On the Life History, Systematics and Ecology of Ruppia maritima L. (Potamogetonaceae) in lower Chesapeake Bay

by

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Abstract

Ruppia maritima is a euryhaline hydrophyte found as a cosmopolitan inhabitant of shallow water habitats. In Chesapeake Bay, Ruppia maritima L. (Potamogetonaceae) and Zostera marina L. (Zosteraceae) form an important submerged aquatic vetetation community. Research in Chesapeake Bay has focused primarily on Zostera marina. Ruppia maritima occurs abundantly in large monospecific stands as well as in mixed stands with Zostera marina. Recent surveys have shown that natural revegetation in some areas has occurred and Ruppia maritima was the primary colonizer in the natural revegetation of some areas.

The objective of this study was to investigate the reproductive biology of Ruppia maritima including the possible function of seed banks and vegetative and sexual propagules on the colonization of new habitats, and the plant's ecological impact around Goodwin Islands, York County, Virginia.

Ruppia maritima rapidly colonized experimental plots that have historically been mixed beds or have been monospecific beds of Zostera marina because it utilized a combination of sexual and asexual reproduction. Ruppia maritima colonized plots by rapid rhizome growth. Seed reserves were probably more important in reestablishing populations than in "maintenance" of populations. Ruppia produces energy costly Post-reproductive shoots. These shoots which produce inflorescenses (and then seeds) remain viable after seeds mature and can detach, disperse, and colonize sites. First year plants were not found to produce an inflorescence. This is significant in the establishment of

new habitats. If a fledgling population is distressed by poor water quality or sediment disturbance, the possibility of producing seeds seems to be eliminated unless the plants have been established for one full growing season. This may explain the ephemeral nature of some Ruppia populations.

To Sarah

In many regions of the world, Spring brings forth changes that we perceive as signs of life. Plants and animals come alive with the warming temperatures.

Lakes, streams, and the coastal areas of oceans once again become baskets of life. The Spring bounty that provides ample nutrients for the new generation of life in a pond has fascinated me since childhood. A catastrophic storm can create new routes for rivers and completely erase the coastal habitats that preceded it. These new habitats can be colonized and become rich and diverse in species in a relatively short period of time; sometimes in days.

The timing and cues effecting changes that we perceive in living things can be due to a number of biotic and abiotic events. The criteria that we outline certainly affect our perception of the causes of an orgainism's life cycle.

Indeed, these and other criteria also strongly influence our perception of what separates species from one another. No matter what the cues or criteria are, the subtle changes that affect the biochemical and, hence, the genetic processes of, say, a seed can stimulate it to germinate at the exact time for it to successfully access its biological niche.

Charles Darwin outlined his hypotheses on the process of natural selection in On The Orginof Species (Darwin 1859). These hypotheses generated 134 years of scientific, philosophic, and sociologic exploration into solving the mysteries of , say, why life comes alive in a pond in New England in Spring. The following is my current contribution to the journey.

Acknowledgments

I thank my advisory committee (Drs. Esen, Johnson, Nilsen, Orth, and West) for their guidance during the project and reviews of this dissertation. I especially with to acknowledge Dr. Orth for extending the facilities and hospitality of the Virginia Institute of Marine Science to me and for spending many hours in the field teaching me about the ecology of Chesapeake Bay.

I also thank Dr. den Hartog, Mr. Ken Moore, Dr. Bruce Parker, and Dr. James Perry for their critical advice on specific aspects of the project. Dr. Gene Silberhorn shared unpublished data with me as well as his vast knowlege of aquatic plants. Dr. Perry provided me with a home and friendship during summers and seasonal trips to Chesapeake Bay. My friends and parents encouraged me, visited me, and helped me with field work during summers.

Finally, I thank Dr. Porter for teaching me by his example. I am truly fortunate to know the path of a scholar.

Preface

Ruppia maritima has received considerable attention in relation to how temperature and salinity affect its distribution, flowering, and seed germination. Taxonomic work has been done on populations occurring in different parts of the world and a number of species of Ruppia have been described. Ruppia maritima has been placed in either its own family (Ruppiaceae) or with the Potamogetonaceae.

The introduction of this dissertation is organized to provide the reader with background information on the systematics of Ruppia maritima and how species theory in Botany is relevant to our knowlege of the taxonomic treatment of Ruppia maritima. Next, hydrophily (water-mediated pollination) is discussed to show how Ruppia maritima achieves pollination compared to other aquatic plants. I then describe the plants which are collectively called seagrasses. Ruppia maritima, while its identity as a seagrass is disputed, is often found growing with other seagrass species.

Contents **Page**

Preface v

List of Tables vii

List of Figures viii

Chapter I. Introduction:
Plant species concepts, systematics and taxonomy of the Nympaeales and Najadales 1

Hydrophily 22

Seagrass Morphology 27

Ruppia maritima in Chesapeake Bay 29

Brief Site Descriptions 32

Chapter II. Pollination of *Ruppia maritima* L. from Chesapeake Bay in a flow-through mesocosm system 40

Chapter III. The seed bank of *Ruppia maritima* L. (Potamogetonaceae) and its importance in establishment and maintenance of beds in lower Chesapeake Bay 53

Chapter IV. Dispersal of *Ruppia maritima* by turions and post-reproductive shoots in Chesapeake Bay 75

Chapter V. Colonization and seasonal succession of *Ruppia maritima* and *Zostera marina* on experimental plots at Goodwin Islands, Chesapeake Bay 83

Summary and Conclusions 114

Literature Cited 116

Appendix 123

Vita 161

List of Tables

Table 1.1. Characters and character states employed in the study of the Nymphaeales. 8

Table 1.2. Data matrix for the character states. The order is separated into five families illustrated here as NELU (Nelumbonaceae), NYMP (Nymphaeaceae), BARC (Barclayaceae), CABO (Cabombaceae), CERA (Ceratophyllaceae). 9

Table 1.3 Characters and character states employed in the study of the Najadales. Values given are for analysis of continuous data and no evolutionary weight is given for data that have continuous values. From Heywood (1985) and Cronquist (1988). 16

Table 1.4 Data matrix for the character states. The Najadales is separated into ten families and the data have continuous values. 17

Table 2.1. Mean number of fruits produced per treatment and percentage of inflorescenses that did not bear fruits in each treatment 47

Table 2.2. ANOVA of pollination treatment vs. the number of seeds produced .. 48

Table 2.3. Summary statistics for inflorescense peduncle growth after fertilization. 49

Table 3.1. Ruppia (Rup), and Zostera (Zos) Shoots (Shts), Seedlings (Sds), and Ruppia Reproductive Shoots (Rep Shts). Total colonization by date for both sites. 64

Table 3.2. T-Test comparisons; York River site vs. Bay site. DF = 7. 65

Table 3.3 T-Test comparisons; Ruppia vs. Zostera Shoots for both sites. DF = 7. 66

Table 4.1. One way ANOVA for number of seeds vs. date for each study site.... 93

Table 4.2. Regression analysis for Ruppia cover in relation to distance from shore comparing the five sites.. 94

Table 4.3. Regression analysis for Ruppia seed bank distribution (seeds in relation to distance from shore). 95

Table 4.4. ANOVA of the number of seeds between sites. The analysis compares the number of seeds along the transect at each site. 96

Table 4.5. Percent viable seeds at each site. Means for the study period. 97

List of Figures

Fig. 1.1 The families of the Nymphaeales as organized by Heywood (1985) and Cronquist (1988) 7

Fig. 1.2 Area display of the data matrix for the Nymphaeales. Valleys represent plesiomorphic character states, peaks represent apomorphic character states. 10

Fig. 1.3 Contour display of data matrix relationships of the Nymphaeales. lighter areas indicate apomorphic character states for a family. 11

Fig. 1.4 Possible cladogram of the Nymphaeales. The cladogram was generated by the Hennig 86 program. 12

Fig. 1.5 Contour graph depicting character relationships between families in the Najadales 17

Fig. 1.6a. Phenogram of the Najadales generated by NTSYS©. Axis indicate matrix correlations. 18

Fig. 1.6b. Phenogram of the Najadales generated by NTSYS©. Axis indicate matrix correlations. 18

Fig. 1.7 Corrotoman River site. 33

Fig. 1.8 Rappahannock River site. 34

Fig. 1.9 Piankatank River (Gwynn Island) site. 35

Fig. 1.10 York River (Goodwin Islands) site. 36

Fig. 1.11 Chesapeake Bay (Goodwin Islands) site. 37

Fig. 1.12 Location of the five study sites in Chesapeake Bay. 38

Fig. 2.1 Pollen grain of Ruppia maritima. Bar = 100 µm 50

Fig. 2.2. Histogram displaying distribution of peduncle growth. 51

Fig. 3.1a Goodwin Islands, York River site colonization plot, April, 1992. 67

Fig. 3.1b Goodwin Islands, York River site colonization plot, May, 1992 68

Fig. 3.1c Goodwin Islands, York River site colonization plot, June, 1992. 69

Fig. 3.1d Goodwin Islands, York River site colonization plot, July, 1992. 70

Fig. 3.1e Goodwin Islands, York River site colonization plot, Aug., 1992. 71

Fig. 3.1f Goodwin Islands, York River site colonization plot, Sept., 1992 72

Fig. 3.1g Goodwin Islands, York River site colonization plot, Oct., 1992 73

Fig. 3.1h Goodwin Islands, York River site colonization plot, March, 1993. 74

Fig. 3.2a Goodwin Islands, Bay site colonization plot, April, 1992. 75

Fig. 3.2b Goodwin Islands, Bay site colonization plot, May, 1992. 76

Fig. 3.2c Goodwin Islands, Bay site colonization plot, June, 1992. 77

Fig. 3.2d Goodwin Islands, Bay site colonization plot, July, 1992. 78

Fig. 3.2e Goodwin Islands, Bay site colonization plot, Aug. 1992. 79

Fig. 3.2f Goodwin Islands, Bay site colonization plot, Sept., 1992. 80

Fig. 3.2g Goodwin Islands, Bay site colonization plot, Oct., 1992. 81

Fig. 3.2h Goodwin Islands, Bay site colonization plot, March, 1993. 82

Fig. 4.1. Corrotoman River. Mean seed reserve, depth profile, and plant cover 99

Fig. 4.2. Rappahannock River. Mean seed reserve, depth profile, and plant cover. 100

Fig. 4.3. Piankatank River. Mean seed reserve, depth profile, and plant cover. 101

Fig. 4.4. Goodwin Islands (York River). Mean seed reserve, depth profile, and plant cover. 102

Fig. 4.5. Goodwin Islands (Chesapeake Bay). Mean seed reserve, depth profile, and plant cover. 103

Fig 4.6. Relationship between Ruppia cover/m^2 and distance from shore. A 2 indicates overlapping data points. 104

Fig 4.7. Relationship between number of seeds and distance from shore. A 2 indicates overlapping data points. 105

Fig. 4.8. Boxplot of the number of seeds at each station compared between the five sites. The graph zeros represent outliers and asterisks represent potential outliers. 106

Fig. 5.1. Study Sites. The Rappahannock River site is marked with a cross-hatched dot. Tangier Island is to the west of the "T". 112

Fig. 5.2. Turions mounted on a herbarium sheet. Collected in the Rappahannock River (Site 2).These turions all have sprouted new leaves. 114

Fig. 5.3. Post-reproductive shoot collected at Tangier Island. 115

Chapter I: Introduction

Plant Species Concepts

Stuessy (1990) has described the chronology of plant species concepts as summarized below:

Morphological Species Concept

This is the classical, or Linnaean, species concept and is based on external and macromorphological characters. This was a very artificial system; however, Linnaeus introduced the use of flower characters during the 1750s, which was somewhat more realistic than using only leaf and stem characters.

Biological (Reproductive isolation) Species Concept

This species concept is most widely applied to animals, but is of limited use with plants. Introduced during the mid 1950s and elaborated until the present time, it is based on actual or potential isolation among species (Mayr 1954).

Biosystematic Species Concept

More recently, the biological species concept has been extended to include the issue of genetic compatibility gradients. That is, the relative compatibility between individuals of the same or different population(s). This species concept is more applicable to plants, especially plants that hybridize.

Ecological Species Concept

This is similar to the biosystematic species concept in that they both allow degrees of compatibility. However, the biosytematic species concept is grounded in the structure or genetics of plants, while the ecological species concept focuses on functional parameters such as resource use, habitat, and species interactions. Stuessy distinguishes between ecospecies (closely related and non-interfertile groups, but with different

distributions) and ecotypes (plants with different distributions, but having some degree of fertility between them).

