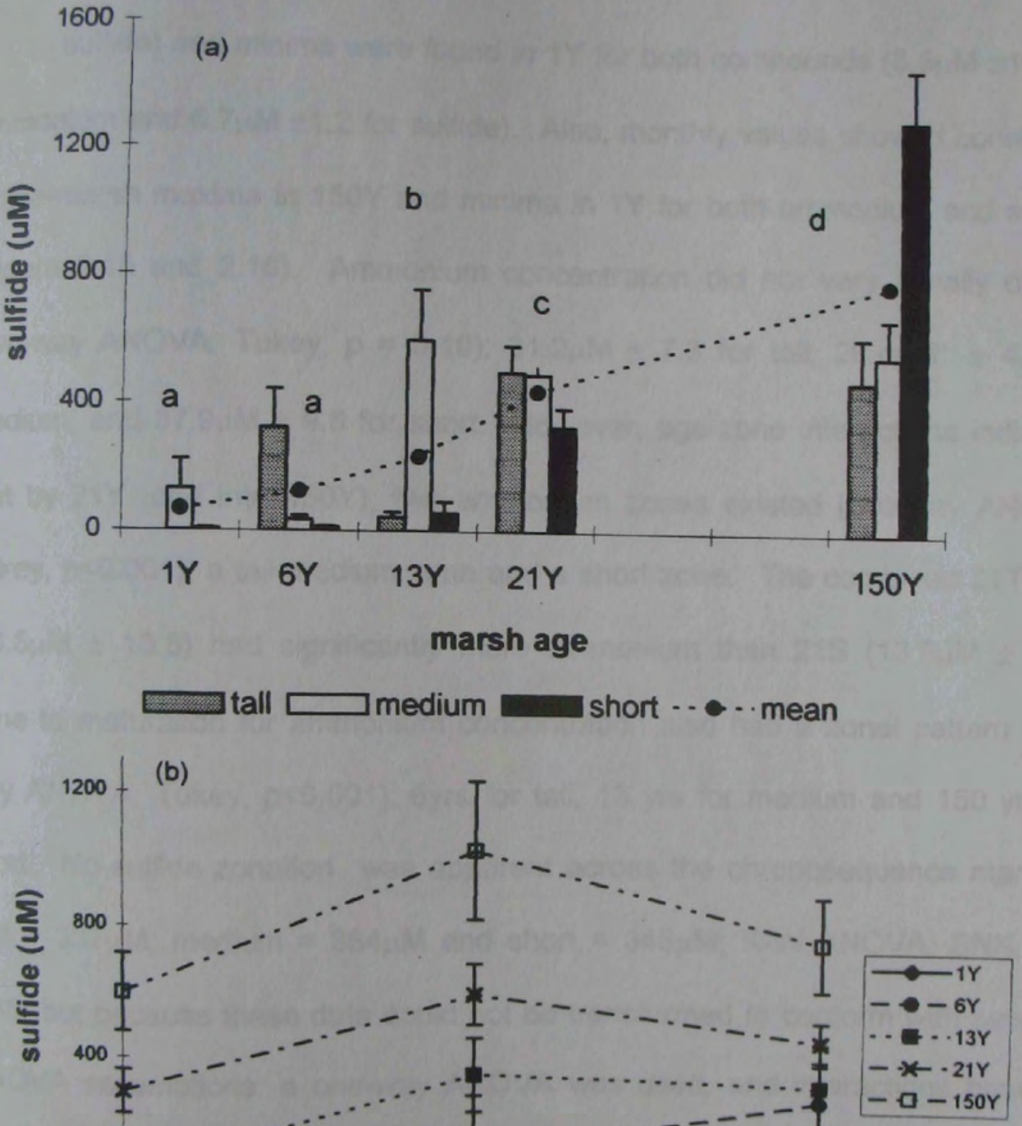


Figure 2. 16 (a) Pore-water sulfide concentration by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-water sulfide concentration.

sulfide) and minima were found in 1Y for both compounds (8.9μM ±1.5 for ammonium and 6.7μM ±1.2 for sulfide). Also, monthly values showed consistent whole-marsh maxima in 150Y and minima in 1Y for both ammonium and sulfide (Figure 2.15 and 2.16). Ammonium concentration did not vary zonally overall (two-way ANOVA, Tukey, p = 0.10): 31.2μM ± 7.3 for tall, 26.4μM ± 4.4 for medium, and 37.9μM ± 9.8 for short. However, age-zone interactions indicated that by 21Y (and into 150Y), two ammonium zones existed (two-way ANOVA, Tukey, p<0.001), a tall-medium zone and a short zone. The combined 21T-21M (50.6μM ± 10.8) had significantly more ammonium than 21S (13.0μM ± 2.7). Time to maturation for ammonium concentration also had a zonal pattern (two-way ANOVA, Tukey, p<0.001): 6yrs for tall, 13 yrs for medium and 150 yrs for short. No sulfide zonation was apparent across the chronosequence marshes (tall = 337μM, medium = 364μM and short = 345μM; K-W ANOVA, SNK, p = 0.35) but because these data could not be transformed to conform with two-way ANOVA assumptions, a one-way ANOVA was used, and interactions between age and zone could not be assessed. Therefore, time to maturity for pore-water sulfide could only be ascertained for whole marshes, and it took 150 yrs before any of the whole marshes contained sulfide levels of the mature (150Y) marsh (K-W ANOVA, SNK, p<0.001).

Figure 2.17 shows pore-water phosphate concentration values by marsh age and height zone (Figure 2.17a), and by month on a marsh-wide basis (Figure

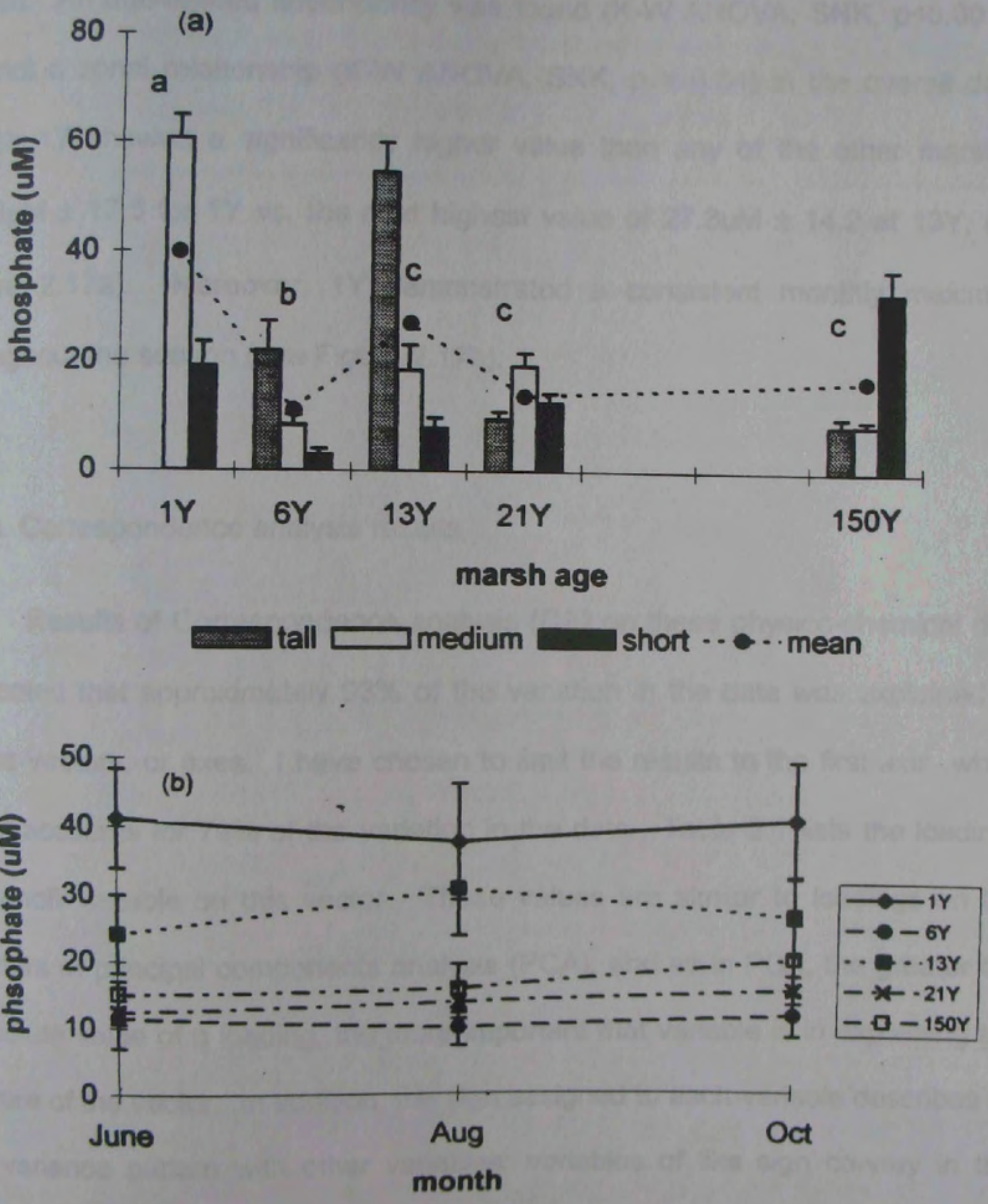


Figure 2. 17 (a) Pore-water phosphate concentration by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide pore-water phosphate concentrations.

2.17b). An age-related dependency was found (K-W ANOVA, SNK, $p<0.001$) , but not a zonal relationship (K-W ANOVA, SNK, $p = 0.84$) in the overall data. Marsh 1Y showed a significantly higher value than any of the other marshes (39.3μM ± 17.5 for 1Y vs. the next highest value of 27.3uM ± 14.2 at 13Y, see Figure 2.17a). Moreover, 1Y demonstrated a consistent monthly maximum throughout the season (see Figure 2.17b).

2.3.4 Correspondence analysis results

Results of Correspondence analysis (CA) on these physico-chemical data indicated that approximately 93% of the variation in the data was explained by three vectors, or axes. I have chosen to limit the results to the first axis, which itself accounts for 79% of the variation in the data. Table 2.1 lists the loadings for each variable on this vector. These values are similar to loadings on the vectors of principal components analysis (PCA), and as in PCA, the greater the absolute value of a loading, the more important that variable is in explaining the nature of the vector. In addition, the sign assigned to each variable describes its co-variance pattern with other variables: variables of like sign co-vary in the same direction, whereas variables of opposite sign co-vary in opposite directions. The most important variable on this vector is pore-water redox

Table 2. 1 Ranked loadings for sediment and pore-water variables on first axis of correspondence analysis. Bold-faced term represents the variable that was chosen to define the vector. Eigenvalue for this axis = 0.33, and data variation explained = 79%.

Variable	Loading
pore-water redox	***111***
sediment sand %	60
elevation	52
pore-water temperature	40
pore-water salinity	40
pore-water pH	39
pore-water phosphate	28
sediment organic content	-21
sediment N	-22
pore-water ammonium	-24
sediment P	-31
pore-water sulfide	-50

(loading = 111). Therefore, I have entitled this axis 'Pore-water Aeration', since this captures the overwhelmingly important variable, pore-water redox, and the nature of the variables of lesser importance. A particular physico-chemical stage can be defined using mean factor scores from the CA output. Like factor scores of PCA, these values represent the position of any sampling quadrat along the pore-water aeration vector. For instance, a positive factor score represents a quadrat with high pore-water redox and low pore-water sulfide values. Mean zonal and whole marsh factor scores can then be used to describe the developmental pattern for each zone and each whole marsh in a multivariate manner. Figure 2.18 shows the development of marshes of the chronsequence by *Spartina alterniflora* height zone. Distinguishing statistically significant zones or whole marshes was determined by performing two-way ANOVA on mean factor scores for a zone or whole marsh, then applying Tukey's post-hoc test to determine significant groupings. Zones or marshes were considered significantly different, and hence constituted separate physico-chemical stages, if their mean factor scores were found to be significantly different at $p \leq 0.05$. Figure 2.18 shows the presence of three physico-chemical stages on a whole marsh basis among chronosequence marshes. Marshes 21Y and 150Y constituted a low-score pair (mean = -54 ± 12), marshes 1Y and 13Y showed an intermediate mean factor score (mean = 90 ± 15), and marsh 6Y had the highest mean factor score (6Y = 144 ± 26). However, marsh age and

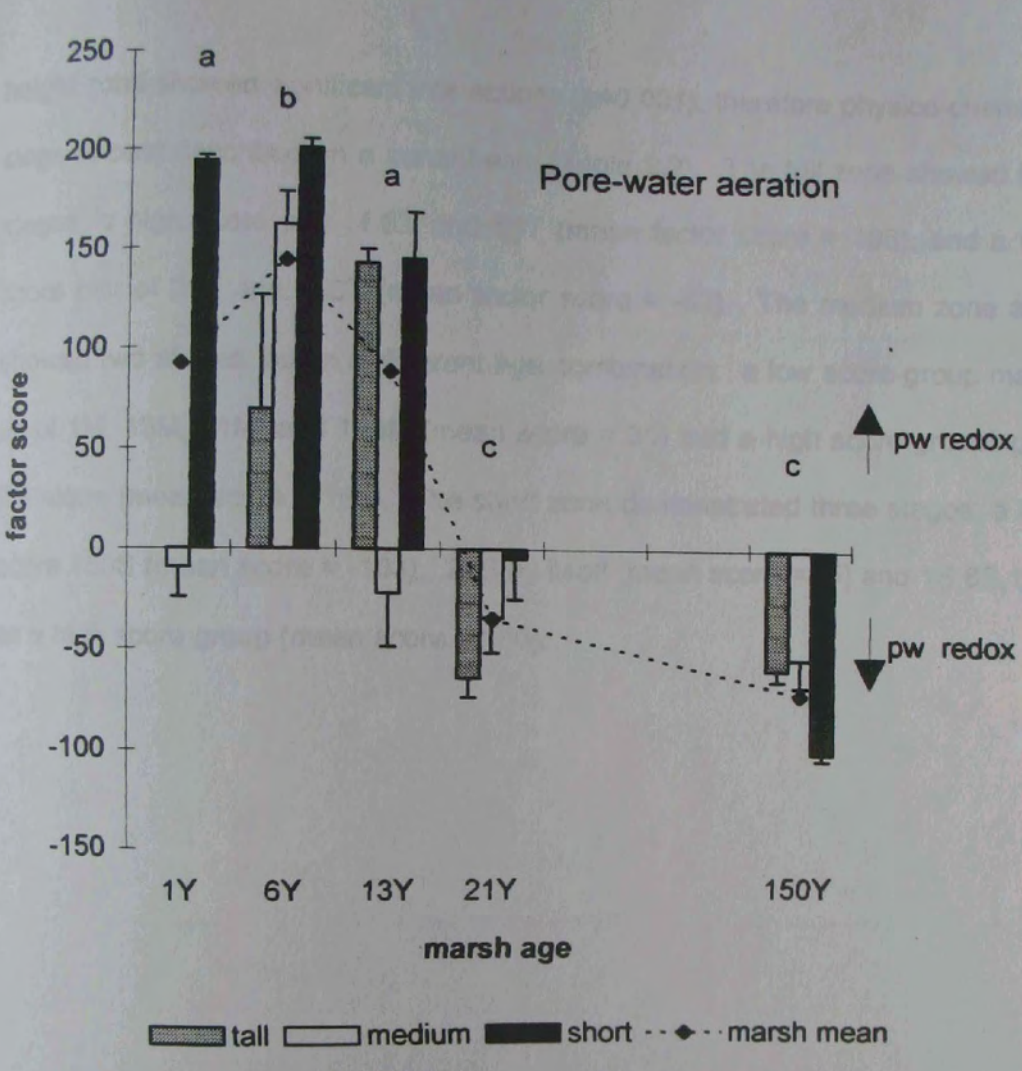


Figure 2. 18 Mean correspondence analysis factor score by marsh age and height zone. Significant whole marsh age groupings as determined by ANOVA are indicated by letters above the bars. The vector, entitled, 'Pore-water Aeration' is characterized by high pore-water redox and low sulfide concentrations for positive factor scores and low pore-water redox and high sulfide concentrations for negative factor scores.

height zone showed significant interactions (p<0.001), therefore physico-chemical stage is best described on a zonal basis (Table 2.2). The tall zone showed two stages: a high score pair of 6T and 13T (mean factor score = 106), and a low score pair of 21T and 150T (mean factor score = -63). The medium zone also showed two stages, but in a different age combination: a low score group made up of 1M, 13M, 21M, and 150M (mean score = 31) and a high score grouping of 6M alone (mean score = 162). The short zone demonstrated three stages, a low score 150S (mean score = -103), 21S by itself (mean score = -5) and 1S,6S,13S as a high score group (mean score = 180).

Table 2. 2 Mean factor score by *Spartina alterniflora* height zone and physico-chemical grouping of marshes as determined by two-way ANOVA, $p \leq 0.05$.

***Spartina alterniflora* height zone**	**Physico-chemical grouping**	**Mean factor score for grouping**
tall	6T, 13T	106 ± 37
	21T,.150T	63 ± 2
medium	6M	162
	1M, 13M 21M,150M	31 ± 9
short	1S, 6S, 13S	180 ± 18
	21S	-5
	150S	-103

2.4 *Discussion*

2.4.1 Marsh re-growth and topographic changes with age

Coastal marsh plants are capable of rapid colonization of suitable unvegetated mud flat areas. In his classic marsh development paper, Redfield (1972) described the extension of back-barrier marsh on Broadway Island, Massachusetts from 1959 to 1967. From his Figure 18, I have estimated the growth rate at about 0.1 ha per year. DeLeeuw, et. al. (1993) reported on establishment and growth of a back-barrier marsh in the Netherlands, and from a figure in their publication, I have calculated a growth rate of approximately 3 ha per year. Furthermore, a one hundred-fold increase in *Spartina* spp. areal coverage over existing mud flat was reported by Hubbard (1965) in Poole Harbor, England over just a four year period. The Hog Island marshes of this study showed a colonization rate equal to DeLeeuw (1993). Between the years 1977 and 1979, about 6 ha of marsh establishment was observed on south Hog Island. Loss of salt marsh is an often-recorded phenomenon that is usually associated with aeolian processes (Redfield, 1972 and Hubbard, 1965). It is likely, therefore, that loss of 1.6 ha of Hog Island marsh area between 1985 and 1990 (Figure 2.3) was due to storm activity.

The theory of marsh development described by Redfield (1972) is a plausable scenario for the development of mainland and lagoonal marshes where sediment accretion elevates intertidal mud flats to mean low water, the minimum elevation for growth of *Spartina alterniflora*. Over-wash marshes, like the Hog Island marshes, however, may develop on platforms that were once above mean high water, the upper extent of *Spartina alterniflora* production. In these cases, marsh genesis depends on a lowering of the over-wash platform to elevations suitable for establishment of *Spartina alterniflora*. Evidence for this type of development would include a fully developed high marsh that existed prior to low marsh development. The 1 year old marsh (1Y) on Hog Island showed this pattern. High marsh extended for hundreds of meters in an upland direction and contained a full complement of typical high marsh plants: *Spartina patens, Distichlis spicata, Limonium* spp., *Borrichia* spp., etc., while the low marsh consisted of a narrow (approximately 4 m wide) strip of *Spartina alterniflora*. While north-east storms have been recognized as important marsh builders, maintainers, and destroyers in the mid-Atlantic region (Godfrey and Godfrey, 1976), the pattern of over-wash marsh development that I have outlined above suggests that north-west winds may also function in the mid-Atlantic region to erode and re-work over-wash platforms to levels suitable for low marsh development.

The elevation profile by age and height zone described in Figure 2.6 shows some interesting topography. Mean marsh-wide elevation decreased from 1Y to 150Y (which escaped burial in 1962). This pattern is probably more related to uneven over-wash deposition along the chronosequence (Fitch, 1991) than it is to marsh age. A general change from 'hummocky' young marshes characterized by scattered, discontinuous *Spartina alterniflora* height zones to older marshes whose surface increased gradually from water's edge to short *Spartina alterniflora* was observed (personal observation). These older marshes thus displayed a gradual decrease in *Spartina alterniflora* height with elevation. Any water - to - high marsh transect through 21Y and 150Y crossed tall, then medium, then short *Spartina alterniflora*. Accumulation of sediment trapped by *Spartina alterniflora* stems probably account for this smoothing with age. Thus these Hog Island marshes took at least 21 yrs to reach topographic maturity, that is to achieve a sediment grade and *Spartina alterniflora* zonation pattern that is associated with 150Y.

2.4.2 Age related differences in sediment and pore-water physico-chemistry

Tables 2.3 and 2.4 compare sediment and pore-water results from this study versus values previously reported in the literature. There is general agreement in magnitude in most cases. The values that I reported are whole marsh figures, with the young marsh being 1Y and the old one 150Y in both tables. Usually a range of values is reported , but when a single figure is given, it represents the mean of an extremely narrow range of values. The works of Osgood, Zieman and Tyler are of special relevance to this study because their efforts involved marshes associated with my sites. Osgood and Zieman (1993) used a 14-16 yr marsh on south Hog Island located about one kilometer south of

Table 2. 3 Comparison of sediment chemical values in young and old natural marshes (modified from Osgood and Zieman, 1993).