Genetic Species Concept

The genetic species concept can also be described under the realm of phenetics. Phenetics develops taxonomic groups based on the degree of similarity between organisms using overall similarity, whether of primitive or derived characters. Developed during the late 1980s, this species concept makes use of statistics to measure the differences between species. The genetic characters used include protein analysis, chloroplast and whole DNA comparisons, and karyotyping.

Evolutionary Species Concept

This is similar to the genetic species concept except that it is concerned with evolving lineages. Therefore, plants which are clones (vegetative propagules) and apomictic groups are included.

Cladistic Species Concept

The cladistic species concept includes characters from all of the above listed species concepts and identifies species as lineages of populations with unique evolutionary trends by identifying groups that share derived characters.

The above species concepts are discussed in detail by Stuessy. The advocates of one or the other of these concepts perpetuate the lack of integration between internal (genetic factors) and external (environmental) influences. An effort to synthesize these concepts has been made by Templeton (1989). Templeton's Cohesion Species Concept synthesizes information from morphology, [systematics], ecology, genetics, [and evolution (cladistics)] to crystallize a species concept in which boundaries of minimal interactions define species. These are quantitative boundaries based on information from the above categories. Populations of a particular species are included based on their statistical "tightness". Critics of the cohesion species concept argue that it is not practical

(Endler 1989). At present, I agree that it is not useful to identify species in the field with the cohesion species concept. But, it really doesn't matter. In the field some system (usually artificial) is used to identify organisms, but usually not to discern relationships. The cohesion species concept may prove to be quite useful in that it moves to synthesize rather than polarize ecological and genetic information. Species concepts are only one area which is affected by ecological and genetic perspectives. Plant biosystematists have differences between studies conducted by ecologists and studies conducted by geneticists due to the hypotheses that they test and the methods used to test those hypotheses.

Plant Biosystematics

Hundreds of reports exist on the ecology of certain aquatic vascular plants. These mostly include weed genera such as Hydrilla, or species such as the seagrass Zostera marina. It is not uncommon to find ecological information on the distribution and classification of such organisms (den Hartog 1977, Helfferich and McRoy 1980, Orth and Moore 1981). Studies have often described the distribution and abundance of an organism and discuss some reproductive ecology. Rarely, if ever, do studies on aquatic vascular plants cover the genetic perspective. Studies conducted on such characteristics as seed germination have investigated environmental effects such as temperature, light, salinity, and less often nutrients (Orth and Moore 1983a, Koch and Dawes 1991). Systematists studying aquatic vascular plants most often investigate morphological or cytological characteristics such as seed coats, meristems, or flowers (Charlton and Posluszny 1991, Shaffer-Fehre 1991a, 1991b).

In a recent systematic survey of 140 species of plants that have water-aided pollination, Philbrick (1991) concluded that although flowering is commonly thought to be due to environmental factors (temperature and light) there is little variation in flowering time along a latitudinal gradient worldwide. Philbrick's study elicits some

interesting questions, such as whether it may be possible for an internal genetic clock to function in anthesis and seed germination. Perhaps flowering occurs regardless of environmental factors (or in combination with environmental factors), and those that survive to reproduction pass on that genome. If this is the case with flowering, then it may also be the case with seed germination.

The taxonomy of aquatic plants has been determined, to a large extent, by morphological and anatomical data only. Whole revisions of groups are sometimes based on data which are exclusive of molecular studies (as described above). I use the following analogy to describe a one-sided approach to a systematic study: birds that nest on cliffs lay eggs that spin in tight circles, yet we don't base the taxonomy of birds on their egg morphology!

The biosystematics of some aquatic plants such as Ruppia maritima is confused. The Najadales (the order in which Ruppia is placed) is treated differently by different authorities (as is discussed below). Family classification within the order varies. For example, Ruppia and Potamogeton differ in floral morphology. However, ecologically, the two genera are very similar, and some systematists argue for placing them in one family rather than two. The order Najadales is organized by morphological and cytological characters. Unfortunately, these plants have not been investigated using any one species concept as a tool for understanding relationships. The morphological species concept has been applied, but little or no synthesis has occurred. Flowering time and seed germination in many genera have been attributed to environmental factors (Verhoeven 1979; Brock 1982a, 1982b). Zostera marina has also been investigated in relation to its value as an important indicator of water quality (Dennison et al 1992). No genetic research has been done with these plants to elucidate phylogenetic relationships.

The crucial early step in taking cladistic or phylogenetic approaches to classification in botany is the assignment of evolutionary polarity (primitive versus

derived) to character states (Stevens 1980). If this is so, then it is equally important to assign proper value (or weight) to characters as well. More simply, the more diverse a character set, the lower the margin of error is in a cladistic study, given that proper polarity is assigned to characters.

In the development of species concepts (and in defining species) the question of whether environmental conditions control adaptation, or whether mutation and adaptation occur because of the probability that a genome survives and is inherited by successive generations, is still pertinent. In plant biosystematics, researchers are engaged with the concepts and conclusions drawn from both the ecological and genetic schools of thought. I am inclined to believe that the genome is a priori to environment, but that environmental effects (physical and biological) pave the path of adaptation to an extent that both perspectives should be weaved together in our emergence beyond the evolutionary synthesis.

An examination of two aquatic orders, the Nymphaeales (Dicotyledonae) and Najadales (Monocotyledonae)

The Nymphaeales

Introduction

"On the first day the flower opens it is in the female stage; the male organs, the anthers, are closed and point straight upwards, forming a slippery surface. The flowers are promiscuous -- that is they attract many different visitors and an assortment of bees and other insects land on the surface formed by the closed stamens and slide down into the bowl-shaped female part beneath, which contains a thin, sugary liquid in which the visitors are quickly drowned. Some of the bigger and more agile ones may manage to get out, but not many" (Bristow 1978). This description of protogeny in Nymphaea citrina

L. (Nymphaeaceae) includes an assortment of descriptive traits which taxonomists refer to as characters. Taxonomists commonly disagree as to the relative importance of these characters or whether or not importance should be applied at all (Cronquist 1988). It is for certain, however, that taxonomists place value on identifying and classifying organisms! Cladistic studies have been used by plant taxonomists as an objective means of estimating the evolutionary history of angiosperms (Meacham 1980).

The Nymphaeales is an order of aquatic dicots containing from two to five families (Heywood 1985, Cronquist 1988). The order includes organisms that have completely submerged leaves, floating leaves, and emergent leaves (Sculthorpe 1967). Some species have both submerged and floating leaves. A comparative study using 15 characters of the Nymphaeales was executed in this study in an attempt to elucidate relationships among groups of plants in this order. Since the Nymphaeales has been proposed as a possible link to the Alismatidae of the monocots (Cronquist 1988), an investigation of the order provides an aquatic cousin in the dicots to the nearly entirely aquatic Alismatidae.

Characteristics of the Nymphaeales

Cronquist:	Heywood:
Ceratophyllaceae Number of genera: 2 Number of species: 2 - 30	Nelumbonaceae Number of genera: 1 Number of species: 2
Nymphaeaceae Number of genera: 9 Number of species: over 90	Nymphaeaceae Number of genera: 5 Number of species: 80
	Barclayaceae Number of genera: 1 Number of species: 3-4
	Cabombaceae Number of genera: 2 Number of species: 7
	Ceratophyllaceae Number of genera: 1 Number of species: 2

Fig. 1.1 The families of the Nymphaeales as organized by Cronquist (1988) and Heywood (1985).

Methods

The characters used in the analysis were chosen from the botanical sources used in Figure 1.1. Character states were assigned for each character and a data matrix was then constructed for these character states. The data matrix was used to graphically display potential relationships between the families. Graphs were produced using Deltagraph® software on a Macintosh® SE/30 computer. A cladogram was also

constructed using the Hennig 86 program on an I.B.M.® computer. Graphical display of the cladogram was created using Superpaint® software on a Macintosh® SE/30 computer.

Results

The characters used in this study are given in Table 1.1; 15 characters with their corresponding character states are listed. The data matrix for these character states is illustrated in Table 1.2.

Table 1.1. Characters and character states employed in the study of the Nymphaeales.

Character	Char. Num.	10=plesiomorphic (primitive)	100=apomorphic (derived)
carpel placement	1	not embedded in large receptacle	embedded in large receptacle
carpels	2	present (1)2-many	reduced (1)
energy supply/embryo	3	abundant endosperm	abundant perisperm
floral arrangement	4	long-pedunculate	sessile
floral sexuality	5	bisexual	unisexual
fruit dehiscence	6	dehiscent	indehiscent
habit	7	aquatic emergent	submerged or floating
integument number	8	bitegmic	unitegmic
leaf attachment	9	petiolate	sessile
ovule shape	10	anatropous	orthotropous
petals	11	present	absent
pollen type	12	aperturate	inaperturate (uni, bi, or tri)
roots	13	rooted to substrate	plants rootless
leaf arrangement	14	alternate	opposite or whorled
leaf type	15	broad or blade-like	dissected

Table 1.2. Data matrix for the character states. The order is separated into five families illustrated here as NELU (Nelumbonaceae), NYMP (Nymphaeaceae), BARC (Barclayaceae), CABO (Cabombaceae), CERA (Ceratophyllaceae).

Character	NELU	NYMP	BARC	CABO	CERA
1	100	10	10	10	10
2	10	10	10	10	100
3	10	100	100	100	100
4	10	10	10	10	100
5	10	10	10	10	100
6	100	10	10	100	100
7	10	100	100	100	100
8	10	10	10	10	100
9	10	10	10	10	100
10	10	10	100	10	100
11	10	10	10	10	100
12	100	100	10	10	10
13	10	10	10	10	100
14	10	10	10	10	100
15	10	10	10	100	100

The order is separated into five families following Cronquist's format. This added more possible relationships to the analysis as well as providing a more detailed illustration of the relationships among families of the Nymphaeales.

Figure 1.2 below illustrates basic relationships among the families. The graph is generated using data from the data matrix in table 1.2.

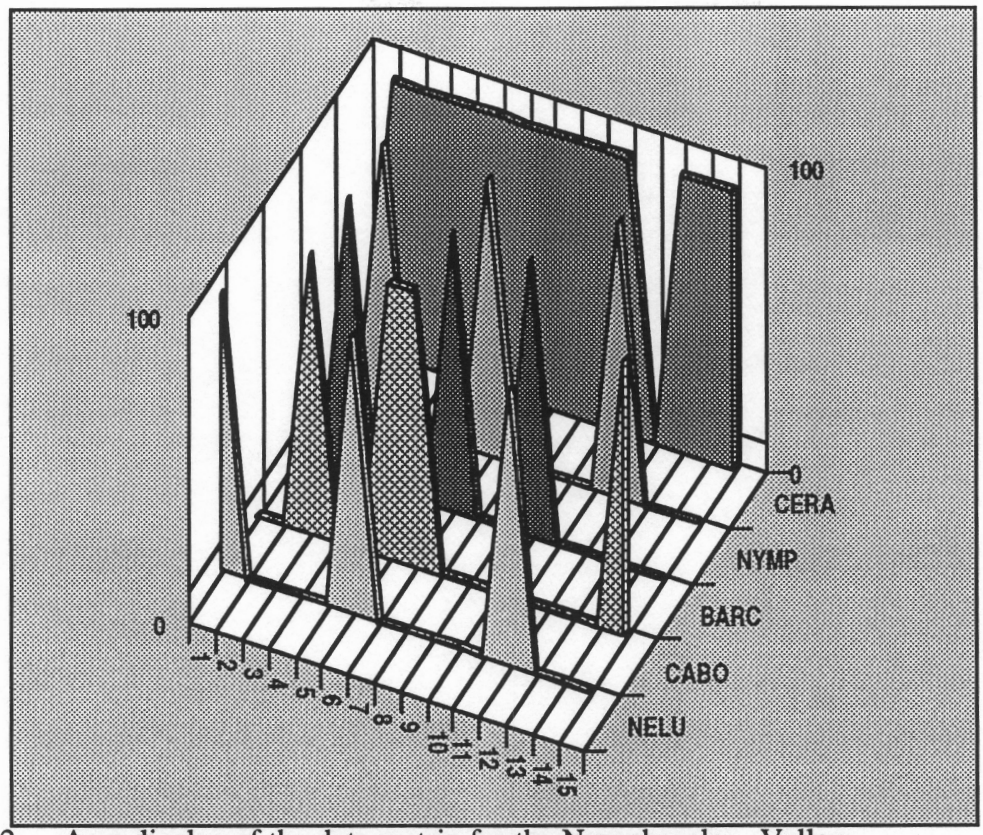

Fig. 1.2. Area display of the data matrix for the Nymphaeales. Valleys represent plesiomorphic character states, peaks represent apomorphic character states.