		Variables			
Author(s)	**Marsh age**	**% Sand**	**% Organic content**	**N (µmole/g)**	**$P0_4$ (µmole/g)**
Broome, et. al., 1875	young	92 - 97	0.2- 0.7		
	old	47 - 93	0.5 - 10.8		
Morris, 1988	young		2 - 6		
	old		6 - 42		
Osgood and Zieman, 1993	young	81 - 88	0.8 - 1.5		
	old	5 - 39	4.1 - 6.4		
Osgood, et. al., 1995	young	90 - 93	0.8 - 1.1	7.2 - 14.3	3 - 26
	old				
Levin, et. al., 1996	young	72 - 88	6.8 - 8.3		
	old				
Tyler, 1997	young	85 - 88	0.8 - 0.9		
	old	17	4.5		
This study	young	90 - 92	0.5	6	2 - 9
	old	21 - 56	5 - 9.5	69 - 110	14 - 29

Table 2. 4 Comparison of pore-water chemical values in young and old marshes (modified from Osgood and Zieman, 1993).

		Variables					
		Salinity (ppt)	**pH**	**E_H (mV)**	**NH_4 (µM)**	**S^{2-} (µM)**	**$P0_4^{3-}$ (µM)**
Author(s)	**Marsh Age**						
Gammill and Hosier,1992	young			+57 - +258			
	old			-103 - -60			
Osgood and Zieman, 1993	young	30 - 38		-81 - +242	20 - 39		26 - 57
	old	34 - 41		-121 - -188	31 - 131		38 - 92
Osgood, et. al., 1995	young	26 - 36	6.7 - 7.0	+4 - +207		1 - 25	
	old						
Tyler, 1997	young	28 - 38	6.6 - 6.9	+110 - +120	10 - 13	10 - 20	4 - 18
	old	34	6.9	0 - -10	42	420	42
This study	young	33 - 35	6.9	+17 - +72	9 - 11	7 - 130	18 - 61
	old	34 - 35	6.8	-31 - -63	29 - 13	482 - 1318	9 - 34

my sites and Tyler (1997) studied creek-bank chemistry from some of the chronosequence marshes of this study.

Decreases in sand content and increases in organic matter content are common sedimentary changes in salt marsh succession (Table 2.3). In fact, Odum (1969) predicted that increasing organic storage was a characteristic of ecosystem development in general. His prediction is borne out in these marshes. Higher levels of pore-water ammonium in chronosequence marshes also suggests that Odum, along with Vitousek and Reiners (1975), were correct about the ability of mature ecosystems to sequester nutrients. However, as Osgood (1995) has shown, standing stock is related to nutrient flux through hydrologic flow. I am unable to say, therefore, if nutrients are more efficiently sequestered in older chronosequence marshes since no hydrologic measurements were taken.

It is likely that *Spartina alterniflora* establishment is responsible for these important low marsh successional changes. Figure 2.19 describes physico-chemical variable interactions in determining marsh ecosystem structure. Plant stems decrease tidal velocity making deposition of finer sedimentary particles (silts and clays) possible. A positive feed-back loop ensues: increased above-ground production resulting from physical conditions that are more favorable to *Spartina alterniflora* growth leads to increased sediment nutrient stocks via decomposition (organic matter, N and P). This increases pore-water nutrient content which then elevates macrophyte production, and so on (Figure 2.19). The results of various authors in Tables 2.3 and 2.4, including this author, confirm

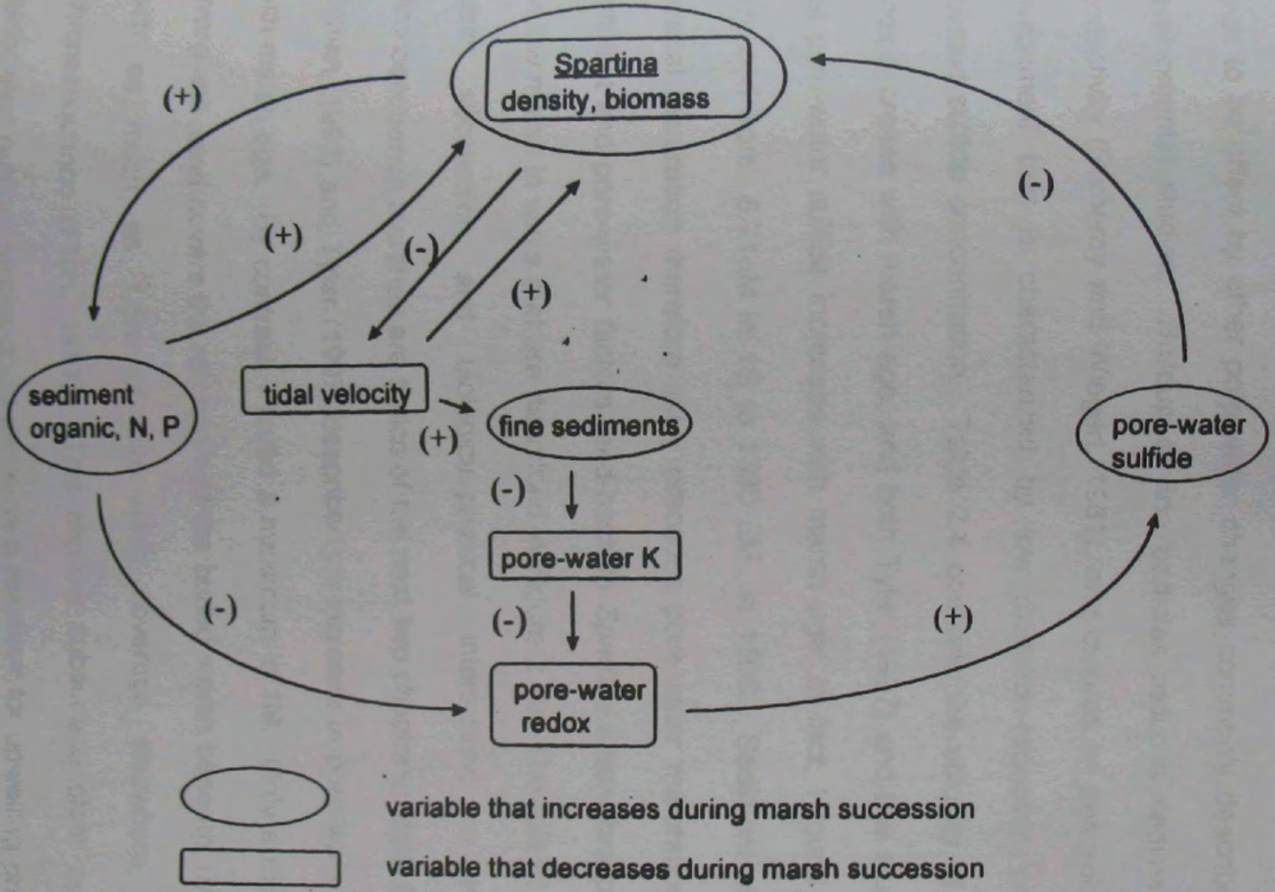


Figure 2. 19 Interactions and feed-backs among salt marsh variables. A **+** sign indicates that an increase in the donor box causes an increase in the recipient box. A **-** sign indicates that an increase in the donor box causes a decrease in the recipient box .

this hypothesis. According to the work reported therein, sediment nutrients increase with age, as does pore-water ammonium concentration. But this pattern tends to be offset by other pore-water changes commonly described in marsh developmental studies. Buildup of fine particles reduces sediment hydraulic conductivity (Pomeroy and Wiegert, 1981), and creates an anaerobic substrate environment that is characterized by low oxidation-reduction potential and elevated sulfide concentration. Table 2.4 confirms the ubiquity of age-related redox decrease with marsh age, and both Tyler (1997) and this study establish that pore-water sulfide increases with marsh age; in fact, I found that sulfide increased from 6.71μM in 1S to 1330 μM in 150S. Sediment chemical and physical maturation therefore likely precedes pore-water maturation, and both sediment and pore-water factors feed-back to *Spartina alterniflora* production in the low marsh in ways that are described in Figure 2.19. The role of biota in low marsh succession and biological-physical interactions in Hog Island chronosequence marshes are topics of the next two chapters. Both Osgood and Zieman (1993) and Tyler (1997) described an increase in pore-water phosphate with marsh age. By contrast, I found a maximum in 1M. Only a thin veneer of over-wash sand covers the remnants of the buried marsh beneath 1M compared with as much as 1.5m of over-wash coverage elsewhere along the chronosequence (Fitch, 1991). This shallow subsurface plant material and associated nutrient stocks could serve as a reservoir for upwelling phosphate to 1M. Indeed, Osgood, et. al. (1995) suggested that a buried mud flat had supplied an overlying sand flat with considerable pore-water nutrients. Pore-water sulfide and ammonium levels, however, are low at 1M.

How long does it take for a sediment / pore-water variable to resemble that of a mature marsh? Osgood and Zieman (1993) found that Hog Island marshes of their study exhibited physico-chemical values of mature marshes by 10 - 13 years of age. Table 2.5 demonstrates a great deal of difference in maturation time by variable and height zone, but it demonstrates an overall trend that was first discovered by Tyler (1997) for creek-bank substrate variables; marsh physico-chemical maturation is more rapid nearer the water's edge, when considering a single variable at a time. The multivariate view described below demonstrates a different pattern.

2.4.3 Physico-chemical stages in chronosequence marshes

The results of correspondence analysis outlined in Table 2.1 verify that a large part of the variation in the physico-chemical data from chronosequence marshes can be identified by a very few variables. In fact, axis one, which is displayed in Table 2.1, explains 79% of the variation in the data. The central role of this vector can be summarized by a single variable, pore-water oxidation-reduction potential (redox). Pore-water redox has long been suggested as a driving factor of wetland chemistry (Mitsch and Gosselink, 1986), and its link to

Table 2. 5 **Maturation time in years for sediment and pore-water variables by height zones.**

	Height zones		
Variables	**Tall**	**Medium**	**Short**
Sediment sand content	6	150	150
Sediment organic content	150	21	21
Sediment nitrogen	6	150	21
Sediment carbon	6	13	21
Sediment phosphate	6	6	6
Pore-water E_H	21	13	150
Pore-water ammonium	6	13	150
Pore-water sulfide	6	13	150

other variables on this vector is clear. For instance, sulfide concentration tends to increase under anaerobic conditions as sulfate is preferred as an electron acceptor in microbial metabolism (Pomeroy and Wiegert, 1981). Thus, the title of this vector, ' Pore-water Aeration' reflects the effect of pore-water oxygen levels on microbial biochemistry.

Although the five marshes included in this study all appear to be identical with respect to plant community, the correspondence analysis results indicated that there are significant age-related differences in the physico-chemical make-up of these ecosystems. Moreover, identification of different systems by use of ANOVA performed on mean factor scores distinguished marshes based on important multivariate groupings, and gives a complete description of what I call PC-stage. The most obvious result of CA is that the five marshes did not constitute five separate PC-stages (Figure 2.18). The young marshes (1Y, 6Y and 13Y) constituted two separate stages, both characterized by relatively high pore-water aeration levels (Figure 2.18). The two older marshes (21Y and 150Y) constituted a low aeration stage.

However, because of the significant statistical interactions between marsh age and *Spartina alterniflora* height zone, each zone's development must be considered separately. Doing so shows that both the tall and short zones displayed decreased mean factor score with age (Table 2.2), that is, pore-water aeration decreased with age. As Table 2.2 points out, two distinct age-related PC-stages existed in the tall zone, and three stages were identified from the short zone. The medium zone groupings also showed a decrease in mean factor score with age, but the groupings placed the youngest and oldest medium zones together as statistically indistinguishable. A possible reason for this unusual similarity may be that 1M is underlain by mature marsh that was buried in the 1962 storm. Thus, 1M appears more mature than it would appear without this sub-surface influence. However, even without 1M, the medium zone matures faster than the other two zones. Using Table 2.2, maturation time for the medium zone (without 1M) was from 6 to 13 years, as compared to 13 to 21 years for the tall zone and 21 to 150 years for the short zone. Thus, Osgood and Zieman's (1993) estimate of 10-13 years for marsh physico-chemical maturation is on the same order of magnitude for two of the three zones in my study (tall and short), and points out the need to discuss marsh development by height zone.

Tyler (1997) found that the tall *Spartina alterniflora* area associated with creek-banks developed chemically faster than areas that I would classify as medium height. The difference in my findings may reflect the larger and more heterogeneous area of marsh that was included in my study, versus the relative homogeneity of creek-bank areas.

A central thesis of this work is the need to view ecosystems, or in this case, physico-chemical stages in a multivariate, rather than a univariate way. Discrepancies in the results between univariate and multivariate analyses showed up in two areas of this work. First, I attempted to narrow the age of marsh 150Y by fitting regression curves of individual variables versus time, and extrapolating the curve to the value of each variable that I had measured for 150Y. Using this technique, I found an age range of 45-70 years for 150Y, a range that, according to aerial photographs and old maps is too young. Using regression analysis on mean factor scores from correspondence analysis however, I obtained an age estimate of 170 years, clearly a more appropriate age. Secondly, estimated time to maturity for the three height zones varied between univariate and multivariate analyses. By using individual variables, it appeared that the tall zone matured faster than the other two zones. However, using factor scores of CA, it was shown that the medium zone matured faster than either the tall or short zones. It is therefore crucial in describing a system of interacting variables, to recognize those interactions through the use of multivariate, rather than univariate methods.

The placement of the mean factor score of a marsh along axis one allowed for the estimation of physico-chemical maturation times by height zone (see the previous paragraph). A description of system dynamics, that is, the change in mean factor score over time, requires that the time intervals between the five chronosequence marshes be standardized. One way to accomplish this is to calculate annual mean factor score difference between marshes of 'adjacent' age. For example, for the adjacent marshes 6Y and 13Y, which differ in age by 7 years, I converted the mean factor score difference between these two marshes to an annual difference by dividing mean factor score difference by seven. Large annual differences between factor scores reflect relatively great year-to-year variations in the pore-water aeration characteristics of that marsh over the time interval in question, and small differences suggest a relative temporal stability in the pore-water characteristics of the marshes in question. Figure 2.20 illustrates these per annum changes in mean factor score over the four marsh age intervals along the chronosequence, 1Y to 6Y, 6Y to 13Y, 13Y to 21Y, and 21Y to 150Y. The graph displays some interesting zonal dynamics. The medium zone showed a great inter-annual factor score difference up until about 13 years of age, when inter-annual factor score difference decreased, and continued to do so, until very little inter-annual difference occurred after about 21 years of age. In other words, the older the medium zone marsh, the greater the inter-annual stability in pore-water aeration characteristics. The tall and short zones showed maximum inter-annual factor score differences between 13 and 21 years of age, and then followed the pattern of reduced inter-annual differences as seen in the medium zone. In all three zones, therefore, inter-annual differences in mean factor score decreased after 13-21 years of age. This suggests that temporal physico-chemical stability in all three zones increased with marsh age from a teen-aged marsh to a mature one of a few hundred years old. A mature marsh, 150Y of the chronosequence for instance, would be expected to demonstrate little inter-annual difference in pore-water aeration characteristics. This 'channeling' effect seen in Figure 2.20 for marshes older than 13 to 21 years of age, suggests a directionality in marsh succession, at least with respect to physico-chemical aspects. Directionality in ecosystem succession toward a 'climax' community has of course been a mainstay idea in succession research over the past 100 years

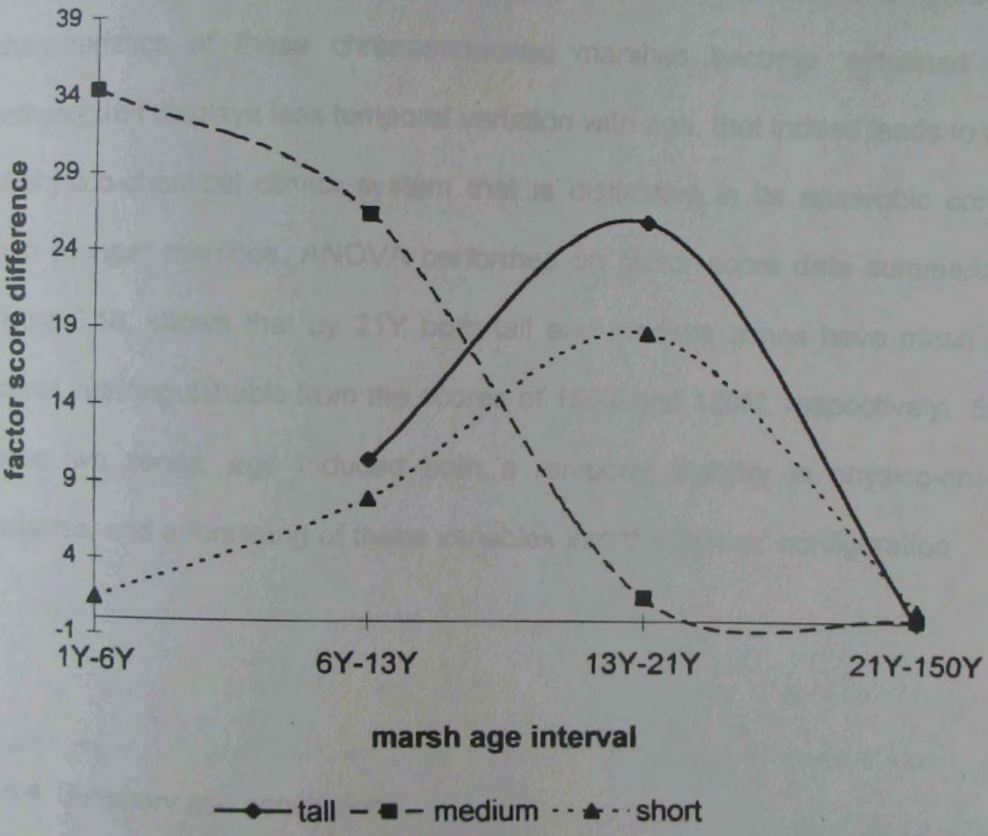


Figure 2. 20 Change in mean annual factor score for four age intervals of adjacent marshes of the chronosequence by height zone. The larger the inter-annual difference in factor score, the more different the pore-water characteristics are from year to year.

(Cowles, 1899, Clements, 1916, 1936, and Odum 1969). However, the focus of the work has been on directionality of plant communities toward a stable array of plants called the 'climax' community. I am suggesting that in the absence of catastrophic over-wash events, salt marsh sediment and pore-water characteristics of these chronosequence marshes become 'entrained' on a pathway that displays less temporal variation with age, that indeed leads to a type of physico-chemical climax system that is distinctive in its anaerobic condition from younger marshes. ANOVA performed on factor score data summarized in Figure 2.18, shows that by 21Y both tall and medium zones have mean factor scores indistinguishable from the scores of 150T and 150M, respectively. So, for these two zones, age induced both a temporal stability in physico-chemical variables, and a funneling of these variables into the 'climax' configuration.

2.4.4 Summary and conclusions

The over-wash marshes of south Hog Island represent a dynamic landscape whose features are ultimately determined by intense storms. Early marsh development at this site did not follow the Redfield (1972) marsh developmental plan, but formed high marsh to low marsh in areas where the over-wash plain was elevated above mean high water. Young marshes of this chronosequence (1Y to 13Y) were characterized by sediments that were sandy, low in organic matter, well drained, and whose pore-water showed the effects of aerobic conditions: high E_H, few nutrients, and low sulfide levels. The mature marsh, 150Y, contained sediment with fine particles predominating, greater amounts of organic matter, and low pore-water E_H, and a buildup of nutrients and sulfide.

In spite of the homogeneity of plant communities along the choronosequence, statistically distinct physico-chemical stages were identified using a multivariate statistical approach that explained a large portion of the variation in the data (79%) by just a few variables. However, physico-chemical succession must be described zonally, and correspondence analysis results indicated that the medium zone matured at a faster rate than the tall and short zones. Moreover, age imposed a temporal stability on these marshes. That is, their interannual variability with respect to pore-water characteristics generally decreased with age, and by 13 to 21 years of age, they became tracked into a physico-chemical sere that resulted in a PC-stage that can best be described as a PC-climax.

How applicable are these findings to salt marshes in general? The successional trends noted herein are probably ubiquitous to all salt marshes, especially those related to the creation and maintenance of anaerobic sediments and pore-water subsequent to the accumulation of fine particles with age: reduced E_H and elevated sulfide and ammonium concentrations. Reasons for deviations from this trajectory include development over a less sandy platform, for instance. Lagoonal and mainland marshes of the Virginia Coast Reserve likely develop on finer sediments than the over-wash sands of south Hog Island, and, although the general developmental picture is probably similar for these marshes, maturation time may be less. Differences in tidal range are also likely to affect the rate of development, rather than the direction. Finally, local landscape factors related to the volume of ground-water flow from upland vegetated areas (Tyler, 1997), the presence of buried nutrient reservoirs (Osgood, et. al., 1995), and salt flat formation in the high marsh (Santos,1996) influence *Spartina alterniflora* production in ways that may alter the rate, but not likely, the direction of substrate succession.

CHAPTER THREE

SUCCESSION IN LOW MARSH BIOLOGICAL COMMUNITIES ALONG AN OVER-WASH SALT MARSH CHRONOSEQUENCE

3. Community succession along an over-wash salt marsh chronosequence

3.1 *Introduction*

Ecosystem succession has long been the territory of plant ecologists. One result of this imbalance has been the use of plant community characteristics to characterize seral stages of an entire biological community. However, as early as 1935, Shelford and Olson recognized the importance of animals in structuring successional stages. In fact, they preferred the term 'spruce-pine-moose' community to describe a boreal forest seral stage, thereby acknowledging the crucial role of at least one mammal in determining community characteristics. Shelford and Olson (1935), in fact, cited other major 'influents' in boreal habitats: caribou, wolves, bears and wolverines. They stated that these large animals:

> '....leave profound effects upon succession which have been all too little studied, due to the fact that plant ecologists have rarely taken animals into consideration.'

Animal communities show varied reactions to successional changes. Bird density and community diversity increase as the structural complexity of old-field seral stages increases. In addition, each seral stage in old field succession possesses a unique assemblage of avifauna. (Luken,1990). Large vertebrates also vary in their successional stage requirements. That is, some vertebrates, like white-tailed deer and moose, require a range of successional stages, while others, like the marten need only single successional phases (seral stages) in which to survive and reproduce (Luken, 1990).

Resident fauna can also influence successional changes. Watt (1962, in Luken, 1990) concluded that high rabbit density on English grasslands caused a retrogression in plant community. Sheep, likewise, have been found to slow succession in *Juncus squarosus* grasslands in Great Britain (Marrs, et al., 1988, in Luken, 1990). Although few generalizations can be made concerning the effects of cattle grazing on grassland succession, it appears that moderate cattle density results in increased plant diversity (Luken, 1990), a characteristic of later seral stages. The most dramatic example of animal regulation of succession is the effect of the African elephant, *Loxodonta africana*, on savanna succession. Because these large herbivores not only graze, but sometimes uproot and overturn trees, their presence significantly reduces tree density and hence slows the rate of succession of savanna to forest (Smart, et al., 1985, in Luken, 19990).

These important forces in terrestrial succession are for the most part large vertebrate herbivores. Can smaller invertebrate herbivores with large populations have similar impacts on intertidal systems? Specifically, do macroinvertebrate assemblages of intertidal systems change with ecosystem succession in ways similar to terrestrial vertebrate assemblages? In one of the few works on intertidal invertebrate community changes during succession, Levin, et al. (1996) compared macrobenthos within created and natural salt marshes within the Newport River Estuary in North Carolina. They found that early salt marsh colonizers consisted of fiddler crabs (*Uca* spp.) and grapsid crabs whose planktonic larvae and rapid growth rates helped to populate the created marsh quickly. Later successional invertebrates consisted of grazing snails. No mention is made, however, of the possible roles of macro-invertebrates in the successional process.

In this Chapter, I describe the biological characteristics of salt marshes of five different developmental ages, with respect to the major primary producer, *Spartina alterniflora*, and the five most common epifaunal macro-invertebrates: two *Uca* spp., *Littorina irrorata, Geukensia demissa*, and *Ilyanassa obsoleta*. The dearth of species throughout the chronosequence marshes begs another question: Do such species-poor communities undergo a process that one could call succession? Organism density and biomass is examined by marsh age and three *Spartina alterniflora* height zones. I also present correlational evidence for possible roles of macro-invertebrates in modifying the speed and direction of community succession through their interaction with physico-chemical variables (Chapter 2). As in Chapter 2, I use a multivariate statistical method, correspondence analysis (CA), to define statistically distinct stages. In the last Chapter, I referred to statistically individual stages as PC, or physico-chemical stages. In this Chapter, distinct statistical entities along the Hog Island chronosequence are appropriately called biological communities. Variables that explain significant amounts of data variation, and thus structure the community are identified, and changes in biological community structure with age are described.

Finally, I examine the application of a few successional theories in these chronosequence marshes. Bormann and Likens (1979) and Odum (1969) predicted that intermediate aged ecosystems are more productive than younger or older ones. Following this logic, we would therefore expect 6Y or 13Y of the Hog Island chronosequence to be the most productive marshes, and 1Y and 150Y to be the least productive. I also evaluate the evidence for a 'climax community' (Clements, 1916). That is, an assemblage of macrophyte and associated epifauna toward which younger marsh communities move with time in the absence of severe disturbance (over-wash). I also evaluate Odum's (1969) idea that biological communities become more stable with community age. I use correspondence analysis factor score changes from year to year as proxy measurements of inter-annual stability of these Hog Island marsh communities.

3.2 *Methods*

3.2.1 Study site

Sampling was conducted on the marshes of the Hog Island, Virginia over-wash marsh chronosequence, which was described in detail in Chapter 2. Sampling quadrat locations within the five different aged marshes were the same as those described in Chapter 2. As in the previous Chapter, marsh age is based on dates of available aerial photographs, and marshes are assigned the maximum age possible given these dates. Moreover, maturation time for a marsh is measured as in Chapter 2. That is, maturation time for any variable, or group of variables is the minimum time that it takes for a variable to be statistically similar in value to the same variable in 150Y, the mature marsh of the chronosequence. A maturation time estimated by this method to be 6 years, is really in the interval 2 to 6 years, based on the dates of aerial photography. This is most crucial for variables whose maturation time is 150 years, since maturation time could be anywhere from 22 to 150 years.

3.2.2 *Spartina alterniflora* sampling

Measurements of *Spartina alterniflora* variables were conducted during the months of May, July, and September of 1995 and 1996, with the exception of individual plant biomass measurements; these were done in September, 1995 only. Graphs of *Spartina alterniflora* height, density, areal biomass, and percent flowering represent mean values of pooled data for two years collection.

Spartina alterniflora height determinations were carried out on 12 randomly chosen plants per quadrat (one square meter) that were found along a diagonal line from corner to corner of the quadrat. Thus, sample size per height zone of a marsh of a particular age was 36 plants. Height was measured from sediment to the tip of the longest leaf, and flowering was also noted at this time.

Spartina alterniflora plant density was assessed by counting plant stems within either a 0.25 m^2 or a 0.0625 m^2 randomly chosen area within each quadrat.

In order to measure end-of-season biomass, all plants within a 0.25 m^2 area adjacent to each sampling quadrat were clipped at sediment level, cleaned of epibionts, measured, and dried at 60 °C for 24 hours, and then weighed. The resulting height-weight regression equations showed a close relationship between these two variables (see Table 3.1 for overall equations for each height zone). The equation derived for each height zone was then used to calculate mean above-ground biomass using 12 randomly selected plants per quadrat (36 plants per height zone comparison). The equations that were derived in 1995 were used again in 1996.

Table 3. 1 *Spartina alterniflora* height to weight regression equations and Pearson correlation coefficients by height zone.

Height zone	**Equation**	**Correlation coefficient**
Tall	$\text{weight} = 0.0096\ \text{height}^{2.06}$	0.81
Medium	$\text{weight} = 0.0013\ \text{height}^{1.92}$	0.91
Short	$\text{weight} = 0.0006\ \text{height}^{2.12}$	0.91

Mean individual plant biomass was calculated using the areal mean derived above (grams per square meter) and the measured density for that quadrat (individuals per square meter).

3.2.3 Macro-invertebrate sampling

The four most common epifaunal macro-invertebrates of the low marsh were sampled: *Uca* spp., that is *Uca pugilator* (the sand fiddler crab) and *Uca pugnax* (the mud fiddler crab), the common periwinkle, *Littorina irrorata*, the mud snail, *Ilyanassa obsoleta*, and the ribbed mussel, *Geukensia demissa*. Organism densities were determined during the months of May, July, and September, 1995 and 1996, and end-of-season biomass was determined in August, 1995, for *Uca* spp., and October, 1995, for the other species.

Density determinations of *Uca* spp. assumed that each crab burrow was inhabited by just one crab (Krebs and Valiela, 1978, and J. Shields, personal communication), thus allowing an accurate fiddler crab density by counting burrows. Fiddler crab species composition was determined in May, 1995, by observing each quadrat during a falling tide, and noting the species composition of emerging fiddler crabs; subsequent observation showed that *Uca* spp. composition did not change over the course of the study in any of the marshes.

Uca spp. biomass estimations necessitated the use of a series of species-specific regression equations that can be found in Table 3.2 and Figure 3.1. Figure 3.1 shows all of the invertebrate allometric regression equations used in this Chapter to estimate organism biomass. The *Uca pugilator* burrow opening size - carapace width relationship was determined by measuring carapace and associated burrow opening for 98 crabs (Table 3.2 and Figure 3.1). In estimating fiddler crab biomass, I assumed that the two oldest marshes included mud fiddler crabs only, and that the three youngest marshes had only sand fiddler crabs; inspection of Figure 3.9 corroborates this assumption. The diameters of twelve burrows were measured per quadrat, and the appropriate equations were applied to each, resulting in estimates of biomass of fiddler crabs per area for each height zone of each of the five marshes of the chronosequence. Individual fiddler crab mass was estimated using the areal biomass and density of burrows for each quadrat.

Shell-free biomass was estimated for the other invertebrate species using the following length measurements: for *Littorina irrorata* and *Ilyanassa obsoleta*, the length from shell apex to tip of the canal, and for *Geukensia demissa*, maximum length along a valve (Figure 3.1). To determine shell length to shell-free body mass for each species, approximately 100 organisms of each species were randomly collected along the chronosequence, cleaned of epibionts, dried at 60 °C for 5 days (*Geukensia demissa* required 7 days to reach a constant weight), and then ashed at 500 °C for 30 minutes (Janet Thompson, personal communication). Shell free dry weight was then calculated by pre and post-

Table 3. 2 Regression equations used to calculate fiddler crab biomass

	Species	
Variables regressed	***Uca pugilator***	***Uca pugnax***
X = burrow opening diameter in cm Y = carapace width in cm	$Y = 0.91X - 0.02$, $r = 0.92$ (this study)	$Y = 0.89X + 0.12$, $r = 0.96$ (Krebs and Valiela, 1978)
Y = carapace width in cm X = crab dry weight in mg	$Y = 0.000072X^{3.27,}$ $r = 0.98$ (Colby and Fonseca, 1984, average values for both sexes)	$Y = 0.00067X^{3.16}$, $r = 0.91$ (Cammen, et. al., 1980)

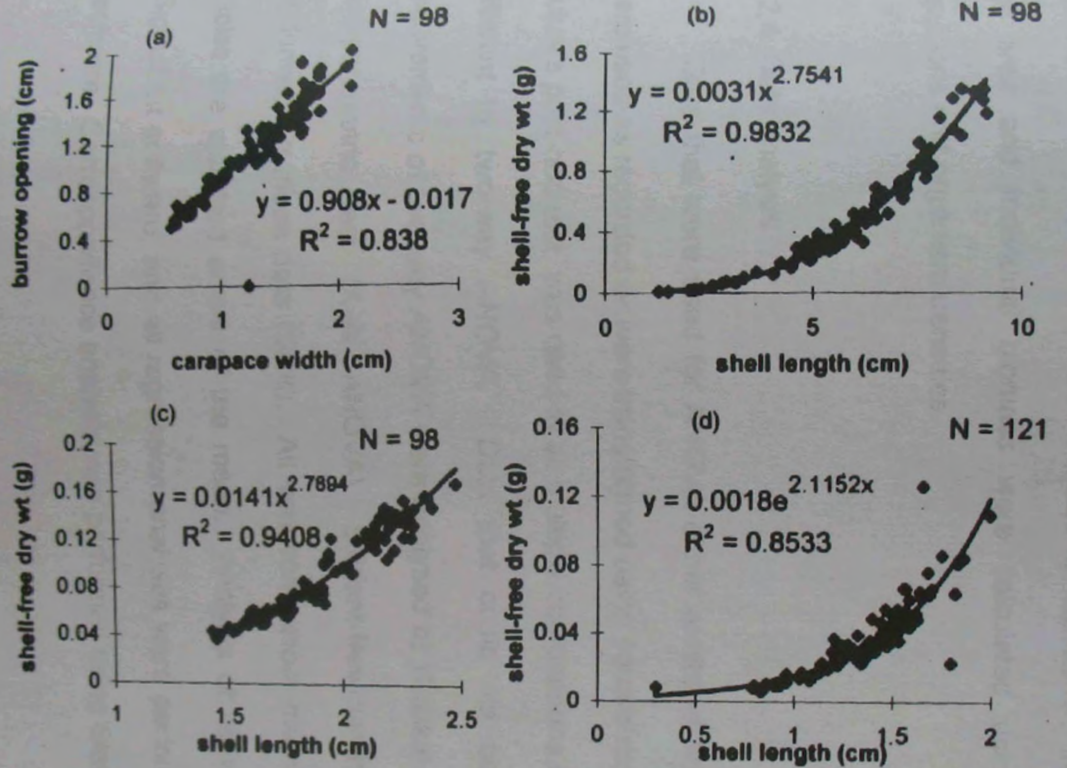


Figure 3. 1 Allometric relationships within each of the four epifaunal groups that were used to generate regression equations in this chapter to calculate biomass. (a) is *Uca pugnax* carapace width vs. burrow opening, (b) is *Littorina irrorata* shell length vs. dry weight, © is *Geukensia demissa* valve length vs. dry weight, and (d) is *Ilyanassa obsoleta* shell length vs. dry weight.

ashing weight difference, and species-specific length-weight regression equations were determined. For each of the non-*Uca* species, 12 organisms were randomly collected in each quadrat (adjacent areas for *Geukensia demissa*) and biomass per area and individual biomass were calculated using these regression equations and organism densities.

3.2.4 Data analysis

Data that were used for ANOVA either exhibited homogeneity of variance and were used as recorded or were transformed using square root and logarithm transforms. Tukey's post-hoc test was used in all multiple comparisons of means found significantly different by two-way ANOVA. Data that could not be transformed to suit the requirements of two-way ANOVA were analysed by Kruskal-Wallis ANOVA on ranks, a non-parametric test (K-W ANOVA); Student-Newman-Keuls post-hoc test was performed on these data (SNK). All variations about the mean shown in graphs and tables are standard errors of the mean. Analysis of variance was performed using SigmaStat software, and all regression analyses were performed using Microsoft Excel software. Correspondence analysis was performed using Statistica software.

3.3 *Results*

Figure 3.2 summarizes the age and zone groupings of each of the biological variables of chronosequences marshes. Age groupings are indicated by letters in cells along the rows of an age-zone matrix . Marshes that are statistically similar for a variable within a height zone show identical letters. Height zone groupings are indicated by shading of cells in a particular column (marsh age). Statistically similar zones of a marsh have identical shading. Marshes whose three height zones demonstrated a pattern that was too complicated to illustrate by this method are shaded in black. Matrices that include only a single row and column represent variables that were analyzed by one-way ANOVA, or by two-way ANOVA that lacked age-zone interactions. In these instances, statistical groupings could only be made by over-all age and height zone similarities. Refer to Figure 3.2 for the grouping of each variable by age and height zone, along with the figures mentioned for each variable in the following text.

3.3.1 *Spartina alterniflora* results

Spartina alterniflora plant heights showed a statistical zonation but failed to demonstrate age dependency. Pooled height measurements differentiated the low marsh into the three height zones that I had distinguished visually (Figure 3.3a). The tall zone had a pooled mean height of 69.2 cm ± 6.8, the medium

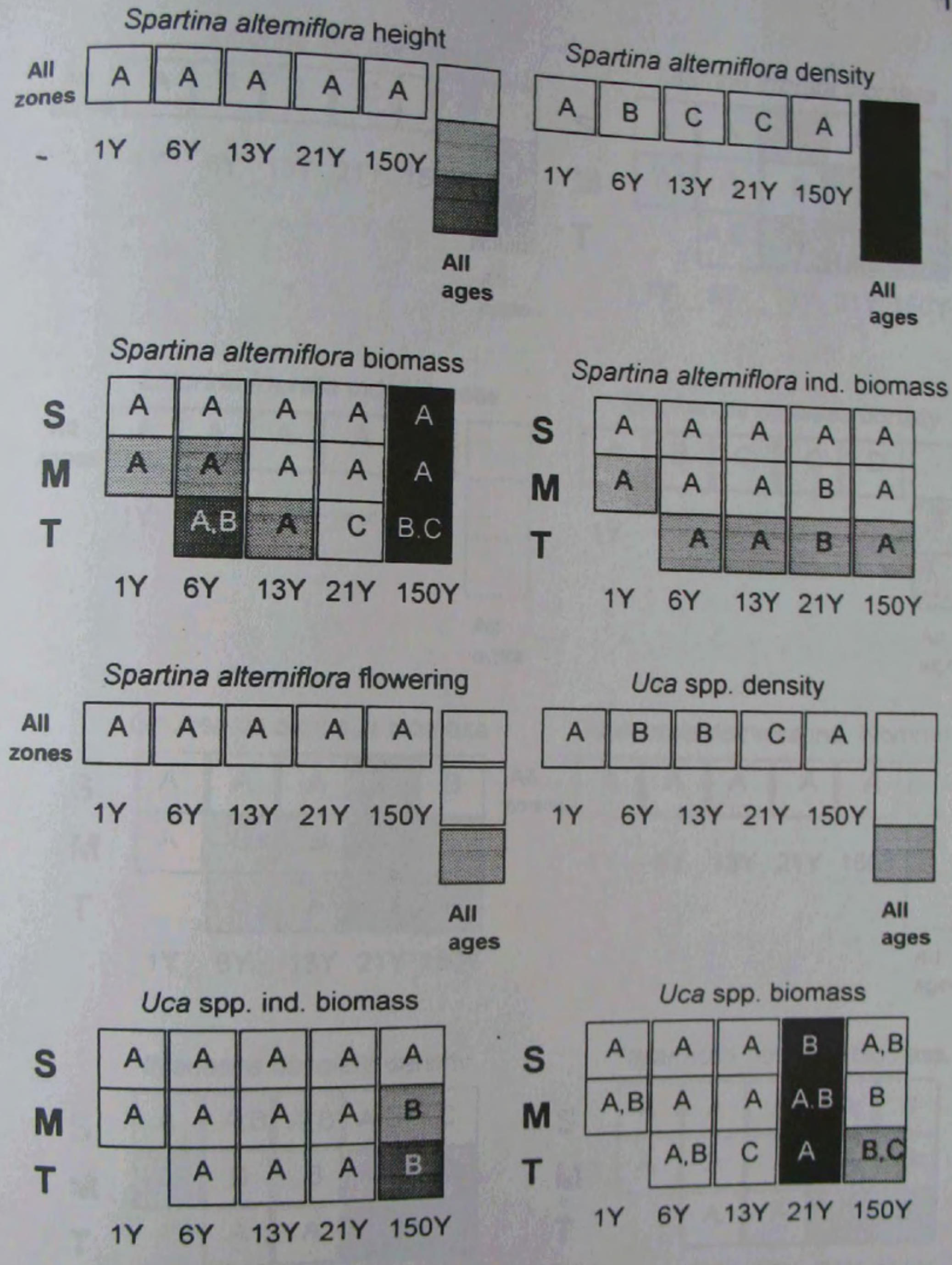
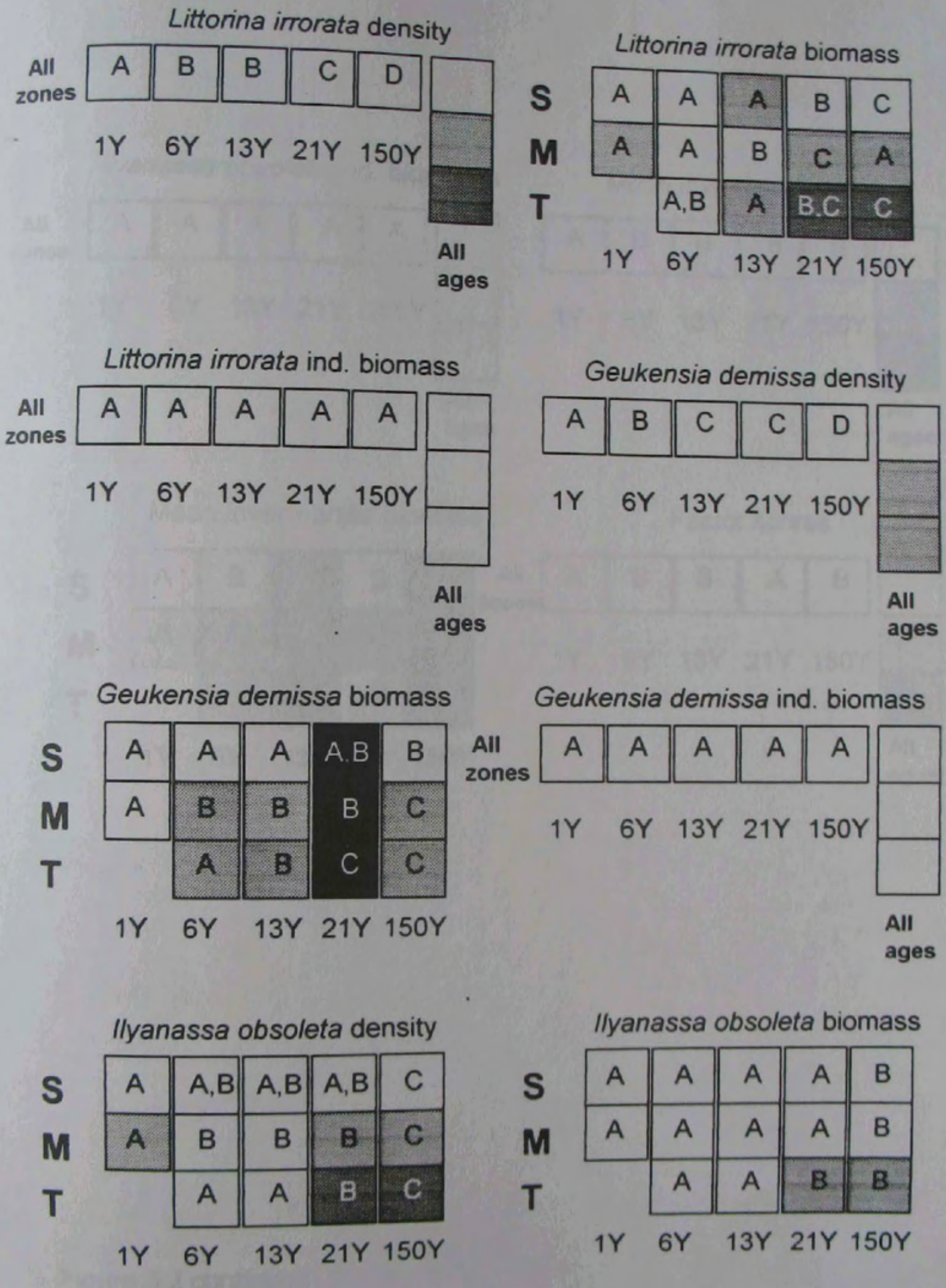


Figure 3. 2 Matrices showing the statistical groupings of each variable by marsh age and height zone. Age grouping is indicated by letters along the rows, and height zones are grouped within a marsh by shading. Marshes whose height zone grouping pattern was too complex to illustrate this way are shaded in black. Matrices that composed of a single row and column were analyzed by one-way ANOVA , and only whole-marsh or zone comparisons could be made.