Relationships are further elucidated using a contour graphing technique as illustrated in Figure 1.3.

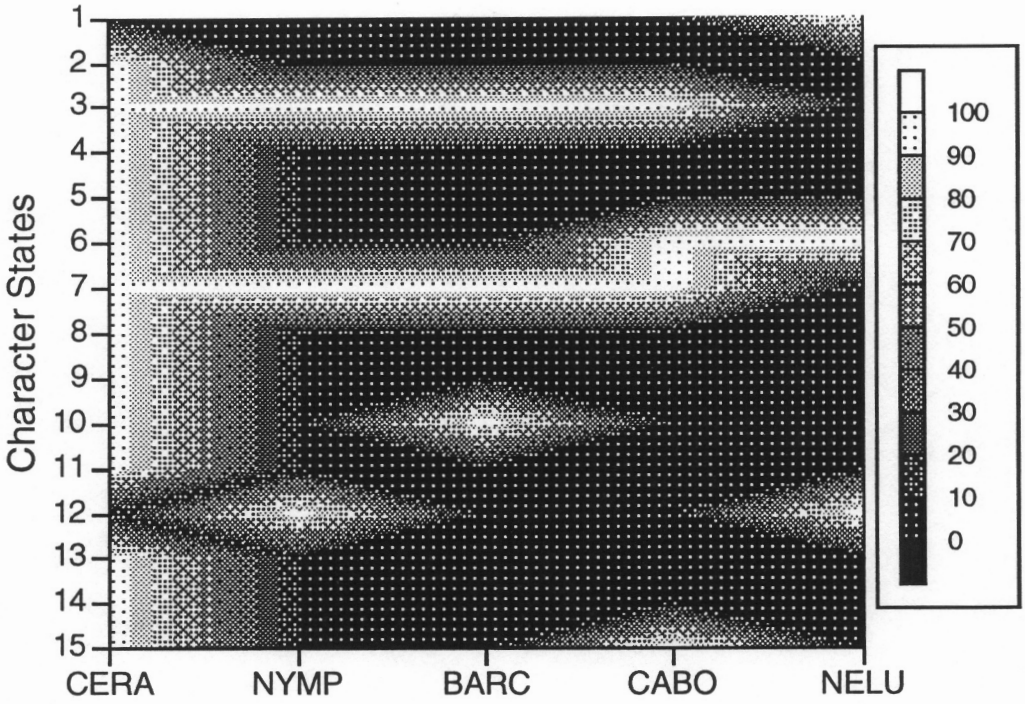

Fig. 1.3. Contour display of data matrix relationships of the Nymphaeales. lighter areas indicate apomorphic character states for a family.

The data illustrated in Figure 1.3 can be compared to an electrophoretic gel. For each of the 15 character states, a band will appear if the character state is apomorphic (derived or advanced). The color shading between character state values is hypothetical. The shading makes display of the data clearer.

The Ceratophyllaceae stood separate from the other families. In addition, the Nelumbonaceae appeared different from the rest. A cladogram of these families is illustrated in Figure 1.4.

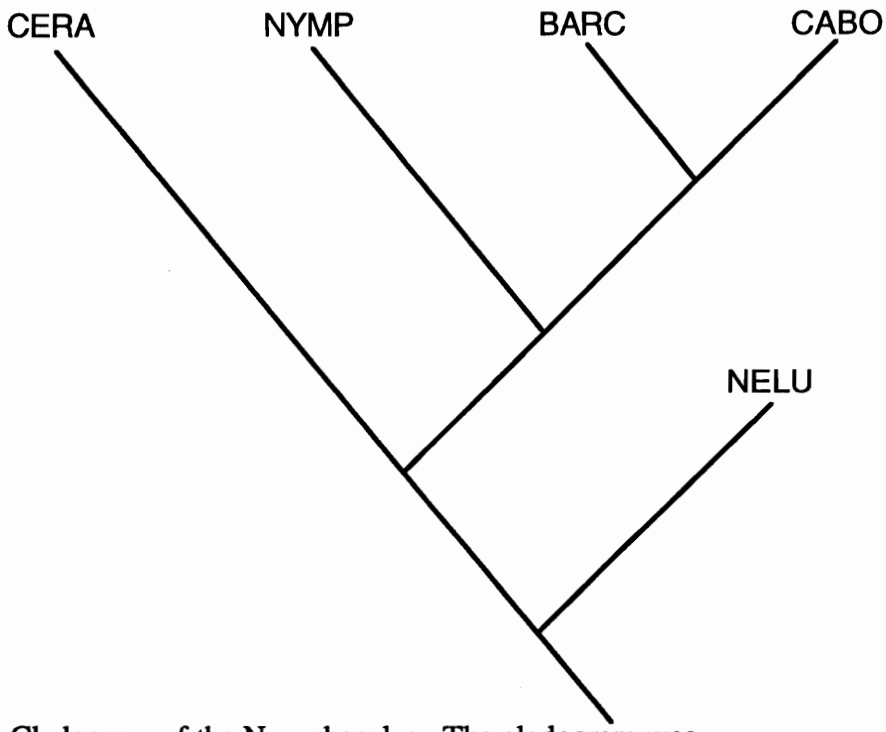

Fig. 1.4. Cladogram of the Nymphaeales. The cladogram was generated by the Hennig 86 program.

Discussion

Figure 1.4 illustrates a five family cladogram for the Nymphaeales. This scheme agrees with Cronquist's key to the five families of the Nymphaeales. The Nelumbonaceae appears to be the oddest family in this analysis. It does not stand as unique, but it is not very similar to the other families either. A three family scheme could be presented for the Nymphaeales where the Cabombaceae, Barclayaceae, and Nymphaeaceae are lumped into one family. This scheme would be more similar to Stebbin's scheme (as seen in Heywood, Figure 1). Figure 1.3 displays the data in a new and interesting way. The contour graph illustrates character similarities among groups as clusters and also highlights apomorphies.

Conclusions

In this study, a number of graphic techniques were used to illustrate relationships based on one data matrix. These data could be criticized as subjective, as the choice of the character states was not blind (they were made by me). However, I am confident that the data show true relationships among at least three families for the Nymphaeales. The contour graph method illustrates a spatial display of the relationships based on apomorphic character states. It is an intuitive method to distinguish how families are related, not just that they are related. It is up to the individual whether or not to create a five family scheme for this order. Are you a "lumper" or a "splitter"? Either scheme seems logical to me. Ceratophyllum will continue to float; they need no roots.

The Najadales

Introduction

According to Cronquist (1988) The Alismatidae includes four orders: the Alismatales, Hydrocharitales, Najadales, and Triuridales. The Triuridales are the most isolated group. These four orders consist of 16 families and perhaps 500 species (Cronquist 1988). Whether or not the Nymphaelaes in the Magnoliidae are the closest link to the Alismatidae and hence a link between dicot and monocot evolution is still up for debate (Les and Schneider 1993).

Ten families have been placed within the Najadales based primarily on floral reduction (Cronquist 1988). As an order the plants range from cold-temperate emergents to tropical marine species. The families can be arranged as follows (from Cronquist 1988):

1. Ovules (1) 2-several in each of the (2) 3-several distinct or proximally connate carpels; fruits follicular; stamens 6 or more:
2. Aquatic plants with floating leaf-blades or with wholly submersed leaves;

tepals 1-3 (6), sometimes petaloid; inflorescence typically a simple or basally forking spike, bractless, although the perianth sometimes consists of a single bract-like tepal; pollen-grains monosulcate, borne in monads ..... **1. Aponogetonaceae**

2. Emergent marsh-plants; tepals 6, never petaloid; inflorescence a raceme, each pedicel subtended by a bract (unique in the order); pollen-grains inaperturate (holoaperturate) borne in dyads ..... **2. Scheuchzeriaceae**

1. Ovules solitary in each distinct carpel or in each locule of a compound ovary; fruits mostly indehiscent or only tardily and irregularly dehiscent, except in the Juncaginaceae; stamens fewer than 6, except commonly in the Juncaginaceae:

3. Leaves all basal, the plants scapose and with a terminal spike or raceme, commonly largely emergent ..... **3. Juncaginaceae**

3. Leaves, or many of them, cauline, sometimes with a floating blade, but not emergent (sometimes exposed at low tide); inflorescence various:

4. Pollen-grains globose or isobilateral, not thread-like; plants of fresh or alkaline or brackish water (Ruppiaceae seldom marine):

5. Flowers perfect:

6. Tepals 4; stamens 4; pollen-grains globose; fruiting carpels sessile; ovule ventromarginal, generally near the base; plants of fresh water. **4. Potamogetonaceae**

6. Tepals 0; stamens 2; pollen-grains of a unique, isobilateral type; fruiting carpels long-stipitate; ovule pendulous from the apex; plants chiefly of brackish or alkaline water ..... **5. Ruppiaceae**

5. Flowers unisexual:

7. Pistil solitary, forming a unilocular ovary surmounted by 2-4 elongate stigmas; ovule basal, erect ..... **6. Najadaceae**

7. Pistils (1) 3-4 (-9), each with a short or elongate style and stigma; ovule ventral-apical, pendulous ..... **7. Zannichelliaceae**

4. Pollen-grains thread-like, plants marine:

8. Flowers perfect; stamens 3, distinct; gynoecium of a single unicarpellate pistil ..... **8. Posidoniaceae**

8. Flowers unisexual; stamen solitary or stamens 2 and connate; carpels 2:

9. Gynoecium of 2 separate pistils; stamens 2, united back to back; tanniferous cells present ..... **9. Cymodoceaceae**

9. Gynoecium of a single unilocular, bicarpellate pistil; stamen solitary; tanniferous cells wanting ..... **10. Zosteraceae**

Character scoring for the Najadales

I developed a character set (Table 1.3) and a data matrix (Table 1.4) for the Najadales. Most of the characters were presence/absence, but three were multiple-state characters. Figure 1.5 depicts a contour graph of relationships between the families. Note that similar shades indicate shared character states between families. This figure can be utilized as a preliminary indicator for a phenetic analysis.

Table 1.3. Characters and character states employed in the study of the Najadales. Values given are for analysis of discrete data and no evolutionary weight is given for data that have continuous values. From Heywood (1985) and Cronquist (1988).

1.	Ovules:	0=two-several in each of the three-several distinct or proximally connate carpels. 1=solitary in each distinct carpel or in each locule of a compound ovary
2.	Fruits:	0=follicular 1=Mostly indehiscent or only tardily and irregularly dehiscent
3.	Stamens:	0=1-3 1=4 2≥5
4.	Tepals:	0=none 1=1-3 3=4 5=numerous
5.	Pollen grains:	0=not thread-like 1=thread-like
6.	Flowers:	0=perfect 1=imperfect
7.	Ovary superior:	0=no 1=yes
8.	Flower unisexual:	0=no 1=yes
9.	Flower bisexual:	0=no 1=yes
10.	Pollination:	0=above water surface 1=submerged
11.	Salt tolerance (o/oo):	0≤10 1≥10
12.	Temp. tolerance:	0=hot tropical 1=cool temperate 2=cold northern latitudes 3=cosmopolitan

Table 1.4. Data matrix for the character states. The order is separated into ten families and the data have continuous values.