Littorina irrorata density

	1Y	6Y	13Y	21Y	150Y
All zones	A	B	B	C	D

All ages

Littorina irrorata biomass

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	B	C
M	A	A	B	C	A
T		A,B	A	B,C	C

Littorina irrorata ind. biomass

	1Y	6Y	13Y	21Y	150Y
All zones	A	A	A	A	A

All ages

Geukensia demissa density

1Y	6Y	13Y	21Y	150Y
A	B	C	C	D

All ages

Geukensia demissa biomass

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	A,B	B
M	A	B	B	B	C
T		A	B	C	C

Geukensia demissa ind. biomass

	1Y	6Y	13Y	21Y	150Y
All zones	A	A	A	A	A

All ages

Ilyanassa obsoleta density

	1Y	6Y	13Y	21Y	150Y
S	A	A,B	A,B	A,B	C
M	A	B	B	B	C
T		A	A	B	C

Ilyanassa obsoleta biomass

	1Y	6Y	13Y	21Y	150Y
S	A	A	A	A	B
M	A	A	A	A	B
T		A	A	B	B

Figure 3.2 continued

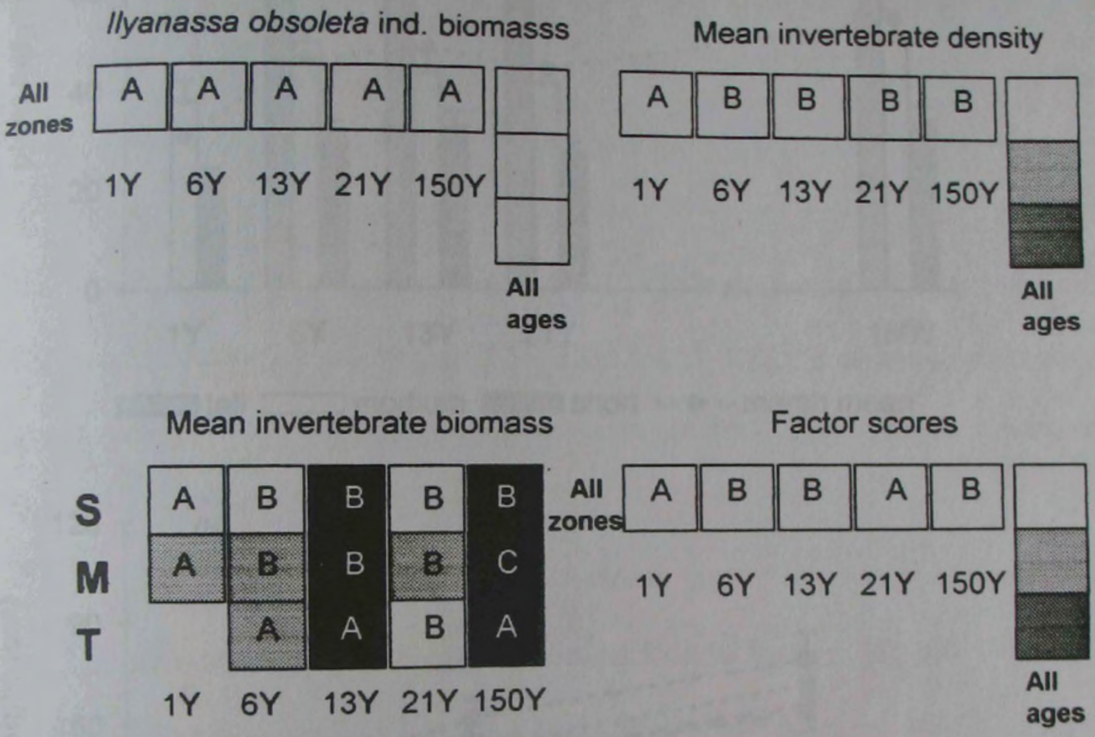


Figure 3.2 continued

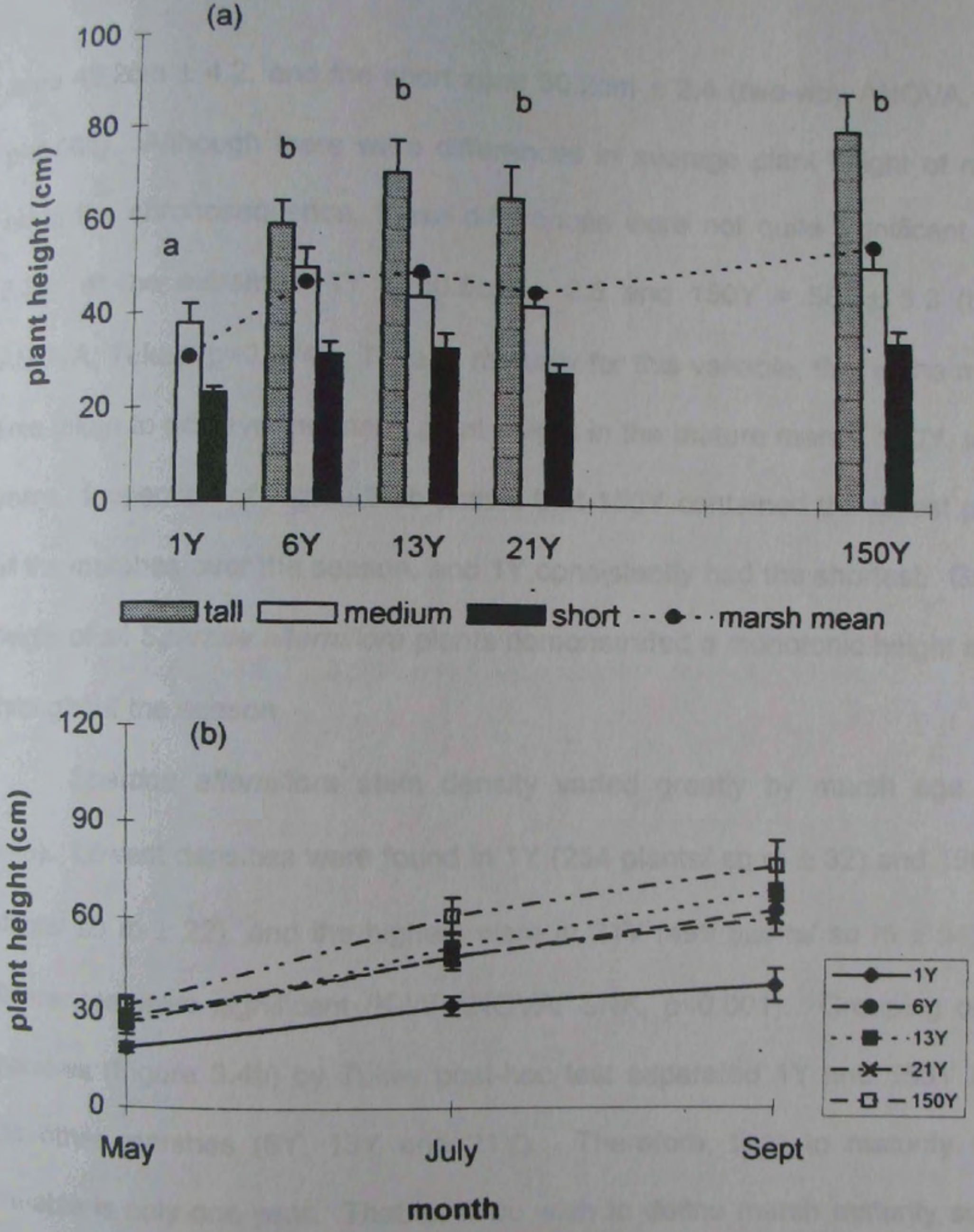


Figure 3. 3 (a) *Spartina alterniflora* plant heights by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide plant heights.

zone 45.2cm ± 4.2, and the short zone 30.2cm ± 2.4 (two-way ANOVA, Tukey, $p < 0.001$). Although there were differences in average plant height of marshes along the chronosequence, these differences were not quite significant (Figure 3.3a): at the extremes, 1Y = 30.5cm ± 2.8 and 150Y = 56.7± 5.3 (two-way ANOVA, Tukey, $p = 0.074$). Time to maturity for this variable, that is the minimum time taken to achieve the mean plant height in the mature marsh, 150Y, is only 6 years. Inspection of Figure 3.3b shows that 150Y contained the tallest plants of all the marshes over the season, and 1Y consistently had the shortest. Growth in height of all *Spartina alterniflora* plants demonstrated a monotonic height increase throughout the season.

Spartina alterniflora stem density varied greatly by marsh age (Figure 3.4a). Lowest densities were found in 1Y (254 plants/ sq m ± 32) and 150Y (270 plants/ sq m ± 22), and the highest were in 21Y (499 plants/ sq m ± 54); these differences were significant (K-W ANOVA, SNK, $p < 0.001$). Grouping of whole marshes (Figure 3.4a) by Tukey post-hoc test separated 1Y and 150Y from all the other marshes (6Y, 13Y and 21Y). Therefore, time to maturity for this variable is only one year. That is, if we wish to define marsh maturity solely by *Spartina alterniflora* stem densities, then this nascent marsh appears more mature (has lower stem density) than one of intermediate age (that has a higher density of plants). Figure 3.4b shows that these age-related differences were

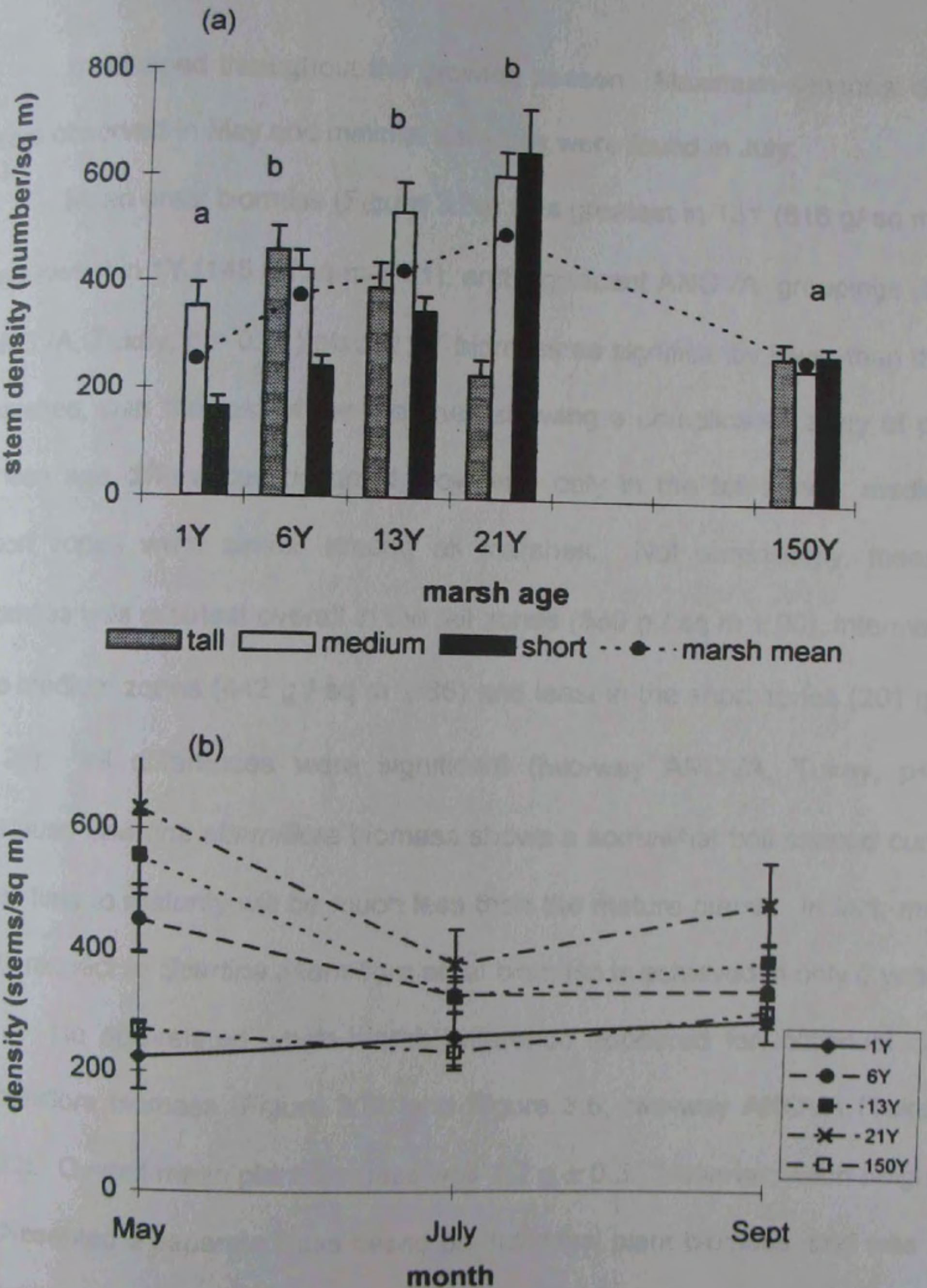


Figure 3. 4 (a) *Spartina alterniflora* stem densities by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars, and (b) monthly marsh-wide stem densities.

maintained throughout the growing season. Maximum seasonal densities were observed in May and minimal densities were found in July.

Mean areal biomass (Figure 3.5a) was greatest in 13Y (616 g/ sq m ± 278) and lowest in 1Y (145 g / sq m ± 91), and significant ANOVA groupings (two-way ANOVA, Tukey, p = 0.01) placed 1Y biomass as significantly lower than the other marshes, with the rest of the marshes showing a complicated array of pairings. These age differences occurred, however, only in the tall zones; medium and short zones were similar among all marshes. Not surprisingly, mean zonal biomass was greatest overall in the tall zones (689 g / sq m ± 90), intermediate in the medium zones (442 g / sq m ± 86) and least in the short zones (201 g / sq m ± 25); all differences were significant (two-way ANOVA, Tukey, p<0.001). Because *Spartina alterniflora* biomass shows a somewhat bell-shaped curve with age, time to maturity will be much less than the mature marsh. In fact, maturity , with respect to *Spartina alterniflora* areal biomass is achieved in only 6 years.

No age-related whole-marsh difference appeared for individual *Spartina alterniflora* biomass (Figure 3.5b and Figure 3.6; two-way ANOVA (Tukey, p = 0.30). Overall mean plant biomass was 1.2 g ± 0.5. However, each height zone represented a separate class based on individual plant biomass, and was strictly related to plant height (two-way ANOVA, Tukey, p<0.001). The tall zone averaged 1.99 g/ individual ± 0.20, the medium zone averaged 0.96 g/ individual ± 0.20, and the short zone averaged 0.56 g/ individual ± 0.07.

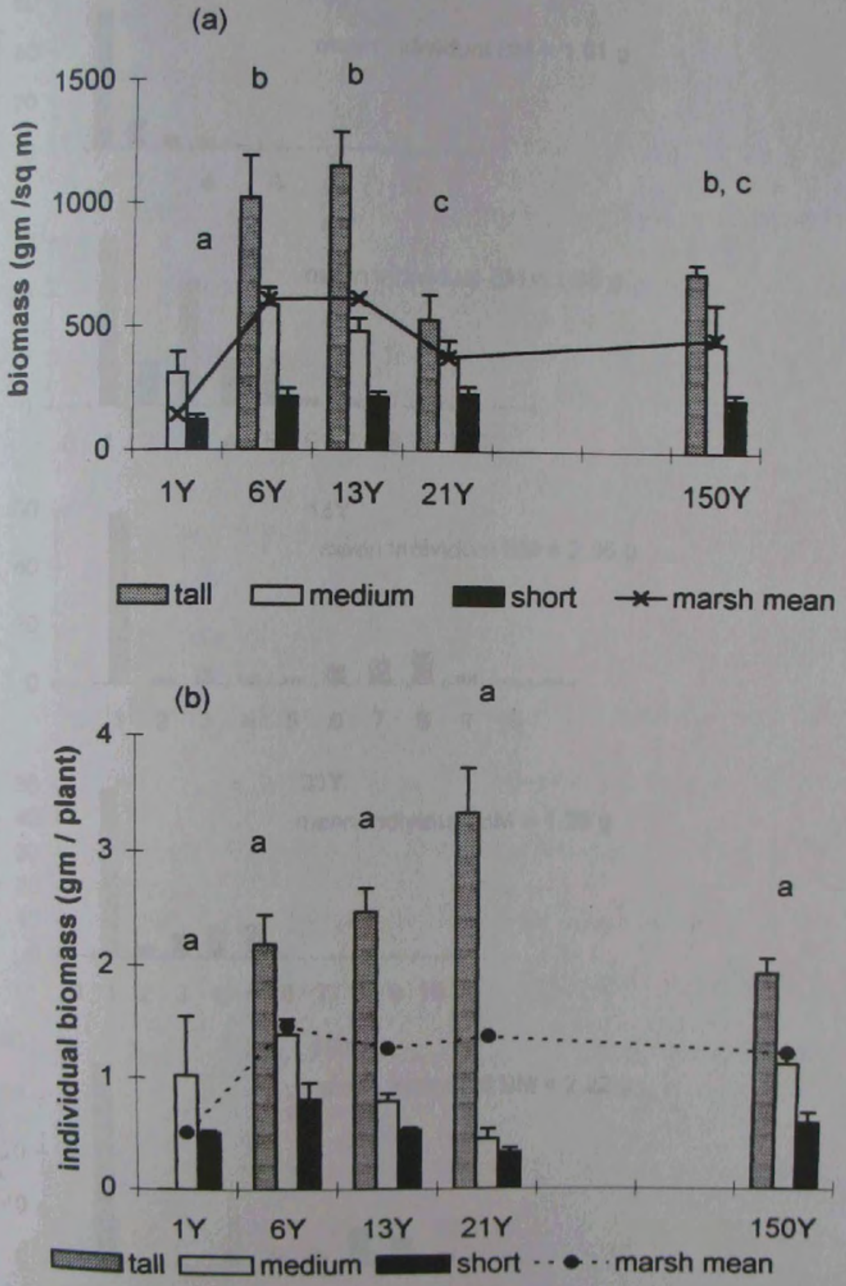


Figure 3. 5 (a) *Spartina alterniflora* mean areal biomass by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars, and (b) *Spartina alterniflora* individual biomass by marsh age and height zone.