Family	1	2	3	4	5	6	7	8	9	10	11	12
Cymodoceaceae	1	1	1	0	1	1	0	1	0	1	1	0
Posidoniaceae	1	1	1	0	1	0	1	0	1	1	1	0
Zosteraceae	1	1	1	0	1	1	0	1	0	1	1	1
Ruppiaceae	1	1	1	0	0	0	1	0	1	0	1	3
Zannichelliaceae	1	1	1	0	1	1	1	1	0	1	0	3
Potamogetonaceae	1	1	1	3	0	0	1	1	0	0	0	3
Najadaceae	1	1	1	0	0	1	1	1	0	1	0	3
Juncaginaceae	1	0	0	5	0	0	1	0	0	0	0	1
Scheuchzeriaceae	0	0	0	5	0	0	1	0	1	0	0	2
Aponogetonaceae	0	0	0	1	0	0	1	0	1	0	0	0

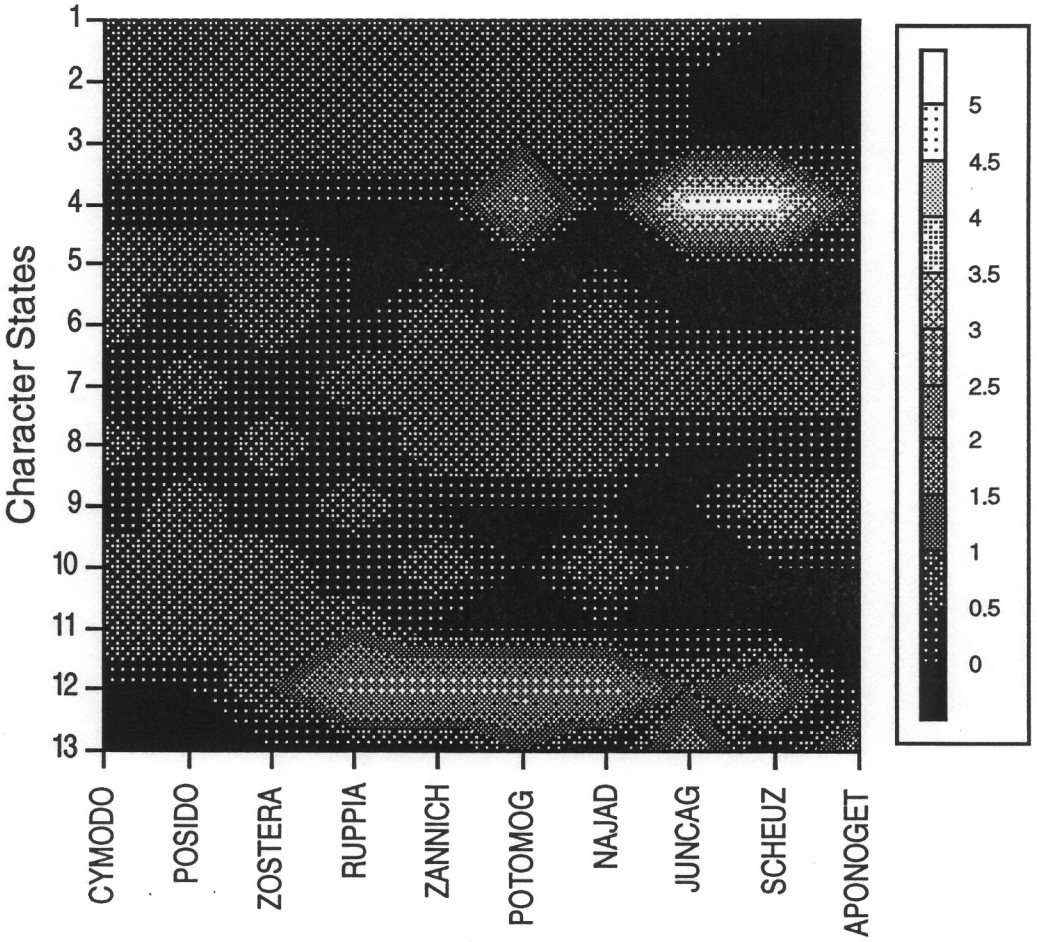

Fig. 1.5 Contour graph depicting character relationships between families in the Najadales

Phenetic clustering of the Najadales

The character set for the Najadales was set up as a data matrix and analyzed using the computer program, Numerical Taxonomy and Systematics© (NTSYS). Two possible phenograms result (Fig. 1.6a, 1.6b). Note that the major difference was that the Potomogetonaceae linked directly to the Zosteraceae in phenogram 1.6b. The matrix correlation (goodness of fit) for both phenograms was high (Fig. 1.6a, 1.6b).

Both phenograms indicated that three "subgroups" may exist within the Najadales. They were: 1. Aponogetonaceae, Juncaginaceae, Scheuchzeriaceae.

2. Najadaceae, Posidoniaceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae.

3. Cymodoeaceae, Zosteraceae. However, the middle cluster had unclear links as indicated by Figures 1.6a and 1.6b.

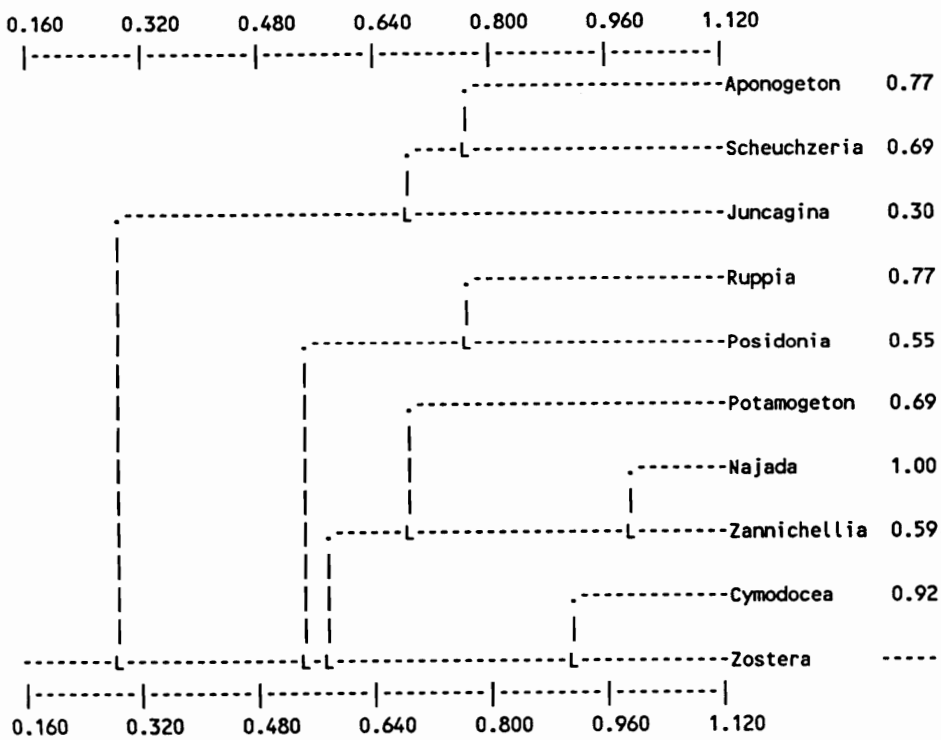

Fig. 1.6a. Phenogram of the Najadales generated by NTSYS©. Axes indicate matrix correlations.

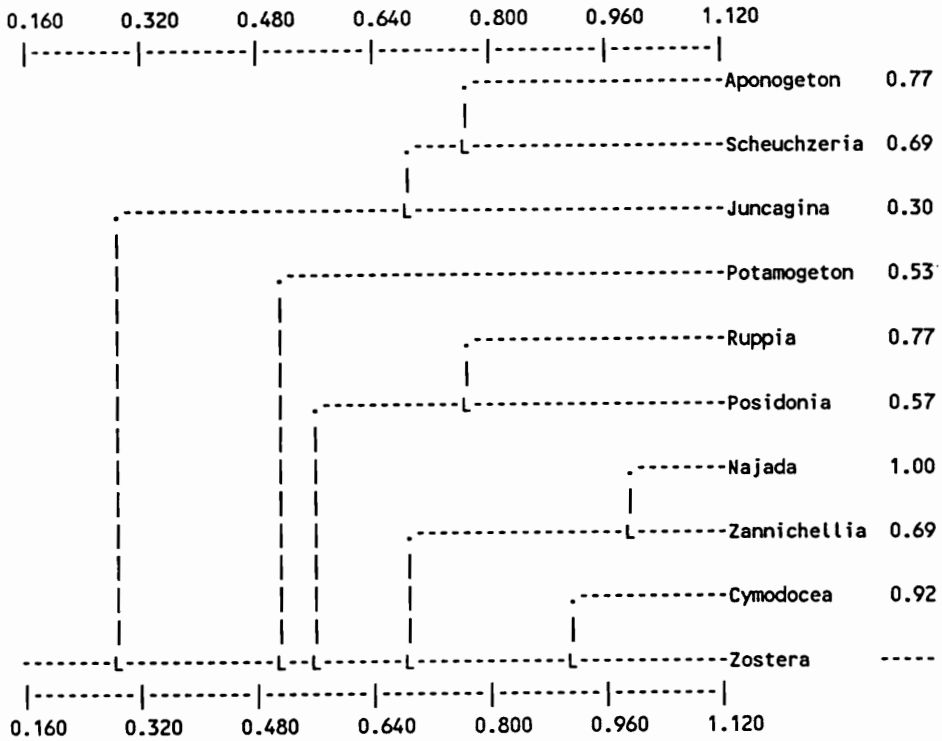

Fig. 1.6b. Phenogram of the Najadales generated by NTSYS©. Axes indicate matrix correlations.

Conclusions

Important differences exist between the phenograms (Fig. 1.6a, 1.6b). The Aponogetonaceae, Juncaginaceae, and Scheuchzeriaceae are emergent plants and they grouped out into a phenetic cluster. The Zosteraceae, Cymodoeaceae, and Posidoniaceae are all marine "seagrasses". In the phenograms, the Posidoniaceae and the Ruppiaceae linked as a group to the Zosteraceae. This is intriguing. Ecologically, the Ruppiaceae is found in estuarine and marine habitats, often as a co-dominant species with other seagrasses (Zosteraceae, Cymodoeaceae, and Posidoniaceae). The results of my analysis

show that the Ruppiacaeae are allied to the seagrass subgroup *and* the "Najadaceae complex" of families. This is in agreement with the current argument. The results of my own research indicate that the Ruppiaceae may be placed within the Potomogetonaceae if you are a lumper, but could be an independent family if you are a splitter and you want to highlight floral construction and the marine habit of this family. The Najadales is a complex group of aquatic families and needs much further study to distinquish true relationships.

Taxonomy and Systematics of seagrasses

The classification of the seagrasses has been handled variously. Stebbins (in Heywood 1985) recognized 44 species in four families: Ruppiaceae (1 genus, 7 species), Zosteraceae (3 genera, 18 species), Posidoniaceae (1 genus, 3 species), and Cymodoceaceae (5 genera, 16 species). Phillips and Meñez (1988) give the following breakdown; 48 species in two families: Potamogetonaceae (9 genera, 34 species) and Hydrocharitaceae (3 genera, 14 species). The following is a general breakdown of the genera. Cymodoceaceae (Tropical and sub-tropical seas): Cymodocea, Halodule, Syringodium, Amphibolis, Thalassodendron. Posidoniaceae (Mediterranean Sea and South Australian coast): Posidonia. Ruppiaceae (Cosmopolitan): Ruppia. Zosteraceae (Temperate coasts): Zostera, Phyllospadix, Heterozostera. Related taxa include Thalassia and Halophila in the Hydrocharitaceae (Hydrocharitales) (Heywood 1985). This discrepancy in seagrass taxonomy causes inconsistency in reporting data and describing taxa. For example, Phillips and Meñez (1988) describe Thalassia (Zanichelliaceae) as a seagrass, while both Heywood (1985) and Cronquist (1988) separate the seagrasses into four "submerged pollination" families and exclude the Hydrocharitaceae (as described above).

Considering that the biology of some seagrass species has yet to be understood (Ruppia maritima, for example), it is not surprising that the systematics of seagrasses is confused. The taxonomy of Ruppia maritima in North America continues to be problematic for some investigators (DenHartog, pers. comm.). Upon my investigation of the herbarium material for this genus at the Royal Botanical Gardens, Kew, I observed that the six taxa represented were clustered around three main areas: North America, Australia and New Zealand, and Europe and the Mediterranean. Ruppia maritima is the only taxon that has been described in all areas and as occurring with all the other taxa (Kantrud 1991). The herbarium material itself showed an astonishing amount of morphological variation even within a taxon. I would conclude that one species, Ruppia maritima s.l. exists with a number of morphological variations (megacarpa, polycarpa, spiralis, cirrhosa, and tuberosa) which now correspond to different taxa. In terms of placement of the genus, I am a lumper, and place it with the Potamogetonaceae. Ruppia, along with Potamogeton filiformis and P. pectinatus, displays a trend toward reduction in floral parts and appears intermediate in the trend towards completely submerged (true) hydrophily in the marine habitat.