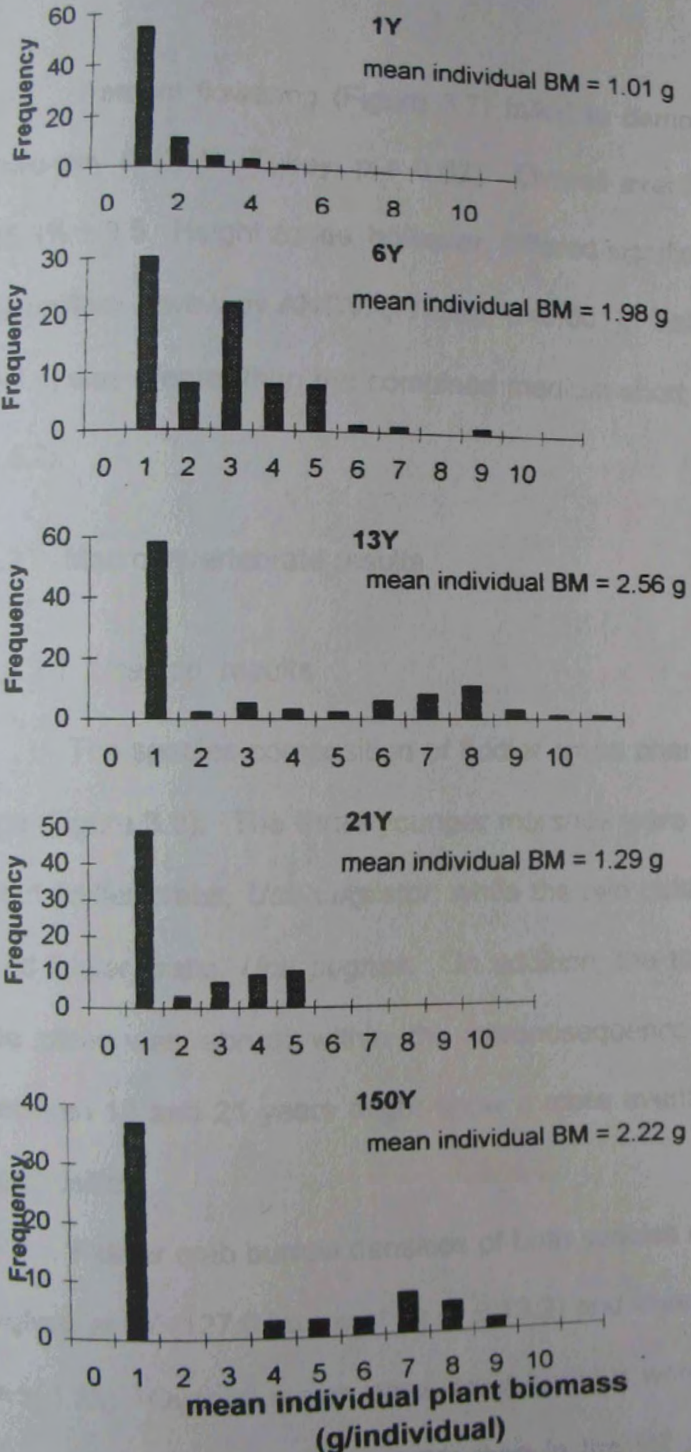


Figure 3. 6 Marsh-wide above-ground individual *Spartina alterniflora* biomass frequency.

Percent flowering (Figure 3.7) failed to demonstrate an age dependency (two-way ANOVA, Tukey, p = 0.62). Overall average for all five marshes was 46.3% ± 9.5. Height zones, however, differed significantly in flowering of *Spartina alterniflora* (two-way ANOVA, Tukey, p<0.001). Tall zone flowering rate (51.1% ± 3.4) was greater than the combined medium-short zone flowering rate (43.95% ± 8.2).

3.3.2 Macro-invertebrate results

3.3.2.1 *Uca* spp. results

The species composition of fiddler crabs changed dramatically with marsh age (Figure 3.8). The three younger marshes were composed almost entirely of sand fiddler crabs, *Uca pugilator*, while the two older ones contained virtually all mud fiddler crabs, *Uca pugnax*. In addition, the transition from one species to the other was abrupt within the chronosequence marshes. A marsh aged between 13 and 21 years might show a more evenly mixed fiddler crab species composition

Fiddler crab burrow densities of both species combined (Figure 3.9a) were highest at 6Y (127.0 burrows/ sq m ± 13.2) and lowest at 150Y (22.1 burrows/ sq m ± 3.33). Over all marsh ages, most burrows were found in the medium-short zone (74.2 burrows/ sq m ± 8.20) than in the tall zone (69.4 burrows/ sq m ± 11.4). These differences were significant ((K-W ANOVA, SNK, p<0.001). Whole

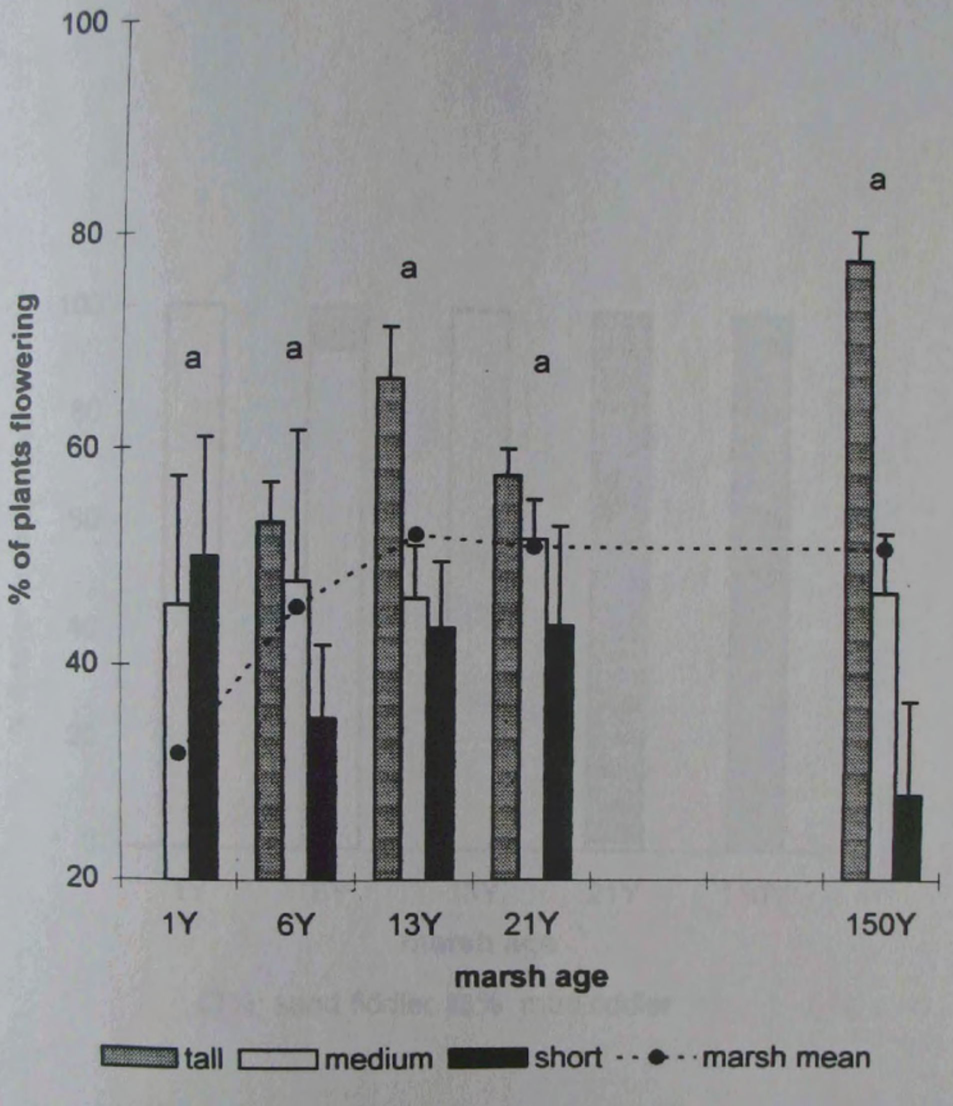


Figure 3. 7 Percentage of *Spartina alterniflora* flowering by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars.

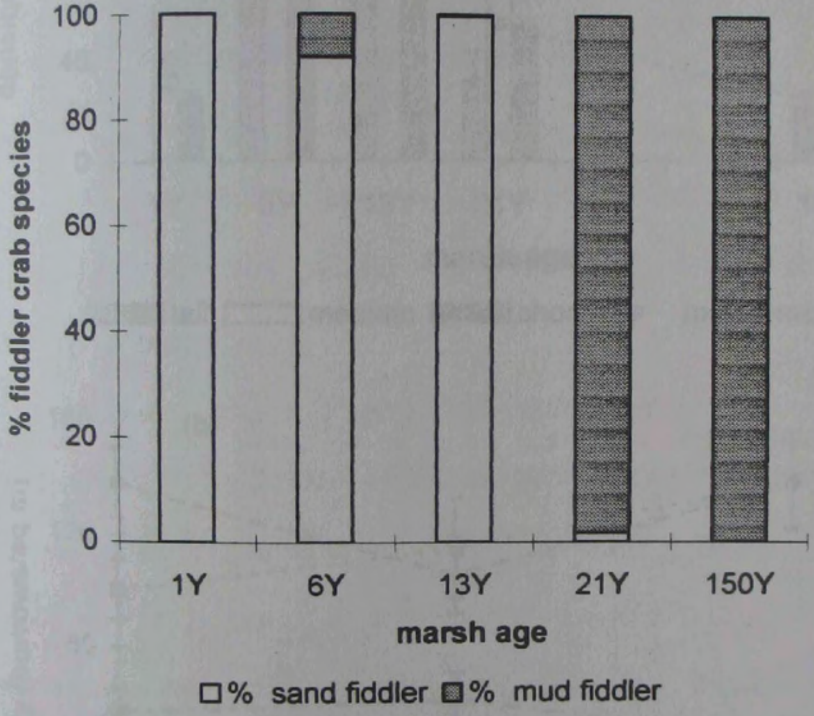


Figure 3. 8 Species composition of fiddler crabs by marsh age.

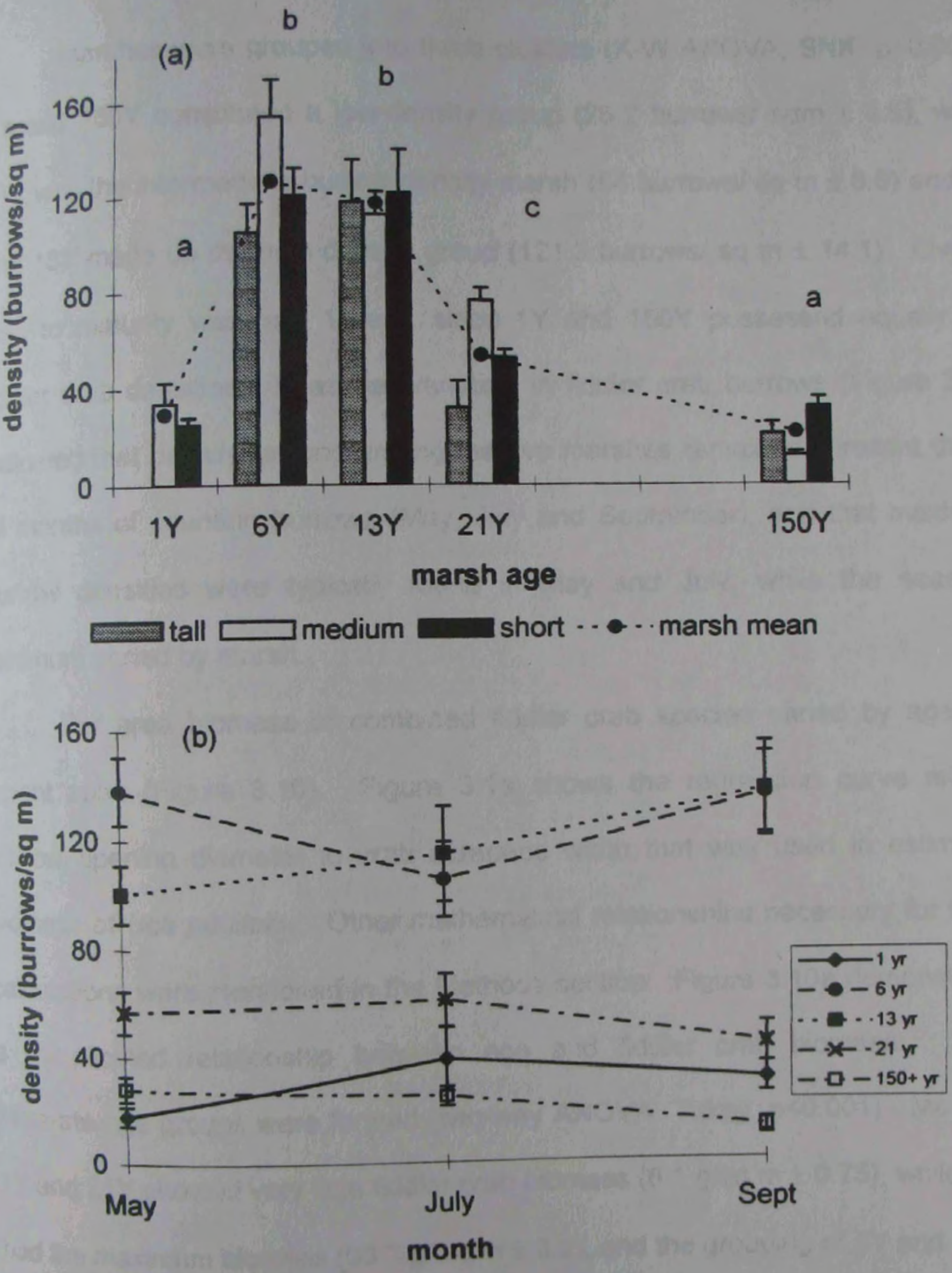


Figure 3. 9. (a) Fiddler crab burrow density by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars, and (b) Monthly marsh-wide fiddler crab burrow density.

marshes were grouped into three clusters (K-W ANOVA, SNK, p<0.001): 1Y and 150Y constituted a low-density group (26.2 burrows/ sqm ± 4.5), while 21Y was the intermediate burrow density marsh (54 burrows/ sq m ± 6.6) and 6Y and 13Y made up the high density group (121.3 burrows/ sq m ± 14.1). Overall time to maturity was only 1 year, since 1Y and 150Y possessed equally low fiddler crab densities. Seasonal variation in fiddler crab burrows (Figure 3.9b) indicated that density ranking among the five marshes remained constant during all months of counting burrows (May, July and September), and that maximum burrow densities were typically found in May and July, while the seasonal minimum varied by marsh.

Per area biomass of combined fiddler crab species varied by age and height zone (Figure 3.10). Figure 3.1a shows the regression curve relating burrow opening diameter to crab carapace width that was used in estimating biomass of *Uca pugilator*. Other mathematical relationships necessary for these calculations were mentioned in the Methods section. Figure 3.10a demonstrates a complicated relationship between age and fiddler crab biomass. Three separate age groups were formed (two-way ANOVA, Tukey, p<0.001). Marshes 1Y and 21Y showed very little fiddler crab biomass (6.1 g/sq m ± 0.75), while 13Y had the maximum biomass (93.7 g/ sq m ± 3.2), and the grouping of 6Y and 150Y was intermediate (50.2 g/ sq m ± 2.2). Time to maturity for this variable is complicated by the presence of two species along the chronosequence. The only

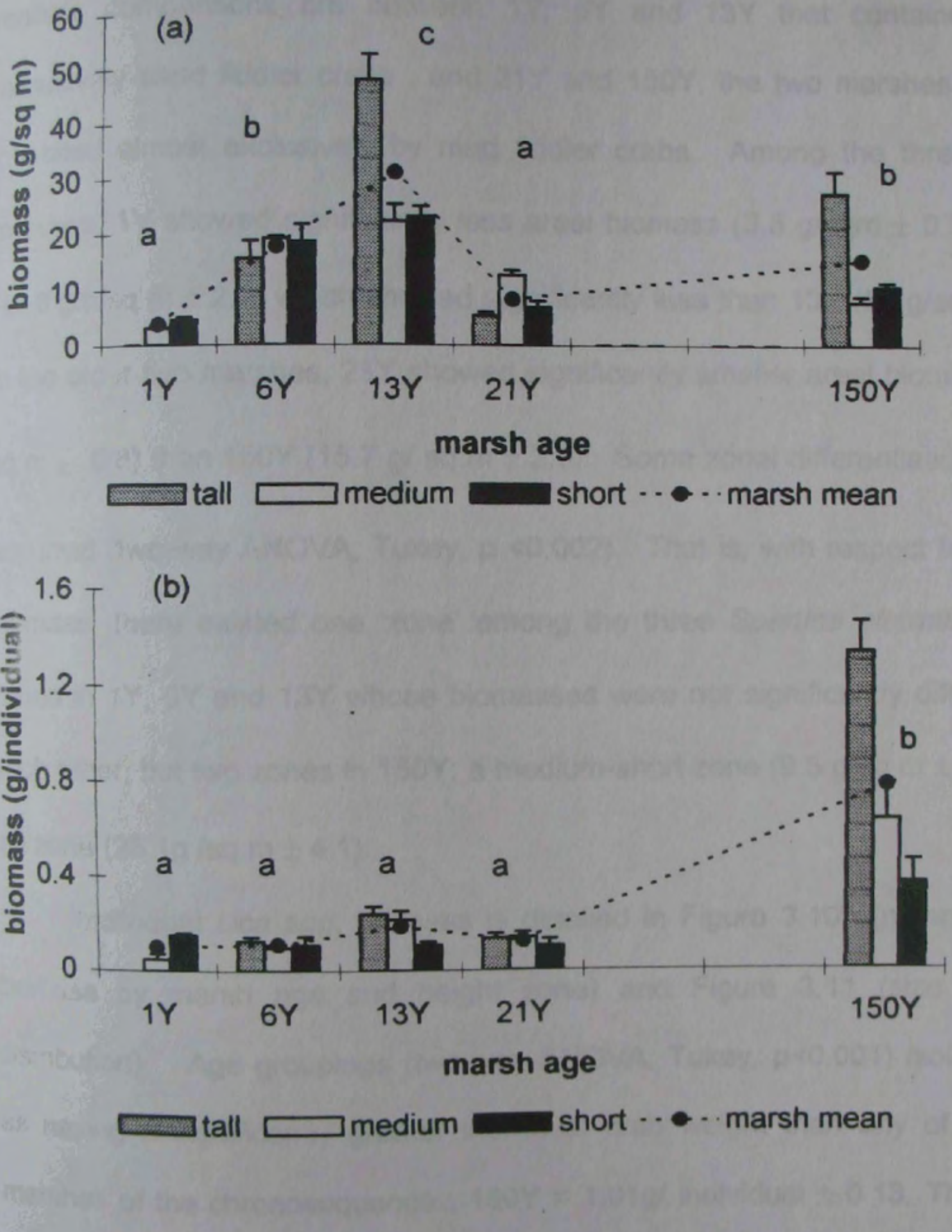


Figure 3. 10 (a) Fiddler crab areal biomass and (b) individual fiddler crab biomass by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars.

realistic comparisons are between 1Y, 6Y and 13Y that contained almost exclusively sand fiddler crabs , and 21Y and 150Y, the two marshes that were inhabited almost exclusively by mud fiddler crabs. Among the three younger marshes, 1Y showed significantly less areal biomass (3.8 g/sqm ± 0.5) than 6Y (17.8 gm/sq m ± 2.2) which showed significantly less than 13Y (31 g/sq m ± 3.2). In the older two marshes, 21Y showed significantly smaller areal biomass (8.4 g/ sq m ± 0.8) than 150Y (15.7 g/ sq m ± 2.3). Some zonal differentiation with age occurred (two-way ANOVA, Tukey, p <0.002). That is, with respect to *Uca* spp. biomass, there existed one 'zone' among the three *Spartina altemiflora* height zones in 1Y, 6Y and 13Y whose biomasses were not significantly different from each other, but two zones in 150Y: a medium-short zone (9.5 g/sq m ± 0.9) and a tall zone (28.1g /sq m ± 4.1).