Cytological examination of these groups has included chromosome counts (Darlington and Wylie 1955; Van Vierssen et al. 1981), but this work has not been included in systematic studies of the taxa. Systematics using molecular approaches is becoming more common in present day investigations (Gibbons 1991). Analysis of chloroplast DNA has been successful in elucidating new characteristics for taxonomic comparisons (Palmer 1986, Sytsma and Smith 1990). Protein sequence analysis has also been employed in molecular evolutionary investigations. Indeed, entire treatises have been written in which molecular techniques are evaluated for the purpose of investigating evolution, taxonomy, and systematics of plants (Palmer 1985). In the most recent text on the biology of seagrasses of Australia (Larkum et al. 1989), not a single

reference is made to molecular approaches. In fact, the term DNA does not appear in the text's reference section. It is clear that some knowledge of the genetic ultra-structure of seagrasses would be beneficial.

Hydrophily

"Whereas the primitiveness of wind-pollination has been a matter for discussion, or by some has been taken for granted, there has never been any doubt that hydrophily is a derived condition, as the aquatic habitat generally is a derived one for higher plants." (Faegri and van der Pijl 1966).

In their introduction to hydrophily, Faegri and van der Pijl (1966) make a comparison between anemophily (wind-pollination) and hydrophily in which the two are juxtaposed. Here anemophily is treated as a commonplace and hydrophily as a peculiarity. While hydrophily may be a rare occurrence when compared to breeding systems of vascular plants in general, some of the morphological characteristics of hydrophilous and anemophilous plants, such as reduced floral structures, increased pollen production, and pollen buoyancy adaptations, are strikingly similar. From an evolutionary standpoint, it should not seem odd that the two pollination media (air and water) would select for some similar characteristics in their resident plants. Both media make possible a passive pollination mechanism independent of other biotic vectors. A number of vascular plant groups such as the Najadales (hydrophily) and the Fagales (anemophily) are successful with these more passive and chancy pollination methods. Others, however, have developed more energy intensive and directional methods, the most familiar method being entomophily (insect pollination). Hydrophily is not peculiar in itself, but variations in pollination strategies within families or genera of hydrophytes are.

Anemophily

Wind pollination (anemophily) is the dominant form of passive pollination and perhaps the most common form of pollination in terms of taxa (Faegri and van der Pijl 1966). While anemophily may be quite common, many unique adaptations have developed to facilitate this strategy. These include number of pollen grains, pollen size, exine characteristics, flower structure and location, timing of flowering, pollen release and pollen buoyancy (Faegri and van der Pijl 1966, Whitehead 1983).

There are many indications that anemophily is a more recent occurrence, derived from entomophilous ancestry. For instance, in many families of entomophilous plants there are anemophilous members (for example in Ambrosia (Asteraceae), Fraxinus (Oleaceae), and Thalictrum (Ranunculaceae). The opposite is also true, for example in Luzula (Juncaceae) and Pariana (Poaceae), (Faegri and van der Pijl 1966). In the latter cases, the entomophilous plants are more primitive.

Some peculiarities exist in these anemophilous plants. For instance, members of the Juncaceae and Poaceae have a greatly enlarged stigmatic surface area for collecting air-borne pollen. The sticky stigmas of many of these plants increases the effectiveness of "catching" the small, dry, and unsticky pollen grains associated with them. This creates a situation where the effectiveness of pollen collection is greater than that of a leaf of the same gross area (Gregory 1951).

Some large conifers, such as Pinus, have buoyant, large pollen grains. Air sacs have been incorporated into these grains to give them a large volume and surface area without appreciably increasing their weight. The result is a pollen grain which has a maximized transport ability (Faegri and van der Pijl 1966).

Entomophily

The parallel evolution of insects and flowering plants has given rise to some beautiful pollination "lures" of all shapes, colors, and odors. A treatise of entomophilous

plants is not my intent here, so I will limit the discussion of entomophily to the peculiar adaptations developed by members of the Nymphaeales as described by Sculthorpe (1967). I chose the Nymphaeales as examples of aquatic vascular plants that have overcome some mechanical problems of living in water, as well as having developed some interesting pollination methods.

In the Nymphaeacae leaves tend to be rounded, notched, and floating. The notch or invagination of the leaves is an added feature to aid the platform-like leaves in staying afloat after being inundated. If part of the leaf is inundated, the notch acts as a water channel while another part of the leaf can surface. A layer of wax also aids in leaf buoyancy. The flowers of these plants are lofted by a sturdy peduncle that, in many cases, is strong enough to actually raise the flower from the water's surface.

In many Nymphaeaceae anthesis is diurnal. In the northern hemisphere, most species of Nymphaea (Water Lily) and some Nuphar (Spatter Dock) species open their flowers during the day either in the early morning or in mid-afternoon. Anthesis in some tropical water lilies as well as in some Victoria species (V. amazonica, V. cruziana, and V. tricheri) takes place at night. In Brasenia schreberi, the flowers emerge from the water, opening during early morning; they are then drawn back into the water, rising and opening again the next day (Sculthorpe 1967).

Generally, the Nymphaeaceae are pollinated by beetles, small flies, and sweat-bees, which crawl indiscriminately over the flowers. The attractants for these insects are probably smell, warmth of the opening flower, and the food value of the stamens. The color of the corolla may also be involved, but may not be as important as the other features. The example of Victoria amazonica is well worth noting. This plant evolves a strong rotting meat-like odor, emanating mainly from the "carmine-red" carpel outgrowths. The flower also generates heat, which may raise its temperature 10° C above its surroundings. Cockchafers and other flying insects are attracted to the flower and will

eat the stamens in the relative warmth of the flower. These organisms may stay inside the flower when it closes, flying away when it re-opens the following evening. Entomophily in these primitive dicots is not unusual.

Self pollination is present in many of the groups described above. In Tenagocharis latifolia (Butomaceae, Alismatales) the wilting petals close in around the dehisced anthers, pressing them close against the stigmas, which consequently become coated in pollen. The Nymphaeales have many primitive Magnoliidae characteristics as described above.

Hydrophily

It is not peculiar that aquatic vascular plants, especially submerged taxa, exhibit adaptations for hydrophily. "Trends of floral modification culminating in the development of submerged water-pollinated flowers are discernable amongst both monocotyledons and dicotyledons." (Sculthorpe 1967 p. 291). Most aquatic plants are still pollinated in air, but some have taken advantage of the water for pollination (Daumann 1963). For example, the rain splash pollination of Ranunculus species can be categorized in this way. For purposes of clarity, I will focus on groups with hydrophilous trends and true hydrophilous species.

In the Hydrocharitaceae a transition from entomophily to hydrophily occurs. Procter and Yeo (1978) discuss that since the actual transfer of pollen takes place in the air, this is not truly hydrophilous pollination at all. However, by comparing the floral morphology of various members of the Hydrocharitaceae a transitional trend from air to water can be observed (Sculthorpe 1967). Certain of these Hydrocharitaceae, both free-floating and submerged, are entomophilous: Hydrocharis, Limnobium (except L. stoloniferum), Ottelia, Stratiotes, and Egeria. In Hydrilla verticillata, Vallisneria spiralis, Lagarosiphon muscoides, and Enhalus acoroides there are definite trends toward hydrophily; the dry microspores are transferred to the stigmas through the air and not the

water (Sculthorpe 1967). In the transition from entomophily to, at least, water-aided pollination there is a marked reduction and specialization of floral parts (Figs. 9.18 and 9.20 in Sculthorpe, 1967). By observing these morphological adaptations, hydrophily can be inferred as the main pollinating agent of these species.

Other morphological adaptations seen in various groups of hydrophilous plants are pollen elongation (which may be aided by early germination) and mechanical actions of pollen grains stimulated by contact with a narrow object (Zosteraceae, Posidoniaceae, Cymodoaceae).

Zostera marina and Ruppia maritima form "seagrass" ecosystems along the Atlantic and Chesapeake shores of Virginia. These plants provide shelter for fish fry and larval stages of molluscs and crustaceans. They provide shore stability and a major contribution to the primary production of the coastal ecosystem. These important plants and their kin, while being quite common, have some curious, but not well studied life histories. In Zostera the female flower consists of an ovary, containing a single ovule, with two long stigmas (much like anemophilous species) at the apex; the male flower, which matures one to three days later, consists of a single anther. Plants are dioecious, with flowers occurring on reproductive shoots as a sessile inflorescense in an elongated spathe. The pollen grains are thread-like and can attain lengths of 0.25 mm. The pollen grains have the same density as sea water and the pollen grain exine is extremely reduced. (Procter and Yeo 1973). Pollen grains often germinate before reaching a stigma, at which time the pollen tube rapidly wrap around it almost ensuring pollination. Zostera is dependant on water currents, and extremely large quantities of pollen grains are produced. Such quantities of pollen are also seen in anemophilous plants. Pollen is probably a food source for some zooplankters. The flowers of Ruppia emerge from the water and large quantities of pollen are released by wave action on the flowers.

Systematics of Hydrophilous taxa

Cladistic analysis of hydrophilous taxa provides some information on the evolution of hydrophily in monocots. The Ceratophyllaceae contain the only hydrophilous dicot (Philbrick 1991). The monocots contain seven hydrophilous families, but 28% of all *aquatic* monocots are hydrophilous (Philbrick 1991). Although it seems clear that hydrophily is polyphyletic in the monocots, it is not clear how many times it arose or from what ancestors it arose. If we allow aerial pollination systems to be derived in some cases, but ancestral in others, a more parsimonious tree evolves for the monocots (Philbrick 1991). It is difficult to accept hydrophily as the primitive characteristic in the development of anemophily since stigmas and anthers are thought to be the result of a terrestrial habit.

Seagrass Morphology

Seagrasses grow in suitable shallow marine waters worldwide and are absent only from the high Arctic and the Antarctic (Helfferich and McRoy 1980). The vegetative and reproductive structures of seagrasses are completely submerged and are anchored to the substrate. Only a few species are adapted to intertidal habitats.

Seagrasses persist predominantly by vegetative growth, but they have evident and important reproductive cycles (Orth and Moore 1983a, Silberhorn et al. 1983). The majority of species have small to very large linear, strap-like leaves (den Hartog 1977). Seagrasses have extensive rhizome systems. Only Phyllospadix (Zosteraceae) occurs obligately on a rocky substrate. All other genera colonize and persist on muddy and sandy unconsolidated substrates (Phillips and Meñez 1988).

The rhizomes of most species have bundles of longitudinal sclerenchyma fibers in the inner and outer cortex that give a structural rigidity to the below ground system. There is a large air space to volume ratio in the roots. The root respiratory oxygen is

produced by photsynthesis in the leaves and a gradient of oxygen exists from the leaf to the roots (Phillips and Meñez 1988). This ability to transport oxygen to the roots allows the plants to grow in anoxic substrates.

The leaves of most seagrasses also have large, longitudinally extended air canals called lacunae (Tomlinson 1980). This enlargement of internal volume neither enlarges the photosynthetic volume nor the surface area to any marked extent. This phenomenon may have no relevance to gas exchange and is found in many aquatic plants to serve in providing buoyancy. The xylem of most seagrasses is poorly developed and the leaves are usually elastic; phloem tissue is well developed. The leaves develop in the usual monocot fashion from basal meristems, with the leaf apex maturing first (Tomlinson 1980). The large air spaces develop from enlarged intercellular spaces.

Many aspects of seagrass physiology and growth patterns have been investigated (den Hartog 1977; Phillips and McRoy 1980; Orth and Moore 1986, 1988; Phillips and Meñez 1988). In addition, ultrastructure, salt and temperature tolerance, and the plant-animal ecology of seagrasses have been studied since the early 20th century (Gibbs 1902; Setchell 1922, 1929; Mazzella and Russo 1989; Waldron et al. 1989; Kuo et al. 1990; Larkum and West 1990; Walker and McComb 1990). However, there is little information concerning the pollination biology of the seagrasses (Phillips and Meñez 1988). All seagrasses have structures adapted for hydrophilous pollination. Other genera have spherical pollen grains that are arranged in floating chains. Most seagrasses are dioecious, and those genera that are monoecious (Zostera, Heterozostera, Halophila) show protogyny (Phillips and Meñez 1988), but there are no comparative studies that explain these variations. Sculthorpe (1967) provides a general discussion of trends toward hydrophilous pollination in vascular plants.