Individual *Uca* spp. biomass is detailed in Figure 3.10b (mean individual biomass by marsh age and height zone) and Figure 3.11 (size frequency distribution). Age groupings (two-way ANOVA, Tukey, p<0.001) isolated 150Y as having a significantly greater individual crab weight than any of the other marshes of the chronosequence : 150Y = 1.01g/ individual ± 0.13. The nearest value, for 13Y is one-fifth the size of the average 150Y crab (0.19 g/individual ± 0.03). Thus, time to maturity is the full 150 years. Age-zone interaction (two-way ANOVA, Tukey, p<0.001) shows some differentiation with marsh age. That is,

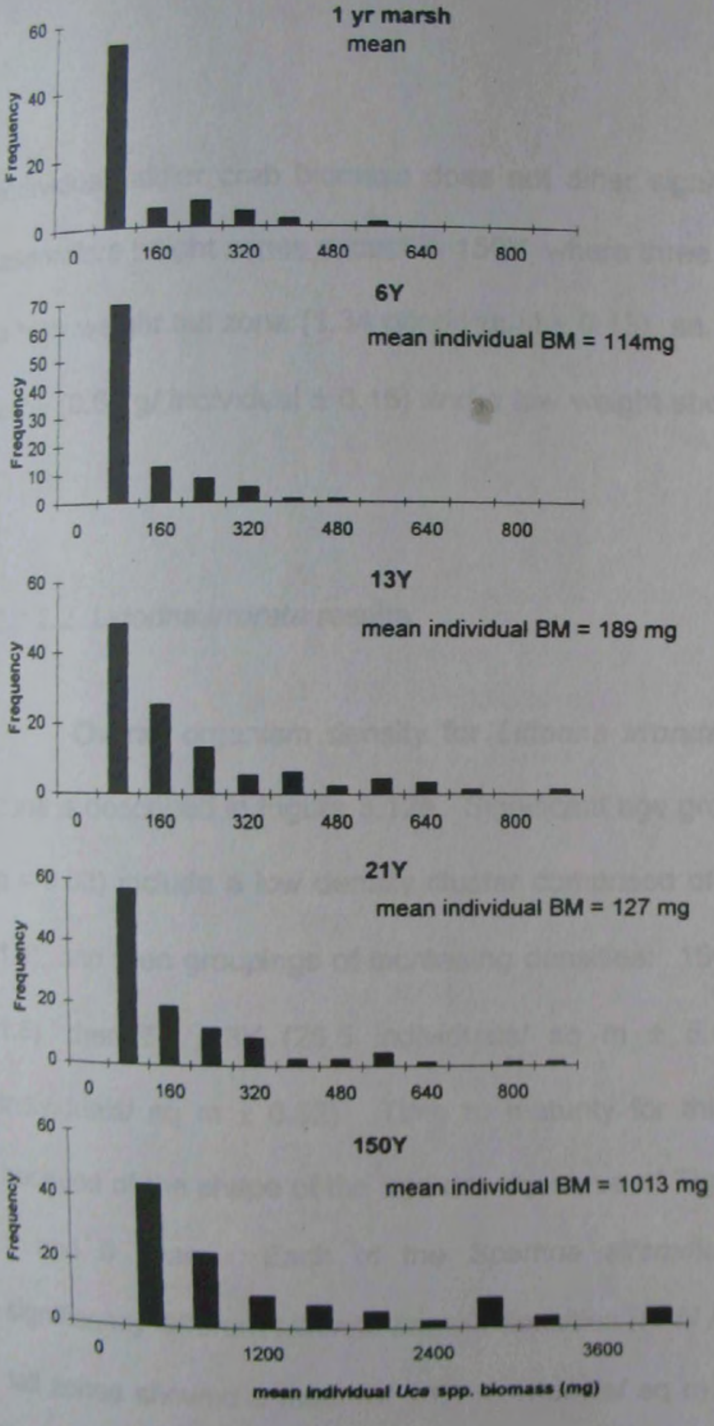


Figure 3. 11 Fiddler crab size frequency distribution by marsh age.

individual fiddler crab biomass does not differ significantly among the *Spartina alterniflora* height zones except in 150Y, where three zones can be distinguished: a high weight tall zone (1.34 g/individual ± 0.13), an intermediate weight medium zone (0.64 g/ individual ± 0.15) and a low weight short zone (0.37 g/ individual ± 0.10).

3.3.2.2 *Littorina irrorata* results

Overall organism density for *Littorina irrorata* by marsh age and height zone is described in Figure 3.12a. Significant age groupings (K-W ANOVA, SNK, p = 0.03) include a low density cluster comprised of 1Y (4.8 individuals/ sq m ± 1.4), and then groupings of increasing densities: 150Y (16.6 individuals/ sq m ± 1.6), then 6Y, 13Y (26.5 individuals/ sq m ± 5.0), and finally 21Y (50.0 individuals/ sq m ± 6.52). Time to maturity for this variable was complicated because of the shape of the age-density curve of Figure 3.12a, but was between 1 and 6 years. Each of the *Spartina alterniflora* height zones exhibited significantly different *Littorina irrorata* densities (K-W ANOVA, SNK, p=0.001). The tall zones showed a mean of 16.1 individuals/ sq m ± 4.33, the medium height zones had 39.1 individuals/ sq m ± 5.01, and the short zones averaged 21.6 individuals/ sq m ± 3.04). *Littorina irrorata* densities were highest in September and lowest in May (Figure 3.12b).

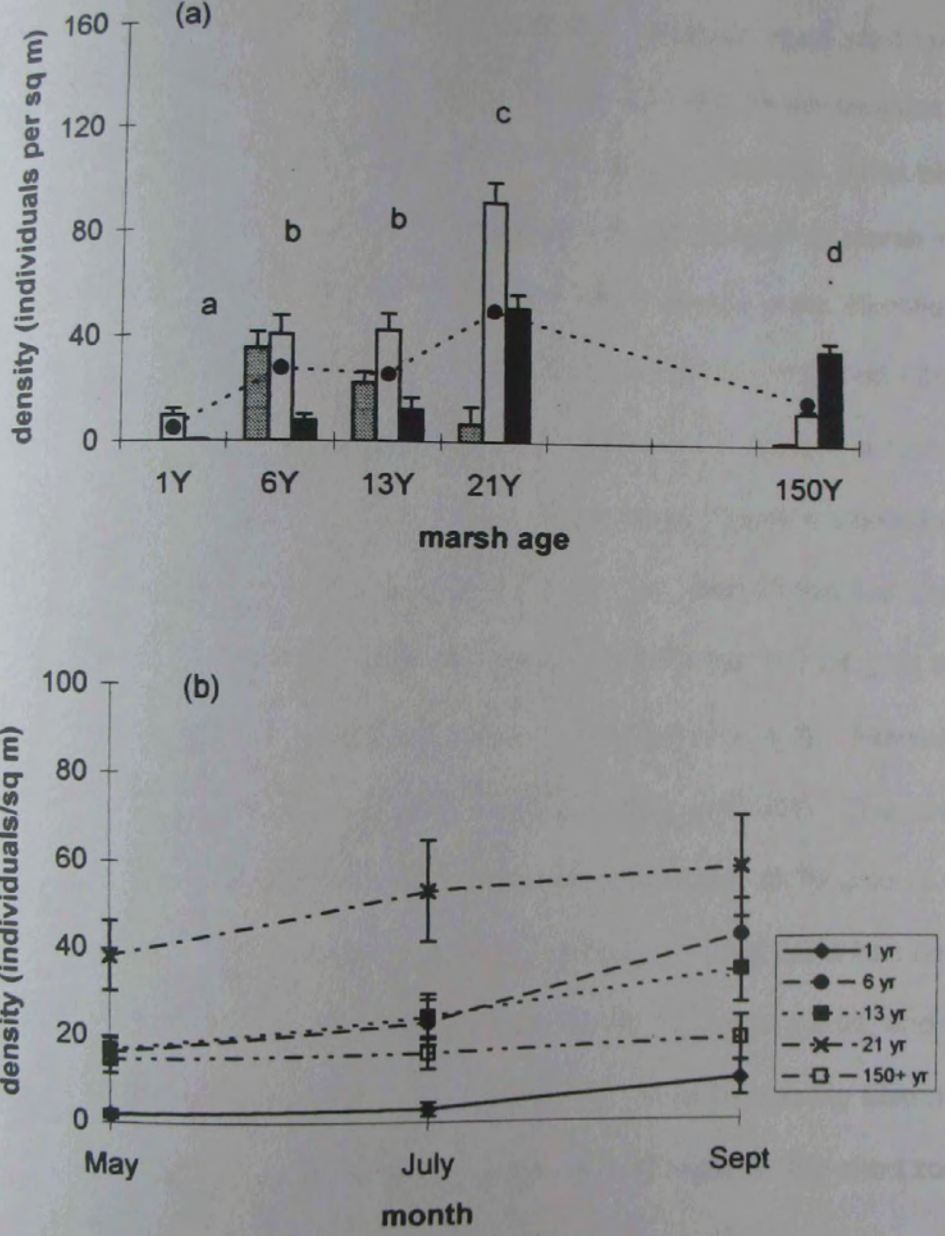


Figure 3. 12 (a) *Littorina irrorata* density by marsh age and height zone. Significant whole marsh groupings as determined by ANOVA are indicated by letters above the bars, and (b) Monthly marsh-wide *Littorina irrorata* density.

intermediate sized snails may be preferred by blue crab predators (Figure 3.14). In fact, size preference for *Littorina irrorata* by blue crabs has been observed elsewhere. Smalley (1959) found that small snails can successfully hide from blue crabs among *Spartina alterniflora* leaves, and large periwinkles climb *Spartina alterniflora* stems to escape tidal predators (in Kneib, 1995), making intermediate sized periwinkles most prone to predation.

Blue crab predation may also be determining *Geukensia demissa* densities across the chronosequence, since tidal crabs are known to prey on these mussels (Seed, 1980). Similar to the pattern found for marsh periwinkles (*Littorina irrorata*), very low mussel densities occurred at 1Y and 150Y. Plant stem density was also very low, and the overall relationship between plant and mussel densities was significant ($r = 0.32$, $p = 0.05$). Like *Littorina irrorata*, *Geukensia demissa* was almost lacking from 21T and 150T, where elevation was lowest among all the marshes of this study. Overall correlation between *Geukensia demissa* densities and marsh surface elevation, however, failed to demonstrate significance, as it did for *Littorina irrorata* ($r = 0.07$, $p>0.1$). Bimodal size frequency distribution (Figure 3.17) for this invertebrate also implies that intermediate sized organisms may be the preferred prey size.

Significant *Ilyanassa obsoleta* densities were found only at 21Y and 150Y, where sufficient silt/clay sized particles made up surface sediments. Densities were particularly high at 150T, significantly more so than at 21T (Figure 3.18). A dense shell fragment layer in 21T probably caused the low frequency of *Ilyanassa obsoleta* (and fiddler crab burrows) in that zone. Areal biomass followed density patterns (Figure 3.19a) and individual biomass was invariant in 21Y and 150Y and across the height zones. No evidence of bimodal size frequency distribution was observed (Figure 3.20) in 21Y or 150Y for this species, as was seen for *Littorina irrorata* and *Geukensia demissa*. If *Ilyanassa obsoleta* is consumed by tidal predators, there does not seem to be a size preference. Moreover, *Ilyanassa obsoleta* shells are known to be 2-3 times more difficult for blue crabs to crack than *Littorina irrorata* shells (B. Silliman, personal communication).

Total invertebrate density and areal biomass shared age-related patterns. For example, both variables peaked at marshes of intermediate age, at 6Y for density and at 13Y for biomass. Moreover, both density and biomass were extremely low at 1Y, emphasizing how biologically depauperate this nascent over-wash marsh is from one that is only a few years older. Both Subrahmanyam, et al., (1976) in a North Florida salt marsh and Levin, et al. (1996) in a North Carolina salt marsh found values for total invertebrate density and biomass that were greater than values found in this study (Tables 3.5 and 3.6). Average invertebrate densities for Wakulla Springs and St. Marks, marshes in northern Florida was 475 individuals/ m^2 compared to a maximum of 236 individuals/ m^2 in natural marshes of the Newport River estuary of North Carolina (Levin, et al., 1996). Marsh 150Y of the Hog Island chronosequence had a value of 178 individuals/ m^2 . Moreover, the Florida biomass was 123 g/m^2 compared to 75 g/ m^2 in 150Y. Both Subrahmanyam, et. al., (1976) and I found greater invertebrate abundance and biomass closer to the water. In these Hog Island marshes, this was due mainly to higher population densities of *Ilyanassa obsoleta* and *Uca* spp. in the tall zones. Figure 3.22 illlustrates the contributions of the four invertebrates monitored in this study to total biomass by marsh age and height zone. The major contributor in most cases were fiddler crabs (66% overall), so it is no surprise that the *Uca* spp. biomass curve (Figure 3.10) so closely parallels the total invertebrate biomass curve. *Geukensia demissa* was next in over-all contribution (18% overall) and *Ilyanassa obsoleta* increased in importance with marsh age in the tall zone only (from 0% in 1Y to 32% in 150Y). Subrahmanyam, et. al. (1976) estimated that *Littorina irrorata* accounted for about 80% of total macrofaunal biomass in trapped samples. This is a very high fraction compared to the Hog Island marshes, especially considering that many more species of invertebrates were sampled in the Florida study than in this one. *Littorina irrorata* accounted for about 7% of total invertebrate biomass in the Hog Island marshes.

The similarity between the *Spartina alterniflora* biomass curve (Figure 3.5a) and the mean total invertebrate biomass curve (Figure 3.21b) reflects the complex relationship between marsh cordgrass and the invertebrate community (Figure 3.24). Facultative mutualism might best describe these interactions. *Spartina alterniflora* can survive without nitrogen input from *Geukensia demissa* feces, and without substrate aeration from fiddler crab burrows, but macrophyte production has been shown to be significantly higher with these inputs (Bertness,1984,1985). Similarly, both species of invertebrates are found in areas devoid of plant cover, but their densities increase sharply in the presence of this plant. The relationship between *Littorina irrorata* and *Spartina alterniflora* however, seems more obligate for the snail, since the periwinkle requires cordgrass stems for food as well as protection from predators.

Time to maturation is the estimated time that it takes for a marsh to demonstrate levels of a single variable (multivariate definition will be given in the next section) that correspond to levels found in a mature marsh. In the case of the Hog Island chronosequence marshes, the mature marsh is 150Y. Marsh maturation with respect to physico-chemical variables was zone specific (see Chapter 2). Table 3.8 lists time to maturation for the biological variables monitored in this study. Keep in mind that '150Y' represents the interval 22 years to 150 years. Because some of these biological variables could only be analyzed by one-way analysis of variance, and also because of the non-linear nature of the 'time series' for many of these variables, only a limited qualitative statement can be made about over-all patterns. In fact, inspection of the three columns of Table 3.8 yields the fact that the three height zones mature at about the same rate for the variables listed.

Table 3. 8 Maturation time in years for biological variables by marsh age and height zone. Asterisks denote variables for which only marsh-wide maturation rates could be determined.

	Height zones		
Variables	**Tall**	**Medium**	**Short**
Spartina alterniflora height	6	6	6
* *Spartina alterniflora* density	1	1	1
Spartina alterniflora biomass	6	6	6
Spartina alterniflora ind. BM	6	6	6
* *Uca* spp. density	1	1	1
Uca spp. biomass	6	21	6
Uca spp. ind. biomass	150	150	150
* *Littorina irrorata* density	6	6	6
Littorina irrorata biomass	6	6	13
* *Geukensia demissa* density	6	6	6
Geukensia demissa biomass	6	6	6
Ilyanassa obsoleta density	150	150	150
Ilyanassa obsoleta biomass	150	150	150
* total invertebrate density	6	6	6
total invertebrate biomass	6	6	6

To summarize this section, both primary and secondary production show peak values at intermediate aged marshes that possess adequate levels of nutrient standing stocks, but have a less toxic substrate than the mature marsh of the chronosequence. Moreover, the two production curves virtually parallel each other with marsh age, evidence of interactions whereby invertebrates create a more favorable environment for plant growth, and *Spartina alterniflora* provides a variety of resources for the animals. Some invertebrate activity accelerates marsh succession, and other activities inhibit it. Predation by tidal invertebrates, notably blue crabs, may structure invertebrate communities along this chronosequence, especially in areas of low marsh elevations, where increased tidal inundation prolongs prey exposure time. Since important feedbacks exist between some of these prey organisms and production in the marsh, succession rate may be partly dependent on such predation pressure. Moreover, since this effect is elevation related, then the level of importance of predation is ultimately linked to depth of over-wash that created these island marshes.

3.4.2 Community succession in chronosequence marshes

Important variable interaction can be assessed through techniques of univariate correlation analysis, as I used in the preceding section to identify interactions within the biological community and between the biota and the physical environment. However, defining statistically distinct communities among chronosequence marshes and discussing their dynamics requires a broader view of these communities using the results of multivariate statistical analysis. Vector one of the correspondence analysis performed on these data explained 49% of the variation in community structure of chronosequence marshes. The vector is entitled 'Snails' because the two most important variables on this vector are snail biomasses, those of *Littorina irrorata* and *Ilyanassa obsoleta*. Age-related differences in these marshes can be described on the basis of whole marshes only, since the two-way ANOVA performed on mean factor scores for each zone indicated that age-zone interactions were not quite significant (p = 0.07). In other words, the effect of age on snail biomass of each *Spartina alterniflora* height zone was constant. Results of correspondence analysis indicate that within these five chronosequence marshes there existed only two distinct biological communities based on the variables that I measured (Figure 3.23). As I reported in Chapter 2 for marsh physico-chemical variables, the number of statistically significant variable groupings (distinct marshes) is less than the number of actual marshes observed. However, the whole-marsh age groupings that were identified using

ANOVA for these biological data were different from the groupings using physico-chemical data in Chapter 2. P-C stages included 1Y and 13Y as a group, and 6Y as a lone statistical marsh, and 21Y and 150Y as a distinct group. Biological communities seem to be less age-related: 1Y and 21Y form a distinct pair, and 6Y, 13Y and 150Y form the other group.

Marshes 1Y and 21Y were the high *Littorina irrorata* biomass marshes and marshes 6Y, 13Y, and 150Y constituted the low *Littorina irrorata* biomass marshes and high *Ilyanassa obsoleta* biomass marshes. The opposite signs attached to these biomass variables does not necessarily indicate direct negative interactions between these two species. It is likely that *Littorina irrorata* depended on *Spartina alterniflora for* food ($r = 0.62$, $p<0.05$, for *Littorina irrorata* biomass versus *Spartina alterniflora* density), whereas *Ilyanassa obsoleta*, a substrate detritus feeder, preferred areas of lower *Spartina alterniflora* density ($r = -0.3$, $p<0.05$), where benthic food sources were more plentiful.

It was surprising that *Uca* spp. and *Geukensia demissa* variables were not more heavily 'loaded' on this vector (Table 3.3), since work by Bertness (1984 and 1985) indicated a close relationship between the densities of each of these invertebrates and *Spartina alterniflora* density. However, as I will show in the next Chapter, fiddler crab density and ribbed mussel biomass are 'loaded' variables on the vector that contains both physical and biological variables. In other words, these invertebrates are not as important in structuring the epifaunal community directly as they are in bio-environmental interactions.

The curve describing changes in factor scores with age for the 'Snails' vector (Figure 3.23) is not unidirectional as was the curve for the physico-chemical vector entitled 'Pore-water Aeration' that I described in Chapter 2. That is, defining marsh age based on these biological characteristics is more difficult than doing so using physico-chemical data. Because the relationship between mean marsh factor score and age is curvilinear, the biological community of relatively young marshes appeared similar to a mature one.

For the Hog Island over-wash marshes, the time to maturity, that is, the time that it took for a whole marsh to have a mean factor score that was statistically the same as marsh 150Y, was only six years (Figure 3.23). That is, marsh 21Y showed a snail community much more similar to 1Y than to 150Y. It is therefore difficult to postulate a 'climax community' sensu Clements (1916) given these results, since age-community variable relationships are not monotonic.