***Ruppia maritima* in Chesapeake Bay**

Seagrasses form dynamic, biologically productive ecosystems in many shallow water coastal habitats of the world (den Hartog 1977, Phillips and McRoy 1980). Special attention has been focused on seagrass communities in the last two decades because these areas have been shown to harbor more animals by orders of magnitude than adjacent unvegetated areas (Orth and Moore 1984). Such communities stabilize sediments, are a food source for waterfowl, and are areas of high primary and secondary production. In many parts of the world, the delicate balance between seagrass ecosystems and their environments is being threatened by anthropogenic inputs, primarily sediments and nutrients that can result in serious, if not catastrophic, losses of seagrass, such as have occurred in Europe, Australia, and the United States (Kemp et al. 1983, Orth and Moore 1983a, Cambridge and McComb 1984).

Seagrass meadows form complex ecosystems that function through detritus-based food webs as well as herbivore food webs. In the latter, living seagrass plants as well as associated epiphytes such as diatoms are grazed. The leaves retard water currents and waves, promoting sedimentation of particulate matter and inhibiting re-suspension of organic and inorganic matter. Seagrasses provide waterfowl, fish, molluscs, crustaceans, protists, and algae with food and/or habitat and breeding grounds (Orth and Moore 1981). Submerged grasses provide food, shelter and breeding areas for birds, fish, shellfish and many other estuarine organisms. In addition to being a basic component of the estuarine food chain, the beds of submerged vegetation are also a habitat for juvenile striped bass (Morone saxitilis) and menhaden (Brevoortia tyrannus), and for the economically important blue crab (Calinectes sapidus) when it is molting. During this time, the softshell crab is especially vulnerable to predators, because of its unhardened, fleshy shell and its inability to move quickly to escape its natural enemies. (Environmental Protection Agency 1980). Chesapeake Bay, the largest estuary in the

United States, has also received considerable attention over the last two decades from scientists, managers, politicians, and the public. Declines in water quality are related to increasing nutrient enrichment, high levels of toxic contaminants, and anoxic or hypoxic conditions. Changes in abundance of living resources is also a major issues facing the bay. Submerged aquatic vegetation (SAV) is one of the living resources that has declined. Declines of SAV have been documented in the past, notably the 1930s eelgrass blight that affected not only the Chesapeake Bay but the entire Atlantic Coast of the United States and Europe (Rasmussen 1977; Orth and Moore 1984). The symptoms of this blight included destruction of rhizome, leaf, and floral stem tissue after previous formation of blemishes on leaves and rhizomes (Rasmussen 1977). Zostera plants with the characteristic symptoms have been found to contain a slime mold, Labyrinthula macrocystis, as well as other Labyrinthula species (Rasmussen 1977). However, the decline that occurred over the last two decades has been unprecedented (Orth and Moore 1983a). This latter decline has affected all SAV species bay-wide, and has been attributed to the increasing amounts of nutrients and sediments entering the bay as a result of the continuing, uncontrolled development of its shoreline and watershed, and poor land use practices associated with this development (Kemp et al., 1983).

The decomposed leaves of seagrasses provide organic matter in detritus-based nutrient cycling (Zieman et al. 1984). High growth rates (600 g dry weight/m^2/yr, not including root production) indicate their importance in detritus-based nutrient cycling. Seagrasses are important in the cycling of sulfur and phosphorus (Zieman et al. 1984). The decaying roots of the plants support sulfate reduction. Phosphorus is directly absorbed through the roots and leaves. Therefore, phosphorus is returned to the water column from sediments via the plants (Zieman et al. 1984). Nitrogen is also returned to the water column in the same way.

Although research on seagrass ecosystems in lower Chesapeake Bay over the last two decades has focused almost entirely on Zostera marina, recent monitoring of SAV populations in the Chesapeake Bay has shown that Ruppia maritima is also very abundant, and in some areas occurs in large monospecific stands (Orth et al. 1989; Orth and Nowak 1990). More recently, natural revegetation has been observed in many areas bay-wide, with Ruppia maritima being the primary colonizer (Orth and Nowak 1990).

Despite this abundance, basic research on Ruppia maritima has been limited in the Chesapeake Bay. The distribution, abundance, and ecology of Ruppia maritima have been the focus of studies in other regions of the United States and elsewhere. Environmental characteristics such as light, temperature, and salinity have been shown to affect the growth and reproduction of this species (Verhoeven 1975, 1979; Richardson 1980; Brock 1982a, 1982b; Evans et al. 1986; Koch and Dawes 1991). Sediment and water column nutrient dynamics have also been shown to affect its physiology and biology (Thursby 1984a, 1984b; Thursby and Harlin 1984). In addition, germination and the seed reserve have been investigated as important factors influencing the colonization and distribution of this plant in suitable habitats (Seeliger and Koch 1984; Van Vierssen et al. 1984; Koch and Seeliger 1988; McMillan 1988). This dissertation investigated the reproductive biology of Ruppia maritima in the lower Chesapeake Bay. Colonization and seasonal changes due to vegetative and sexual reproduction was also investigated as well as the role of seed banks in the establishment and maintenance of populations.

Brief Site Descriptions

Five sites in lower Chesapeake Bay were chosen by the following criteria:

- Presence of monospecific beds of Ruppia maritima.
- Presence of mixed Ruppia maritima and Zostera marina beds.
- History of previous investigations by Virginia Institute of Marine Science.
- Use as a current study site by VIMS scientists.

The following are short descriptions of each site with corresponding aerial photographs:

Corrotoman River

Latitude/Longitude (on shore, beginning of transect) = 37°40'08" / 76°27'51".

Monospecific bed of Ruppia maritima from shore extending over 400 meters (Fig. 1.7).

Rappahannock River

Latitude/Longitude (on shore, beginning of transect) = 37°39'55" / 76°27'44".

Monospecific bed of Ruppia maritima from shore extending to approximately 200 meters (Fig. 1.8). The water clarity at this site was very good and visibility was more than two meters.

Piankatank River (Gwynn Island)

Latitude/Longitude (on shore, beginning of transect) = 37°30'55" / 76°17'29".

Mixed bed of Ruppia maritima and Zostera marina from shore extending to over 400 meters. This was a mixed bed near the north-west point of the island and the largest mixed bed on the west side of Gwynn Island (Fig. 1.9).

York River (Goodwin Islands)

Latitude/Longitude (on shore, beginning of transect) = 37°13'12" / 76°23'90".

Mixed bed of Ruppia maritima and Zostera marina from shore extending to about 200 meters (Fig. 1.10).

Chesapeake Bay (Goodwin Islands)

Latitude/Longitude (on shore, beginning of transect) = 37°13'15" / 76°22'94".

Mixed bed of Ruppia maritima and Zostera marina from shore extending to over 400 meters (Fig. 1.11). This site included a number of sand bars. These bars had patches of Ruppia and Zostera growing in the deeper trenches between the bars.

Chesapeake Bay Region

Sites are located as listed above from north to south (Fig. 1.12).

The following chapters investigate reproductive and ecological features of Ruppia maritima at these sites. Comparisons between sites are made when appropriate. Data from this study are also compared to other ongoing studies on submerged aquatic vegetation at these and other sites in order to shed light on ecological and management issues in Chesapeake Bay.

Fig. 1.7. Corrotoman River site. North ↑

Fig. 1.8. Rappahannock River site. North ↑

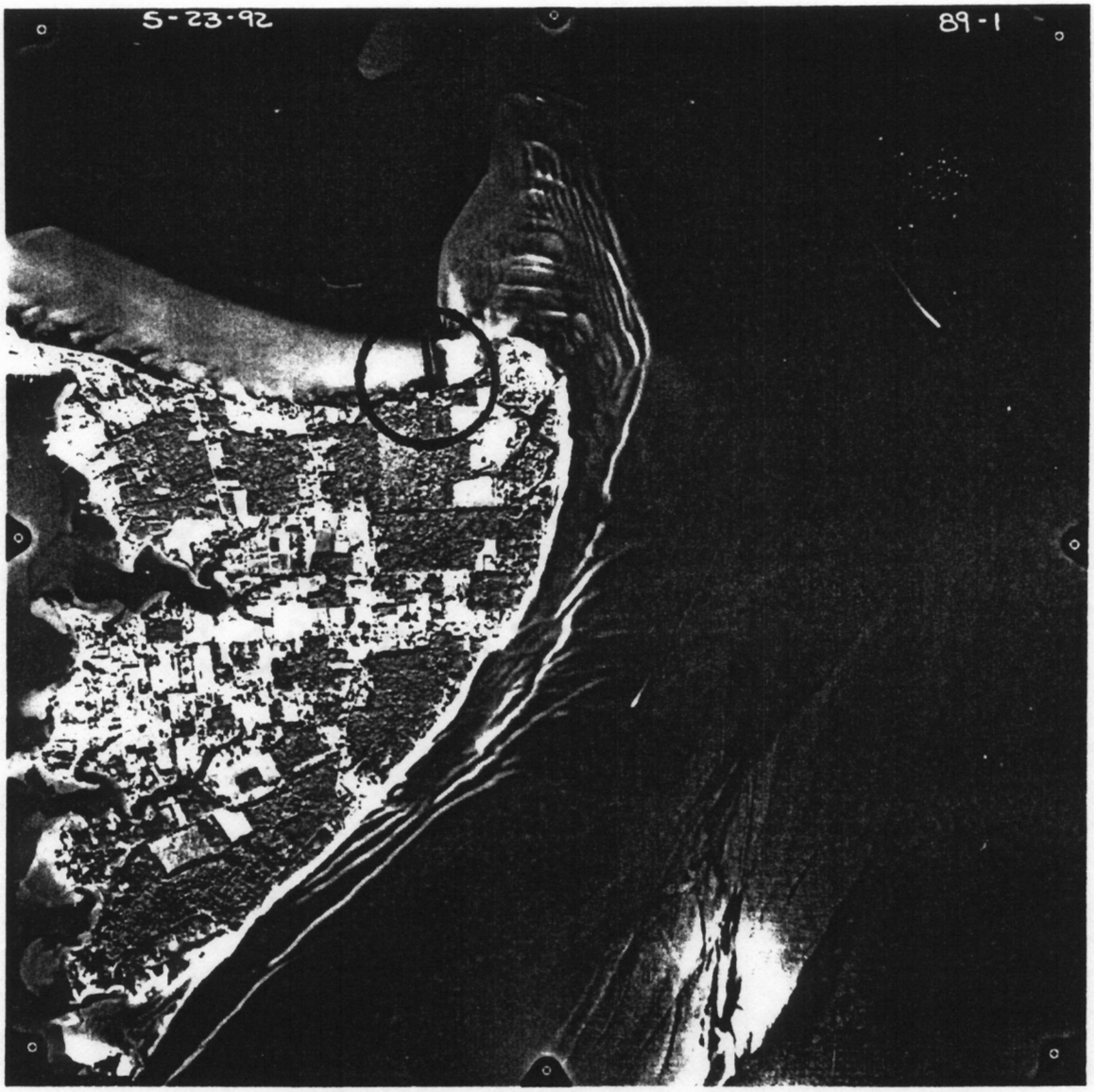

Fig. 1.9. Piankatank River (Gwynn Island) site. North →

Fig. 1.10. York River (Goodwin Islands) site. North ↑

Fig. 1.11. Chesapeake Bay (Goodwin Islands) site. North ↑

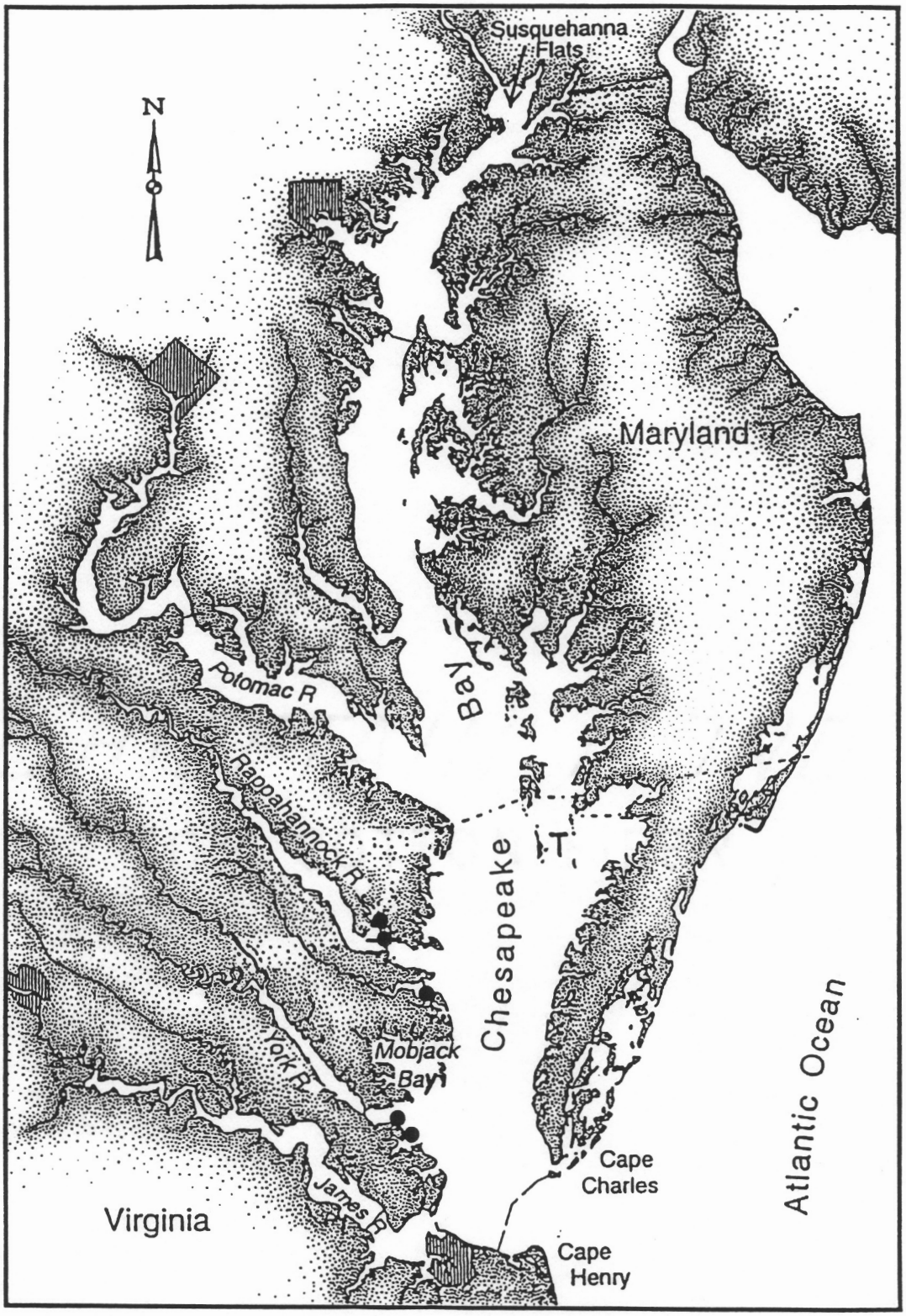

Fig. 1.12 Location of the five study sites in Chesapeake Bay.

Chapter II.

Pollination of *Ruppia maritima* L. from Chesapeake Bay in a flow-through mesocosm system

* In preparation as a manuscript to be submitted to *Estuaries*.

Abstract

In lower Chesapeake Bay, Ruppia maritima occurrs in monospecific stands as well as in communities with Zostera marina. The establishment and maintanence of Ruppia in these habitats is by both sexual and asexual propagules. The importance of sexual reproduction in the ecology of these plants has not been determined and may pose a vital link in the timing and methods used to preserve and manage Ruppia and Ruppia/Zostera habitats. The purpose of this study was to examine pollination of Ruppia and to explore the possibility that a biological gradient of population isolation can result in lower seed production from outcrossed individuals from the same and separate populations. During the course of this study I observed that the inflorescence peduncle grew back down into the water upon fertilization and before the fruits developed. This provided the fruits with a protective advantage from dessication and, perhaps, from predation by water fowl.

Introduction.

Pollination systems of aquatic vascular plants present some unique and dramatic ecological and evolutionary characteristics. Taxa exhibiting water-mediated pollination (hydrophily) are infrequent in angiosperms, with only about 140 of the total 225,000 taxa or 0.00062% exhibiting some kind of hydrophilous pollination system (Philbrick 1991). Hydrophily occurs in only one dicot (0.3%) and seven monocot (10.6%) families. The taxa exhibiting hydrophily are found in one dicot order (Nymphaeales) and in one monocot order (Najadales). Of the 140 total taxa, only six are in the Nymphaeales. Philbrick (1991) discusses the taxonomic and phylogenetic distributions of hydrophily as well as some ecological and biological factors that may influence the distribution of hydrophilous taxa in relation to wind-pollinated plants. Here he describes hydrophilous systems as perhaps the best examples of evolutionary plasticity of angiosperm floral

biology, in that the aerial floral system that dominates angiosperms has been essentially abandoned and the infrequent occurrence of hydrophily makes it possible to gain an overall understanding of its evolution respective to other pollination systems. He concludes that because of the degree of specialization and reduction in hydrophilous flowers, it is difficult to construct phylogenetic hypotheses based on floral structures alone, and molecular based data may prove to provide exciting insights.

With this in mind, I examined the pollination of biology of Ruppia maritima in Chesapeake Bay. The pollination of Ruppia taxa has been examined in western Europe (Verhoeven 1979) and in Australia (Brock 1982a, 1982b). I will summarize the results of these studies in relation to pollination biology of Ruppia maritima in Chesapeake Bay.

The flowers of Ruppia are arranged in a spike. Each spike bears two hermaphrodite flowers, each with two sessile stamens between which lie four or more stipitate carpels, each with a campylotropous ovule (Sculthorpe 1967). McCann (1945) reported that in Ruppia maritima the stalks of the carpels elongate, so that the discoid peltate stigmas form a loose canopy above the anthers. Long reniform microspores, often adherent in strings, float upwards and are caught beneath the stigmatic canopy of the same or higher inflorescences. They tend to drift out from under the canopy and around its margins to the receptive stigmatic surface, where some adhere and germinate. In the related Potamogetonaceae, most taxa produce an aerial spike and wind pollination occurs. In Potamogeton filiformis and Potamogeton pectinatus, the spike floats on or near the water surface, and pollen floats to the stigmas of the same or other inflorescences (Daumann 1963). These two species often extend into brackish waters, as does Ruppia maritima. These two genera appear intermediate in the trend towards completely submerged (true) hydrophily in the marine habitat.

Verhoeven (1979) reported that when Ruppia spikes become submerged by high tides, a pocket of air can form around the inflorescences. Pollen release is promoted by

desiccation of the anther during exposure and pollen can stick to the inner surface of air bubbles and be transported mechanically to stigmas of the same inflorescence. I observed the air bubble phenomenon on inflorescences at my study sites in lower Chesapeake Bay. Presumably, the same form of pollination can occur here as well. In addition, spikes exposed by low tides, or by extension of the peduncle above the surface, can be pollinated when pollen is released and transported across the water surface to the same or other inflorescences (Verhoeven 1979). In another description (Richardson 1980) anthers burst and pollen is released, aided by gas bubbles that accumulate inside the anther sac. Pollen can be trapped within the inflorescence and some can cling to the surface of the gas bubbles. In this way, most of the eight pistils that are usually found in each inflorescence are self-pollinated, but cross-pollination occurs from pollen-laden bubbles that rise to the water surface, and pollen is transported to other flowers. At my study sites, in all cases, the reproductive shoots grew to about mean low water. During peak times of flowering, pollen was spread as a visible layer across the surface of the water. Brock (1982b) describes the pollen of Ruppia tuberosa as generally elongate, dumbbell-shaped, and comparatively longer than those of Ruppia megacarpa. The latter were squat, elliptical or dumbbell shapes. Pollen grains of Ruppia polycarpa were elongate and boomerang-shaped at maturity. The pollen grains that I collected were all dumbbell-shaped and twice as long as wide (Fig. 2.1). Pollen grains stained with either 10% ethyl alchohol or 2% IKI appeared to be high in starch grains and lipid droplets. The lipid droplets probably aid in the buoyancy of the pollen.

In Chesapeake Bay Ruppia maritima occurs in monospecific stands or with Zostera marina. The reproductive biology of Ruppia maritima has not been extensively studied in Chesapeake Bay. Silberhorn (unpublished manuscript) has provided some information on seed production, but the importance of asexual and sexual modes of reproduction has not been addressed in relation to the occurrence of Ruppia maritima,

either with or without Zostera marina, in Chesapeake Bay. The relative abundance of Ruppia in the lower bay and its ecological importance to the bay ecosystem adds importance to understanding the pollination system of Ruppia maritima in Chesapeake Bay. The sensitivity of submerged vegetation to disturbance alone warrants a better understanding of the pollination biology of Ruppia maritima in Chesapeake Bay.

In this study, I focused on pollen transfer and degree of selfing and crossing quantified by seed production. This study does not disprove the possibility of agamospermy. However, all spikes that produced fruits in this study exhibited a downward growth of the peduncle after pollination. All other spikes died. I presume here that, at least, pollination if not fertilization must occur for the plants to produce fruits. In addition, I quantified the downward peduncle growth of fertile inflorescences. Both studies were conducted at the Virginia Institute of Marine Science (VIMS), Gloucester Point, Virginia, in controlled chambers in a flow-through tank that used water pumped from the York River, a major tributary of Chesapeake Bay.

Methods and Materials

The experiments were conducted in a fiberglass tank set up in a greenhouse located next to the York River at VIMS. Water was pumped from the York River, filtered twice through
sand filters, and then pumped through the greenhouse. Nylon mesh material was placed over the tank to decrease sunlight and, hence, algal growth in the tank.

I constructed two acrylic plastic chamber units, each consisting of a grid of chambers measuring 14 cm X 14 cm X 30 cm deep for total of 130 chambers. One mm screening was added to the bottom of each unit in order to hinder the movement of particles and pollen into each chamber. The chamber units were immersed in the tank

and held down in the water by weights. Air stones were placed around the tank to aid in water circulation.

Experimental Design

Reproductive shoots were collected from one of my study sites on the Bay side of Goodwin Islands. In addition, reproductive shoots were also collected from one other site approximately three miles away from Goodwin Islands at Sandy Point, on the north shore of the York River near the mouth of Mobjack Bay (Fig. 1.12). All reproductive shoots had one or more inflorescence that was still enclosed in its sheath. The 130 chambers contained a total of 205 inflorescences. Emergence and development of the inflorescence took place in pollination chambers to insure that no pollination had taken place in the field. Reproductive shoots were placed in pollination chambers using a four treatment design. The treatments were

1. One inflorescence to test for selfing.
2. Two inflorescences from the same reproductive shoot.
3. Two inflorescences each from a different reproductive shoot from the same ramet.
4. Two inflorescences each from a different reproductive shoot from different populations.

Seed production in the field was also monitored during the duration of the study as a comparative control. Seed production and number of seeds produced were used as the outcome to test for relative degrees of selfing and outcrossing. ANOVA was performed on the data to test for significance within and between treatments. To quantify peduncle growth as an indication of fertilization, reproductive shoots from the Goodwin Islands site were placed in the chambers and peduncle growth was measured after the dehiscence of pollen. Linear regressions were performed to test for the relationship between downward peduncle growth and seed production.

Results

Raw data tables for this study can be found in Appendix 1. Of the 205 inflorescences, only 21 (10.2%) did not develop fruits. The mean number of fruits produced and the percentage of non fruit-bearing inflorescences in each treatment are tallied in Table 2.1. ANOVA showed no differences within treatments. Although there were no significant differences between treatments for degree of pollination as quantified by seed production, treatment two (two inflorescences on the same reproductive shoot) generally produced fewer seeds (Table 2.2) and also had a higher percentage of non-bearing inflorescences (Table 2.1).

Eighty one inflorescences were tested for peduncle growth after fertilization. Of these, 80 displayed a downward growth of the peduncle before fruits developed. Only one did not have a peduncle that grew down into the water, and that inflorescence was the only one that did not produce fruits. Summary statistics for peduncle growth are displayed in Table 2.3. Most peduncles grew between 1 and 3 cm, and Figure 2.2 displays a histogram of the overall variation of peduncle growth. The was a 100% correlation between peduncle growth and fruit production. That is, all inflorescences that were borne on a peduncle that exhibited the downward growth into the water produced fruits.