Figure 3.25 illustrates the inter-annual changes in mean factor score by *Spartina alterniflora* height zone for the four marsh age intervals along the Hog Island chronosequence. These values were obtained by dividing the mean factor score difference for each age interval by the number of years in that interval. For instance, for the interval 6M-13M, the mean factor score difference was 48. Since the time interval was 7 years, the mean annual factor score difference was

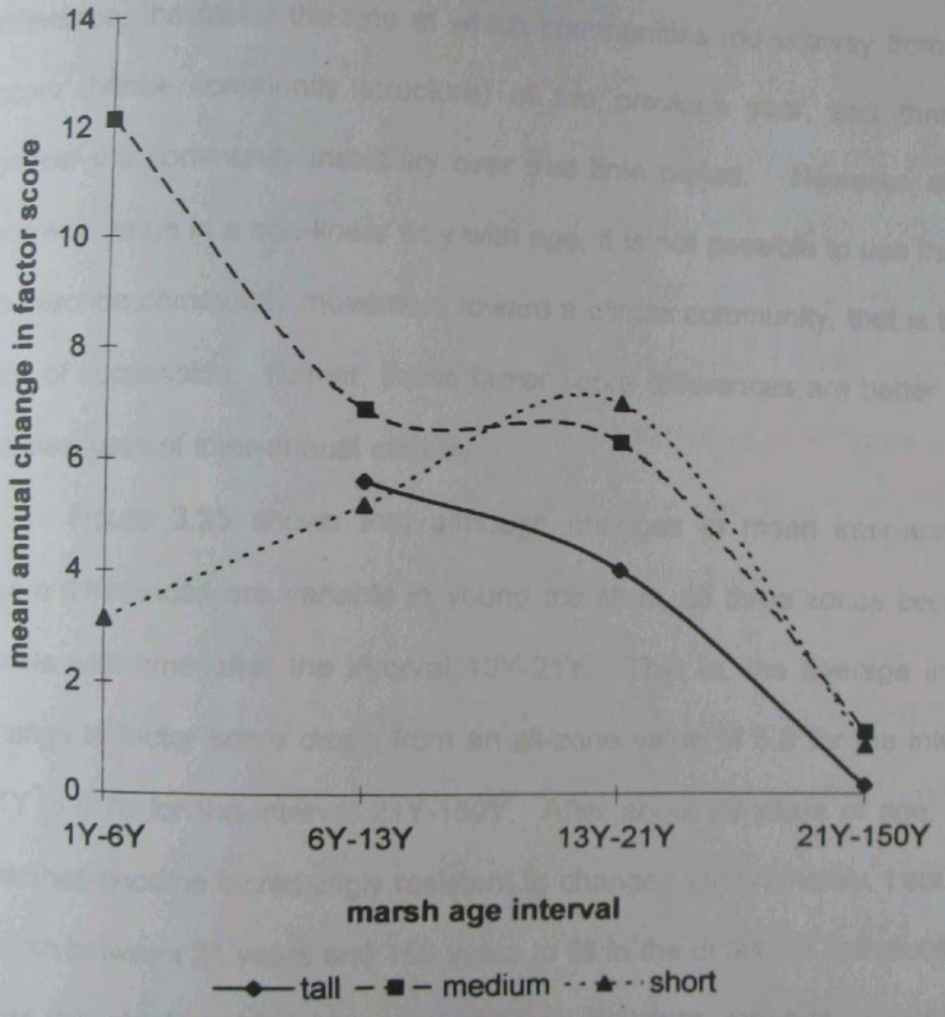


Figure 3. 25 Mean inter-annual factor score differences for the time intervals represented by adjacent marshes of the Hog Island chronosequence by height zone.

calculated to be 48/7 = 6.9. These year -to -year factor score differences can be used as estimates of inter-annual change. The greater the factor score difference, the faster the rate at which communities move away from the factor score (hence community structure) of the previous year, and therefore, the greater the community instability over that time period. However, since factor scores change in a non-linear way with age, it is not possible to use these values to describe community movement toward a climax community, that is to estimate rate of succession. Rather, these factor score differences are better thought of as measures of inter-annual stability.

Figure 3.25 shows that although changes in mean inter-annual factor score differences are variable in young marshes, all three zones become more stable with time after the interval 13Y-21Y. That is, the average inter-annual change in factor score drops from an all-zone value of 5.9 for the interval 13Y-21Y to 0.70 for the interval 21Y-150Y. After about 20 years of age, these low marshes become increasingly resistant to change. Unfortunately, I could find no marsh between 21 years and 150 years to fill in the details of community stability over this considerably long period of time. However, these results indicate that Odum's (1969) idea that ecosystems become more stable with age is appropriate for these marshes.

3.4.3 Summary and conclusions

Spartina alterniflora production pattern with age supported the theory of Odum (1969) and Bormann and Likens (1979) that intermediate aged ecosystems have higher primary production than younger or older systems. Moreover, primary production was related to density of fiddler crabs and ribbed mussels. Burrowing activity of fiddler crabs tended to maintain the marsh surface in a more oxidized juvenile state, whereas ribbed mussel fecal matter (as well as snail feces?) may have accelerated marsh succession by increasing nutrients that accumulated in sediments. These invertebrate-macrophyte relationships were found in all marshes along the Hog Island chronosequence.

The invertebrates of the chronosequence marshes showed a variety of changes that were related to marsh age. *Uca* spp. composition for instance, changed with marsh age. Young, sandy marshes were populated almost totally by sand fiddler crabs, whereas older marshes whose sediments contained finer particles, contained mud fiddler crabs. In addition, mean individual fiddler crab size increased greatly with marsh age. The density of the marsh periwinkle, *Littorina irrorata*, also showed age related changes that were dependent on *Spartina alterniflora* stem density patterns. Density of the ribbed mussel decreased with age, and the mud snail, *Ilyanassa obsoleta*, was confined solely to the two older marshes of the chronosequence.

Total invertebrate density and mean biomass paralleled changes in primary production with marsh age, peaking at 13Y. The correlation between these two curves is likely the result of complex animal-plant interactions that shape the biological community of any salt marsh (Figure 3.24). For instance, *Spartina alterniflora* stems and roots provided burrowing stability for fiddler crabs (Bertness, 1984), and in turn, crab burrows elevated pore-water redox, and thereby reduced the accumulation of pore-water toxins (sulfide) that stunt plant growth. Ribbed mussels and marsh periwinkles were also related to *Spartina alterniflora* growth, and were provided in turn with protection from predation by blue crabs.

Multivariate analysis of these biological communities depicted two distinct communities, not five in the five chronosequence marshes. Community structure was best characterized by its snail populations. Age-related patterns with respect to snails was complex and non-linear, thus snail variables, although the best biological descriptors of these communities, were not as reliable a predictor of marsh age as were certain physico-chemical variables (see Chapter 2). Younger marshes of this chronosequence showed greater inter-annual variability in community structure than older marshes. In fact, each height zone became stable after about 20 years of age.

CHAPTER FOUR

ECOSYSTEM-LEVEL SUCCESSION ALONG AN OVER-WASH SALT MARSH CHRONOSEQUENCE

4. Ecosystem scale succession along an over-wash salt marsh chronosequence

4.1 Introduction

In Chapter 2 I described salt marsh succession only in terms of changes in physico-chemical stages. In Chapter 3 successional changes in biological communities were described, and biological-environmental interactions that occur during salt marsh succession were discussed. In this Chapter, all variables that were measured (Table 4.1) are analyzed together in order to fulfill the description of the process of succession in these over-wash marshes of Hog Island. It has been implied that succession is a process that involves the entire ecosystem (Odum, 1969), and not just plant community. Therefore, a system-wide description of this process must utilize a multivariate statistical approach that identifies suites of defining variables (biological and physical) as distinct seral stages that change with time (van der Maarel and Werger, 1978). Indeed, a focus of research at the Virginia Coast Reserve, the site of this work, is to identify ecosystem stages, and describe successional processes using multivariate means (Hayden, et al., 1995).

Perhaps because of the physiological demands that anoxic, saturated sediments impose on wetland plants, successional studies in wetland ecosystems have included physico-chemical variables as part of a multivariate description of succession. Bernard et al. (in Peet, 1985) used de-trended correspondence analysis (DCA) to separate fens in western New York into communities according to bottom type (marl versus peat). Dunn and Sharitz (1987) studied re-vegetation of a bald-cypress-water tupelo swamp in South Carolina following thermal disturbance from a nuclear reactor. Using DCA, they found that species composition correlated with water depth, substrate type and severity of disturbance. They also discovered that re-vegetation pattern depended on substrate type. Succession in aquatic macrophyte communities in Indiana dune ponds was found (using DCA) to be associated with changes in sediment chemistry that were driven by age-related hydrologic regimes (Wilcox and Simonin, 1987). Ordination techniques revealed that hydrologic disturbance was also implicated as a driving force in succession in English valley mires (Fojt and Harding, 1995). Finally, canonical correspondence analysis was used to identify peat nutrient level and pH as the important variables in succession in Finnish pine mires following water level draw-down (Jukaine and Laiho, 1995).

This work constitutes the first description of salt marsh succession that includes traditionally pertinent physical and biological variables combined into a description of ecosystem seral stage, as well as descriptions of the changes that occur in these stages during marsh succession. Invertebrate variables must be included in such a comprehensive view, since some organisms have been shown to be intimately related to macrophyte production. It is this macrophyte production that is the basis of marsh formation and is central to its development (Bertness, 1984, 1985, and Chapter 3 of this work). In this Chapter, I briefly review the variables that were measured at the Hog Island chronosequence marshes, then report the results of correspondence analysis (CA) performed on these variables. The combinations of variables that best define separate seral stages are identified. The process of succession, that is, the change of seral stages with time, is then described for each of the three *Spartina alterniflora* height zones. Time to maturity for each height zone is estimated, and successional rate of each seral stage over time is calculated.

4.2 Results

Table 4.1 reviews the list of variables that were measured at chronosequence marshes in the course of this work, and Table 4.2 lists the CA loadings for all variables. I have chosen to describe these marsh ecosystems using only vector one because of the large variation explained by it (51%) and to maintain a consistency with analytical methods used in Chapters 2 and 3. The most heavily loaded variables on this vector were: pore-water sulfide, ammonium, redox, sediment phosphate, mud snail biomass, and fiddler crab density (Table 4.2). The title of this vector, 'Bio-Aeration', recognizes the importance of fiddler crab burrowing to sediment and pore-water oxidation-reduction potential and to associated variables also present on this vector. The negative sign associated with both *Uca* spp. density (loading = -50) and pore-water redox (loading = -72), indicates that as *Uca* spp. density increases, so does pore-water redox. That is, fiddler crab burrowing which has been proven to elevate pore-water oxidation-reduction potential (Bertness, 1985), seems to slow the trend in marsh maturation toward more anaerobic sediments (Osgood and Zieman, 1993, and Chapter 2 of this work).

Table 4. 1 Variables measured at the Hog Island chronosequence marshes.

Physico-chemical variables		**Biological variables**	
sediment variables	**pore-water variables**	***Spartina alterniflora* variables**	**epifaunal macro-invertebrate variables**
surface elevation	temperature	plant height	*Uca* spp. composition
total phosphate	salinity	stem density	organism density
nitrogen	pH	above-ground biomass	organism areal biomass
surface grain size	oxidation-reduction potential	individual plant biomass	individual organism biomass
organic content	ammonium	percent flowering	total invertebrate density
	sulfide		total invertebrate biomass
	phosphate		

Table 4. 2 Ranked loadings for all variables on first axis of Correspondence Analysis. Eigenvalue for this axis = -0.2, and data variation explained = 51%. Variables and loadings in bold type represent those that have been chosen to define the vector.

Variable	Loading
pore-water sulfide	**81**
sediment phosphate	**65**
pore-water ammonium	**63**
***Ilyanassa obsoleta* biomass**	**50**
sediment nitrogen	48
sediment organic content	48
Littorina irrorata biomass	33
pore-water phosphate	7
Spartina alterniflora density	-10
pore-water temperature	-11

Table 4.2 (continued) Ranked loadings for all variables on first axis of Correspondence Analysis. Eigenvalue for this axis = -0.2, and data variation explained = 51%. Variables and loadings in bold type represent those that have been chosen to define the vector.

Variable	Loading
pore-water salinity	-11
Spartina alterniflora flowering %	-15
total invertebrate density	-17
elevation	-17
Spartina alterniflora biomass	-26
sediment sand %	-31
total invertebrate biomass	-32
Uca spp. biomass	-38
***Geukensia demissa* biomass**	**-48**
***Uca* spp. density**	**-50**
pore-water redox	**-72**

Although *Geukensia demissa* biomass co-varies in the same direction with *Uca* spp. density on this vector, the relationship between ribbed mussel biomass and the other physico-chemical variables is unclear. Ribbed mussel filter feeding activity tends to increase sedimentation rate through production of pseudofeces (Bertness, 1984). Furthermore, the formation of byssal threads that attach ribbed mussels to *Spartina alterniflora* stems binds sediment and prevents erosion (Bertness, 1984). But Bertness (1984) found no effect of ribbed mussel presence or absence on substrate redox, and there exists little relationship between the two variables in this study ($r = 0.15$, $p > 0.05$).

Along this vector, a positive factor score is associated with a marsh that is high in pore-water redox, *Uca* spp. density, and *Geukensia demissa* biomass, but low in pore-water sulfide and ammonium and sediment phosphate concentration. Conversely, a marsh that has a negative factor score is one with a low density of fiddler crabs, ribbed mussels and pore-water redox, and high pore-water sulfide and ammonium, and also high sediment phosphate content.

Figure 4.1 describes the distribution of mean CA factor scores by marsh age and *Spartina alterniflora* height zone for vector one. The general trend in Figure 4.1 is clear: mean factor scores decreased with marsh age. That is, young marshes displayed a high pore-water oxidation that was related to elevated densities of fiddler crabs (Bertness, 1985). Pore-water oxidation decreased with marsh age, as increased deposition of fine grained sediments and reduced fiddler crab densities lowered pore-water redox. Results by whole marsh indicated that there existed four seral stages along the chronosequence, with mean factor score generally decreasing with age: 1Y (mean factor score = 36 ± 9), 6Y and 13Y (mean factor score = 84 ± 15), 21Y (mean factor score = -35 ± 15), and 150Y (mean factor score = -104 ± 15).

Two-way ANOVA performed on mean factor scores across the chronosequence indicated significant interactions between marsh age and height zone ($p < 0.001$). Therefore, discussion of seral stages must consider *Spartina alterniflora* height zone, and discussion of zones must be done by marsh age. There were two seral stages in the tall zone: marshes 6T and 13T (mean factor score = 88 ± 16) and 21T and 150T (mean factor score = -43 ± 8). For the medium height zone, there existed two seral stages: 1M, 13M, 21M and 150M constituted had a mean factor score of -44 ± 30, while 6M constituted the high factor score marsh (mean factor score = 111 ± 6). Three seral stages were found in the short zone: a high factor score group consisting of 1S, 6S and 13S (mean factor score = 119 ± 6), an intermediate score group of 21S alone (mean factor score = -16 ± 16), and a low score group of 150S alone (mean factor score = -209 ± 5).

Zonation showed an alternation of one and two height zones in chronosequence marshes, with the youngest and oldest marshes separating into two zones. Marsh 1Y had a medium zone with low factor score (mean factor score = -55 ± 21) and a short zone with high factor score (mean factor score =

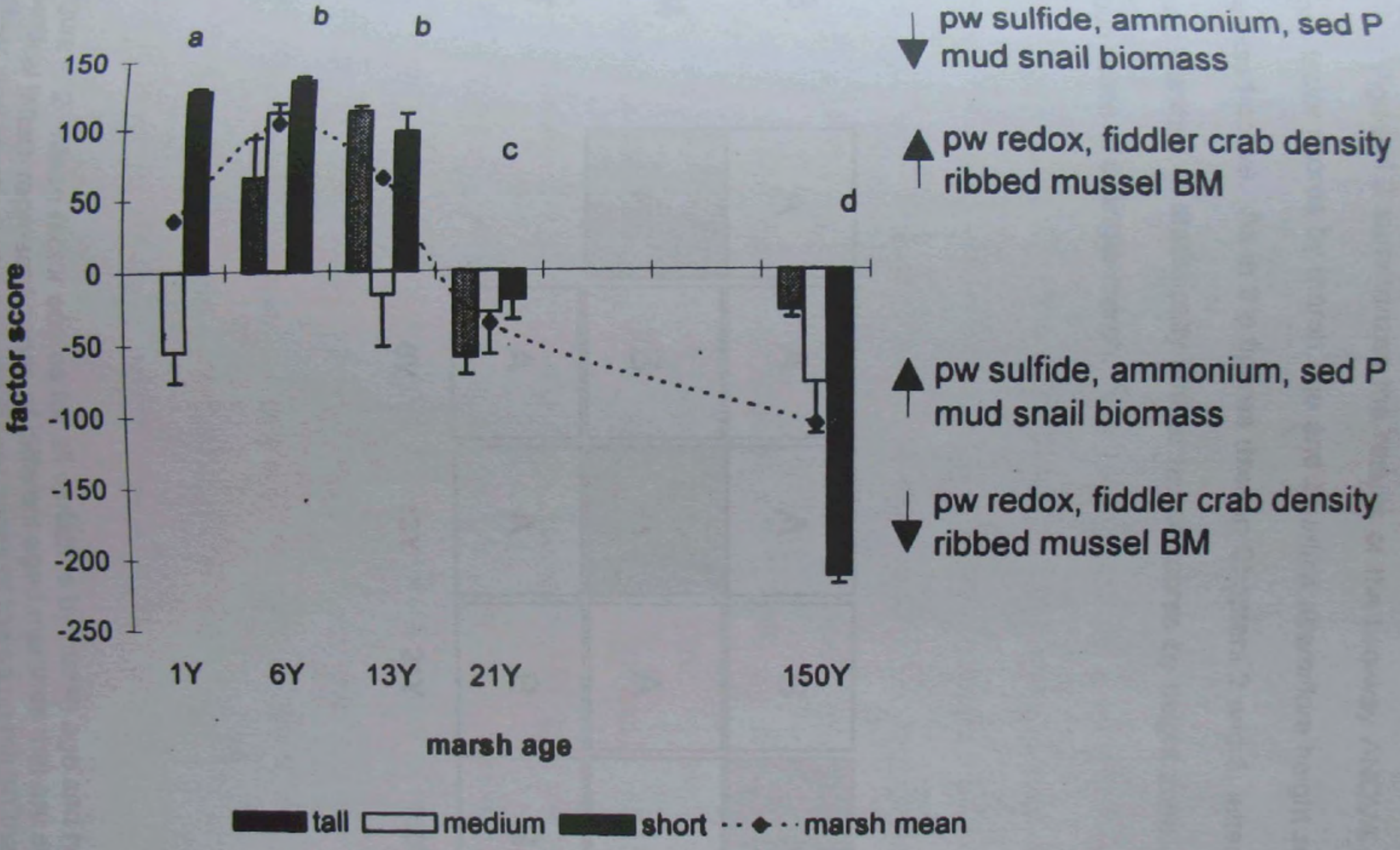
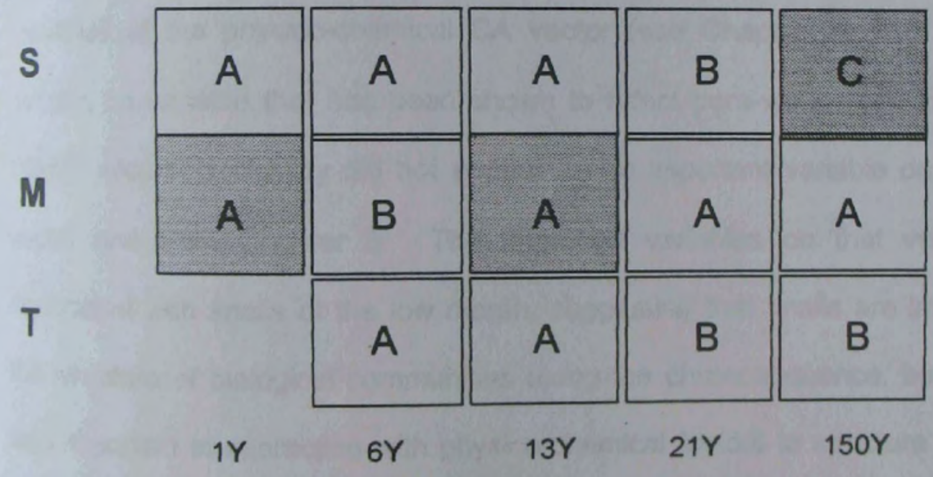


Figure 4. 1 Mean factor score for all variables measured in chronosequence marshes by marsh age and height zone. Letters above the bars indicate statistically different groupings based on two-way ANOVA.

Figure 4.2 summarizes the results of the two-way ANOVA performed on mean factor scores by marsh age and *Spartina alterniflora* height zone that were discussed above. As in the figures used in Chapters 2 and 3, letters are used to group marshes of statistically similar factor scores by height zone, and shadings group zones of a single marsh.



	1Y	6Y	13Y	21Y	150Y
S	A	A	A	B	C
M	A	B	A	A	A
T		A	A	B	B

Figure 4. 2 Mean factor scores for all variables by marsh age and height zone. Identical letters represent zones of different aged marshes that are statistically similar, and identical shading represent zones of the same marsh that are statistically similar with respect to factor score.

4.3 Discussion

4.3.1 CA vector one: Bio-Aeration

A central question to this work has been whether it is possible to describe succession for a species-poor ecosystem, such as these low marshes that are composed of a single species of macrophyte and a few species of macro-fauna. The results of CA confirm that sets of variables do indeed exist, and for the most part they make ecological sense. Vector one, entitled 'Bio-Aeration' combines variables of the physico-chemical CA vector (see Chapter 2), plus *Uca* spp. density, a variable that has been shown to affect pore-water redox (Bertness, 1985). *Uca* spp. density did not appear as an important variable on biological vector one from Chapter 3. The important variables on that vector were associated with snails of the low marsh, suggesting that snails are important in the structure of biological communities along the chronosequence, but they are less important in interacting with physico-chemical factors to structure the entire ecosystem. The inclusion of fiddler crab density as an influencing variable on this vector but not on the community vector associates *Uca* spp. with interactions involving physico-chemical processes and less so with strictly biological interactions. By virtue of their burrowing, fiddler crabs inhibit the age-related decrease of pore-water redox. In this way, fiddler crabs act as organisms that have come to be termed 'ecosystem engineers' (Jones, et. al., 1997). That is, they are influential more for their physical activities which significantly alter environmental conditions, rather than for trophic interactions only. It is known that *Spartina alterniflora* also aerates the substrate by pumping oxygen through its root system (Teal and Kanwisher, 1966), but this effect seems to be much less important in a system-wide sense than the effects of fiddler crab burrowing, since *Spartina alterniflora* density had a small loading on vector one (loading = -10).

The role of *Geukensia demissa* biomass on this vector is speculative. It is known that ribbed mussel filter feeding results in production of pseudo-feces that increases sedimentation rate. Moreover, their attachment by byssal threads stabilizes sediment and prevents erosion (Bertness, 1984). Kraeuter (1976) estimated that *Geukensia demissa*, the most abundant filter feeder in a Georgia salt marsh, was responsible for removing 549 g/m^2/yr of sediment from the water column, and depositing it on the marsh surface. These activities should accelerate marsh succession by increasing sediment deposition from the water column, and by stabilizing sediment, thus encouraging anaerobic substrate conditions. However, *Geukensia demissa* biomass co-varies in the same direction as pore-water redox, which is opposite of the above prediction. Moreover, *Geukensia demissa* biomass co-varies in opposition to pore-water sulfide and ammonium concentrations, variables that ought to change in the same direction as ribbed muscle biomass.

The general trend in marsh succession outlined in Figure 4.1 clearly points to a pattern that I described in the last two Chapters: a buildup of pore-water ammonium, sulfide and sediment phosphate concentrations, with reduced populations of fiddler crabs and ribbed mussels with marsh age. The biological-environmental mechanisms of these trends was posited in Chapter 3 (Figure 3.24).

4.3.2 Marsh maturation by height zone

How long does it take for an over-wash marsh to mature? As in the last two Chapters, I estimated time to maturity by *Spartina alterniflora* height zone, recognizing again, that these estimates are subject to the age intervals of marshes along the chronosequence. A marsh height zone is mature when it displays a mean factor score that is statistically similar to the same height zone in 150Y, as determined using two-way ANOVA. To say, for example that it takes 150 years for maturation of this system means that it takes between 21 and 150 years, the time interval between available aerial photographs of this area of the chronosequence.

Using this system of estimation, the tall zone shows two distinct seral stages by mean factor score, a low score group (6Y and 13Y) and a high score group (21Y and 150Y). The implication of these two ecosystem stages is that the tall zone takes only 21 years to appear mature with respect to the 22 variables measured. For the medium zone, though, no difference was seen between 1Y and 150Y. This abnormal result was probably due to the existence of a buried marsh at the edge of 1M. Referring to Figure 4.1, 1M showed a mean factor score of 55, that is statistically similar to the 76 recorded for 150M. By comparison, the 1S factor score was -127 and that of 150S was 209. Clearly, the proximity of 1M to this buried marsh gave the appearance of accelerated development in this zone. That a buried intertidal system could affect the rate of development of an overlying one was first suggested by Osgood, Santos, and Zieman (1995) for a salt marsh sitting atop a mud flat. Interestingly, the buried marsh at 1M had no influence on the apparent development of 1S located just three meters away. Even after removing 1M from consideration, the medium zone took about 20 years to become mature, that is, to appear statistically similar to 150M. In contrast, the short *Spartina alterniflora* zone took somewhere between 21 and 150 years. Therefore, estimating time to maturity must be performed on a height zone basis, since these zones mature at different rates.

Why might the short zone take so much longer than the other two zones to mature? Fiddler crab densities are higher in the medium and short zones (Figure 3.9, $p = 0.05$) than in the tall zone. It would therefore be expected that both the short and medium zones age slowly, given the retarding effect of fiddler crab burrowing on development. However, the medium zone aged faster than the short zone. Higher fiddler crab density is not the reason for developmental delay in the short zone. It is likely that a combination of elevation, local topography, and developmental distance are responsible. Vector two, which accounted for 20% of the variation in the data, showed two heavily loaded variables at one end of the vector: pore-water redox (loading = 50) and marsh surface elevation (loading = 47). This vector obviously related elevation to redox. Therefore, quadrats at higher elevations should also show higher levels of pore-water aeration, and short zone quadrats were significantly higher in elevation than the other two zones: mean short zone elevation = 27.4 cm above MSL, mean medium zone elevation = 8.5 cm above MSL, and tall zone mean elevation = 26.7 cm below MSL (Figure 2.6). Not surprisingly then, mean pore-water redox for all the short zones (mean redox = 27.5 mV), was significantly higher than for all combined tall-medium zones (mean redox = 1.0 mV). Short zone maturation lagged behind the other two zones because of reduced inundation time that resulted in elevated pore-water redox and lower sedimentation rate, both characteristics of younger marshes. Local topography may also have been a factor. Young short zones along the chronosequence had a 'bumpier' surface than older marshes (personal observation). These micro-topographic features can lead to unexpected local differences. Kindra Loomis (personal communication) has studied 'hummocks' that are found in older marshes along the Hog Island chronosequence. These are small hills (approximately 20-30 cm in height) that probably formed along a past over-wash feature. The *Spartina alterniflora* production along these hummocks is significantly higher than that of surrounding, flatter areas. She hypothesizes that increased drainage along these hummocks leads to a more favorable growth environment for *Spartina alterniflora*. It is possible then, that a more 'hummocky' surface in the young short zones lead to increased local drainage and higher pore-water redox potential, helping to maintain the short zone in a juvenile state. Maturity was accelerated as these hummocky areas were leveled out by sedimentation. Perhaps the most important factor, though is that short zones have a greater factor score 'distance' to cover to become mature. Using the youngest marsh that contains all three *Spartina alterniflora* height zones, that is 6Y, the difference between the mean factor score for 6T and 150T is 92 units, the difference between 6M and 150M is 187 units, and between 6S and 150S is fully 343 units (Figure 4.1).

4.3.3 *Spartina alterniflora* height zones reconsidered

Although I separated these marshes initially into three height zones based on visual observation, the presence of three *Spartina alterniflora* height zones was confirmed statistically (Figure 3.2). Moreover, I have considered the distribution of each variable and factor score by height zone. Does this zonation by *Spartina alterniflora* height represent equally distinct ecosystem variable configurations? That is, does mean factor score for a height zone suddenly change significantly at its border? Figure 4.2 suggests that height zones did not represent individual ecosystem configurations of combined biological and physico-chemical variables. None of the five marshes showed three distinct zones. Some had one factor score zone (6Yand 21Y) and others had two (1Y, 13Y and 150Y), but none had three zones. Using the comparable figure from

Chapter 2 (Figure 2.18), it is clear that physico-chemical stages also did not correspond to *Spartina alterniflora* height zones. However, Figure 3.23 shows the existence of three distinct biological communities corresponding to each of the three *Spartina alterniflora* height zones. Therefore, the *Spartina alterniflora* height zones had a purely biological meaning in that they defined three statistically unique epifaunal communities.

4.3.4 Rates of succession and the 'climax' ecosystem

Figure 4.3 illustrates the mean change in inter-annual factor score for the four marsh intervals that existed along the chronosequence. I have already explained the method of calculating these mean values in Chapters 2 and 3. Each point on the curve in Figure 4.3 represents the rate of succession for that height zone over the time interval indicated on the abcissa. Each height zone started at a different point (mean factor score) and developed over time toward the mean factor score of the same zone in 150Y. If we eliminate 1M from Figure 4.1 (because of its proximity to a buried marsh, see above), then it is clear that the general trend for all three height zones is in the direction of the factor score configuration of 150Y. Therefore, inter-annual changes in factor score (the points

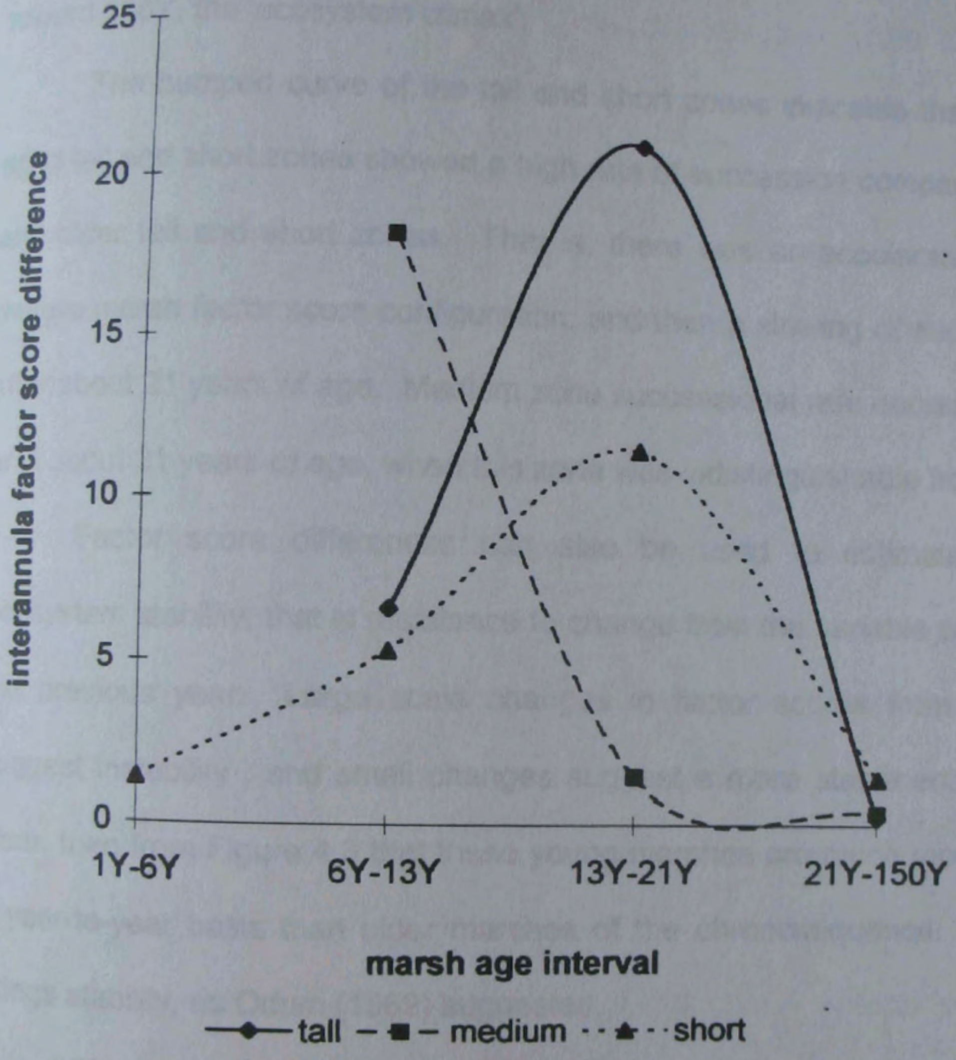


Figure 4. 3 Inter-annual mean factor scores for various marsh age intervals by height zone.

of each curve on Figure 4.3) describe the mean annual rate of change toward 150Y, the 'ecosystem climax'.

The humped curve of the tall and short zones indicates that intermediate aged tall and short zones showed a high rate of succession compared to younger and older tall and short zones. That is, there was an acceleration toward the mature marsh factor score configuration, and then a slowing of successional rate after about 21 years of age. Medium zone successional rate decreased with age, until about 21 years of age, when this zone was indistinguishable from 150M.

Factor score differences can also be used to estimate year-to-year ecosystem stability, that is resistance to change from the variable configuration of the previous year. Large scale changes in factor scores from year to year suggest instability , and small changes suggest a more stable ecosystem. It is clear, then from Figure 4.3 that these young marshes are much more variable on a year-to-year basis than older marshes of the chronosequence. That is, age brings stability, as Odum (1969) suggested.

Marsh 150Y can be considered, then to be a 'climax ecosystem' in the Clementsian sense (Clements, 1916). To use the parlance of dynamical systems, the three height zones of 150Y represent an 'attractor' (Gleick, 1987), a state that systems approach asymptotically with time. In this work, the attractor (150Y) is a set of factor scores toward which younger marshes evolve in the absence of significant disturbance. Moreover, because this set of factor scores includes both physico-chemical variables and biological variables, the attractor is more than a biological community, it is an entire ecosystem consisting of interacting physico-chemical and biological variables (see Figure 3.27).

That such a highly disturbed ecosystem would approach a Clementsian climax state was surprising. As I stated in Chapter 1, my expectation was that poly-climaxes in over-wash marshes were to be expected because of the high frequency of disturbance of the system (see Figure 1.2). Certainly, over-wash events and aeolian disturbance of significant intensities have occurred along this strip of marshes in the last 20 years or so. Yet, there is little sign of developmental reversion along the chronosequence. Perhaps this stability is testimony to the resistive power of bio-physical feedback systems as described above that help to buffer these marshes from all but the most severe events. Indeed, another Ash Wednesday storm would demonstrate the ultimate frailty of these over-wash marshes to physical events, and would re-set the developmental clock as did the 1962 storm. However, in the absence of such a catastrophic event, these marshes will develop toward the climax ecosystem that I have described above. It is obviously imperative to study similar chronosequences to verify that this developmental pattern is universal in coastal marshes.

4.3.5 Summary and conclusions

A species-poor ecosystem, even a monoculture as found in the low marshes of the Hog Island chronosequence, undergoes succession that tends toward a climax ecosystem or attractor. The important aspects of this process can be summarized by the variables on correspondence analysis vector one, entitled 'bio-aeration'. This vector explained 51% of the variation in the data using six of the 22 variables that were measured during this study. Factor scores of vector one generally proceeded from values associated with low levels of pore-water sulfide, ammonium, redox and high *Uca* spp. density in young marshes to the opposite variable values in 150Y, the mature marsh of the chronosequence. The variable '*Uca* spp. density' related the burrowing activity of fiddler crabs to retardation of marsh substrate development by means of enhanced pore-water aeration.

Maturation time must be considered on a height zone basis. Tall and medium height zones reached factor scores of 150T and 150M, respectively, in about 20 years, while maturation time for the short zone was much longer, up to 150 years. Reduced inundation time, more irregular local topography, and especially a greater factor score difference between young and mature short zones, explained the short zone's lagging development.

Young marshes of this chronosequence were more unstable on a year-to-year basis than were older marshes. Moreover, after about 21 years of age, these ecosystems demonstrated increasing inter-annual stability as they approached what for them will be a climax ecosystem.

CHAPTER FIVE

SUMMARY AND CONCLUSIONS

5. Summary and conclusions

The over-wash marshes of the south Hog Island chronosequence exhibited age-related physico-chemical changes, many of which were monotonic. Young marshes of this chronosequence (1Y to 13Y) were characterized by sediments that were sandy, low in organic matter, well drained, and whose pore-water showed the effects of aerobic conditions: high E_H, few nutrients, and low sulfide levels. On the other hand, the mature marsh, 150Y, contained sediment with fine particles predominating, high organic matter content and the following anaerobic characteristics: low pore-water E_H, and a buildup of nutrients and sulfide.

In spite of the monoculture that existed along the choronosequence, statistically distinct physico-chemical stages were identified using a multivariate statistical approach that explained a large portion of the variation in the data (79%) by a single vector, entitled 'Aeration'. However, patterns of physico-chemical succession were height zone dependent, and correspondence analysis results indicated that the medium zone matured at a faster rate than the tall and short zones. Moreover, inter-annual variability of pore-water characteristics generally decreased with age, and by 13 to 21 years of age, these marshes became tracked into a physico-chemical sere that resulted in a PC-stage that can best be described as a PC-climax.

Spartina alterniflora end of season production pattern supported the prediction of Odum (1969) and Bormann and Likens (1979) that intermediate aged ecosystems have higher primary production than younger or older systems. Moreover, primary production was most related to epifaunal invertebrate variables, rather than purely physico-chemical ones. Especially important was burrowing activity of fiddler crabs which probably maintained the marsh surface in a more oxidized juvenile state.

The invertebrates of the chronosequence marshes showed a variety of changes that were related to marsh age. Young, sandy marshes were populated almost totally by sand fiddler crabs, whereas older marshes whose sediments contained finer particles, were comprised of mud fiddler crabs exclusively. In addition, mean individual fiddler crab size increased greatly with marsh age. Density of the ribbed mussel decreased with age, and the mud snail, *Ilyanassa obsoleta*, was confined solely to the two older marshes of the chronosequence. The density of the marsh periwinkle, *Littorina irrorata*, showed changes that were dependent on *Spartina alterniflora* stem density, whose patterns were themselves related (in a non-linear way) to marsh age.

Total invertebrate density and mean biomass paralleled changes in primary production with marsh age, peaking at 13Y. The similarity between these two curves is likely the result of complex animal-plant interactions that shape the biological community of any salt marsh. For instance, *Spartina alterniflora* stems and roots provided burrowing stability for fiddler crabs (Bertness, 1984), and in turn, crab burrows elevated pore-water redox, thereby reducing the accumulation of pore-water toxins (sulfide) that stunted plant growth. Ribbed mussel density was also related to *Spartina alterniflora* biomass, and these bivalves were likely provided in turn with protection from predation by blue crabs.

Multivariate analysis of these biological communities depicted two distinct communities, not five along the five marshes of the chronosequence. Community structure was best characterized by populations of its two snails, the marsh periwinkle and the mud snail. Age-related patterns with respect to snails is complex and non-linear. Thus snail variables are not as reliable as certain physico-chemical variables in predicting marsh age. Younger marshes of this chronosequence showed greater inter-annual variability in community structure than older marshes. In fact, each height zone became stable after about 20 years of age.

An ecosystem-wide approach was taken by analyzing all 22 variables in a multivariate analysis. Results from correspondence analysis demonstrated that a species-poor ecosystem, even a monoculture as found in the low marshes of the Hog Island chronosequence, undergoes succession that tends toward a climax ecosystem or attractor. The important aspects of this process were summarized by the variables on vector one, entitled 'Bio-Aeration'. Using six of the 22 variables, this vector explained 51% of the variation in the data collected during this study. Factor scores of vector one generally proceeded from values associated with low levels of pore-water sulfide, ammonium, redox and high *Uca* spp. density in young marshes to the opposite variable values in 150Y, the mature marsh of the chronosequence. The variable '*Uca* spp. density' related the burrowing activity of fiddler crabs to retardation of marsh substrate development probably by means of enhancing pore-water aeration.

Ecosystem maturation time was height zone dependent. Tall and medium height zones reached factor scores of 150T and 150M, respectively, in about 20 years, while maturation time for the short zone may have been much longer, up to 150 years. Reduced inundation time, more irregular local topography, and especially, a greater factor score difference between young and mature short zones, explain the short zone's lagging development.

Young marsh ecosystems of this chronosequence were more variable in their multivariate structure on a year-to-year basis than were older marshes. Moreover, after about 21 years of age, these ecosystems demonstrated increasing temporal stability as they approached a climax ecosystem. This trend can be reversed by over-wash storms that introduce sand into the sediments of affected marshes.

Although this study examined one salt marsh chronosequence, the results can be applied with caution beyond Hog Island. Because of the reduction in tidal velocity that *Spartina alterniflora* stems induce, certain successional changes in physico-chemical factors that were observed in the Hog Island marshes can be expected to be ubiquitous. Most importantly, reduction in surface grain size and pore-water oxidation-reduction potential, and increased organic matter storage, are predictable changes in the development of all salt marshes. The biological changes that I have documented herein may be less predictable. It remains to be seen if the changes that I observed with marsh age, such as invertebrate densities, areal biomass, and individual organism biomass are replicated in other over-wash marshes, or indeed in different salt marsh types. However, the biotic-abiotic and biotic-biotic interactions that I alluded to in this work, and that have been verified experimentally elsewhere, can be expected to be widespread in salt marshes. Therefore, the description of succession in virtually all coastal marshes must acknowledge the importance of such interactions.

Finally, it is clear from this work that ecosystems, not just biological communities move through the seral stages of ecological succession. Thus, descriptions of this process for any ecosystem must be system-wide to be complete. Even whole classes of variables (biotic versus abiotic) may provide incomplete information on successional processes. Had this description included physico-chemical variables only, or even biological variables in isolation, important abiotic-biotic interactions would have been missed, and succession in these marshes would have appeared to be solely driven by physical forces. Although the limits of system structure are indeed set by physical forces for any ecosystem, the between-event, day-to-day processes of development, even in a vulnerable system like an over-wash marsh, depend on interactions between the living and the abiotic.

Eugene Odum (1969) recognized two aspects of ecological succession that have been re-inforced in this work. The title of his influential paper ,'The Strategy of *Ecosystem* Development' suggests that ecosystems, not simply plant communities are affected by, and in turn, effect successional processes. Secondly, Odum, as well as Clements (1916) included directionality to succession. Odum was cautious, however, and described ecosystem development as only 'reasonably directional' (Odum, 1969). The chronosequence marshes of Hog Island demonstrated such a directionality, as well as temporal stability with age.

My approach has differed from Odum's construct in an important way. In his 1969 paper, he makes assumptions about which variables are important in ecosystem development, then predicts changes in those variables with ecosystem age. In this work, I collected data on a wide variety of variables and allowed my statistical analysis to define which variable set, biotic and abiotic, best defined a seral stage. Using this statistical method for defining seral stage, I was then able to recognize the emergence of distinct stages in the process of ecological succession.

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