Discussion

Morphological plasticity is common in aquatic vascular plants. Variation in leaf structure in Myriophyllum has lead to taxonomic problems in the past (Sculthorpe 1967) and to reorganizing of present groups (Cronquist 1988). A biological gradient of population isolation resulting in lower fruit production from outcrossed individuals did not occur. In addition, the taxonomy of Ruppia is based mostly on morphological differences of fruit size and peduncle length and shape (straight vs. spiraled).

I have observed both straight and spiraling peduncles within the same ramet in very shallow (10 - 20 cm) and hot (> 30°C) water .

The production of fertile fruits without fertilization (apomixis) is still a possibility in Ruppia since no observations have been made of the pollen tube growing to the ovule. Even so, the possibility seems slight given the peduncle growth data presented in this study. In every case when the peduncle grew back down into the water, fertile fruits were produced. Peduncle growth began shortly after pollination (and presumably fertilization) occurred. Ecologically, no matter how the fruits were formed, the growth back down into the water may provide them with a very important protective advantage from both desiccation and predation. In many habitats, Ruppia grows in areas that are exposed during low tide. I have observed waterfowl grazing through these shallow exposed areas during low tide. Subsequent floodings during high tide may permit fruits to wash out and disperse into deeper habitats or other sites.

Ruppia maritima is a main source of primary production in some areas of Chesapeake Bay and totally dominates certain portions of estuaries where proper conditions of depth, salinity, and temperature exist (Kantrud 1991). The rapid growth of this plant is due mostly to vegetative expansion, but prolific fruit production under optimum conditions can lead to near anoxic conditions of decay in certain types of isolated lagoons when reproductive shoots are released. In areas where Ruppia coexists with Zostera marina, the age of plants and timing of reproductive cycles has led to a symbiotic community able to support a myriad of species important to Bay- wide ecology and to human fisheries. The pollination strategies of R. maritima provide some information as to the effectiveness of sexual reproduction at maintaining populations as well as to the ability of the plant to disperse to new habitats.

Table 2.1. Mean number of seeds produced per treatment and percentage of inflorescenses that did not bear fruits in each treatment.

	T1	**T2**	**T3**	**T4**
Mean # Fruits	2.8	2.5	3.0	3.2
% Non-bearing	7.7	18.3	2.9	13.2

Table 2.2. ANOVA of pollination treatment vs. the number of seeds produced.

SOURCE	DF	SS	MS	F	p
FACTOR	3	13.31	4.44	1.38	0.250
ERROR	201	647.00	3.22		
TOTAL	204	660.31			

```
                                INDIVIDUAL 95% CONFIDENCE INTERVALS FOR
                                MEAN BASED ON POOLED STANDARD DEVIATION
LEVEL    N    MEAN  STDEV   ----------+---------+---------+------
Seeds T1 39   2.821 1.760     (----------*-----------)
Seeds T2 60   2.500 1.918  (--------*--------)
Seeds T3 68   2.971 1.648        (-------*--------)
Seeds T4 38   3.211 1.877         (----------*-----------)
                              ----------+---------+---------+------
POOLED STDEV =                1.794   2.50      3.00      3.50
```

Table 2.3. Summary statistics for inflorescense peduncle growth after fertilization.

N	MEAN	STDEV	SEMEAN	MIN	MAX
81	1.2879	0.4123	0.0458	0.0000	2.3000

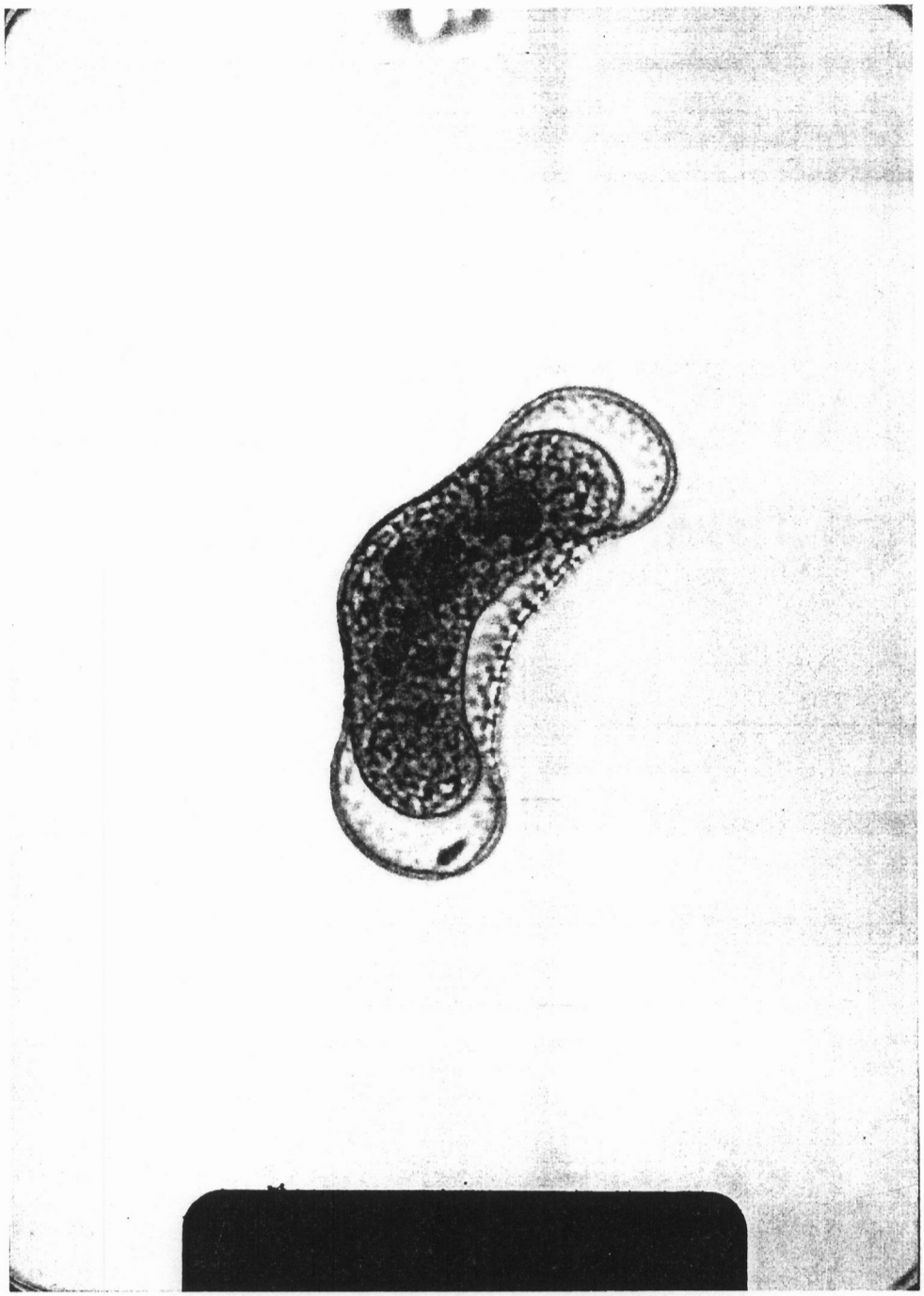

Fig. 2.1 Pollen grain of Ruppia maritima. Bar = 100 μm.

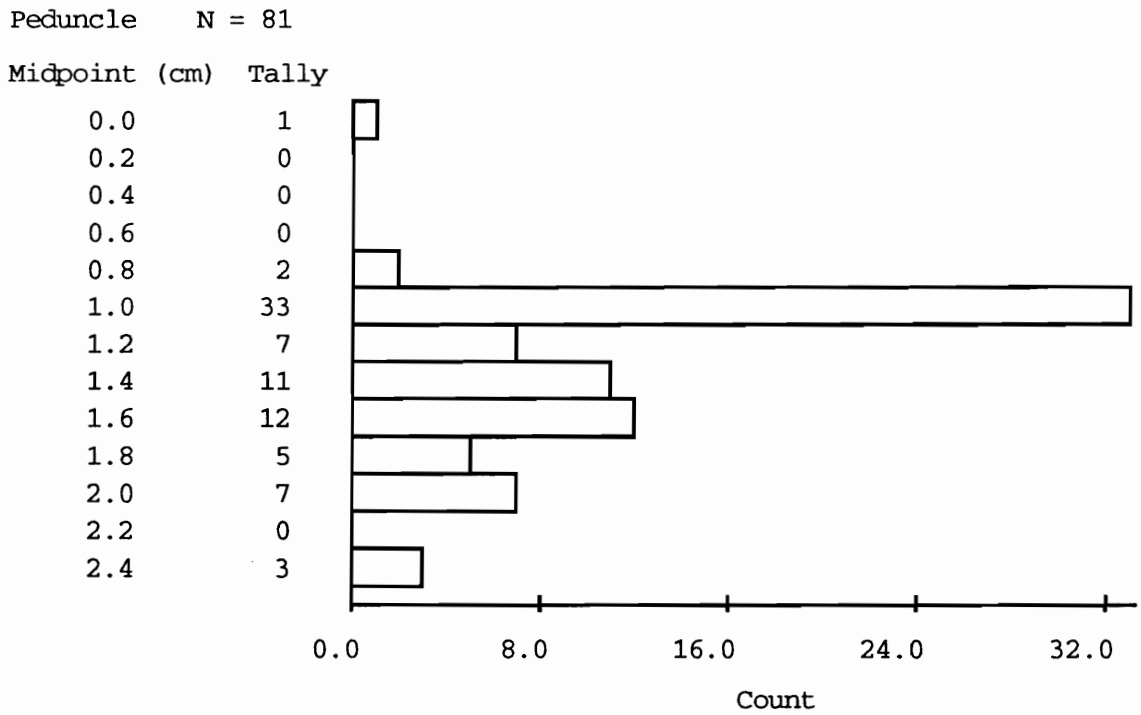

Fig. 2.2. Histogram displaying distribution of peduncle growth.

Chapter III.

The seed bank of Ruppia maritima L. (Potamogetonaceae) and its importance in establishment and maintenance of beds in lower Chesapeake Bay.*

* In preparation as a manuscript by Michael S. Rosenzweig and Robert J. Orth to be submitted to Aquatic Botany.

Abstract

Ruppia maritima coexists with Zostera marina to form seagrass communities in Chesapeake Bay. Ruppia is often a primary colonist of sites that have previously lost plant populations due to poor water quality, storms, or perturbation by animals such as the Cow-nose ray (Rhinoptera bonasas). Ruppia maritima forms extensive rhizome networks, and is the primary form of vegetative propagation. In addition, the plants also produce high numbers of seeds during the second year of growth. The seeds may germinate soon after fruit dehiscense, or they may form viable seed reserves. This study characterized the seed bank of Ruppia maritima at five sites in the lower Chesapeake Bay. Seeds were collected from the sediments and tested for viability. 100% of the whole seeds that were tested were viable. The remaining portion were empty seed coats and seed coat fragments. Seeds can remain viable in the sediments for at least one year. The number of seeds in the sediments varied between sites and also by season. There was a significant relationship between plant cover and the number of seeds present and also between distance from shore and number of seeds present. Perennial plants are important in the maintenance of Ruppia beds by producing seeds in addition to spreading vegetativly. The knowlege of when and where to find viable seeds can help in planning conservation efforts since the seed reserve may also function to maintain plant populations in Chesapeake Bay.

Introduction

A comprehensive volume of information on the ecology of seed banks has recently been made available (Leck et al 1989). This compilation of articles is the first to address the ecology of seeds and their importance in developing theory in population and community ecology. Most submersed macrophytes have the ability to reproduce vegetatively and sexually (Sculthorpe 1967). However, without sexual reproduction (seed production), loss of vegetative portions because of water quality or other

perturbations could mean complete loss of plant populations. Seed reserves, therefore, are important to maintenance as well as reestablishment of populations of submersed macrophytes. The seed reserves of Halodule wrightii and Syringodium filiforme have been investigated from the western Atlantic (McMillan 1983). McMillan found that the seeds of these seagrasses can remain dormant for up to two years and that their germination is staggered over a period of weeks. The seed reserves and germination for other genera such as Phyllospadix, Amphibolis, Posidonia, Thalassodendron, Enhalus, Thalassia, Najas, and Zostera have been studied (McMillan 1982, 1983, 1988; Orth 1984). In addition, the importance of the genetics of seed dormancy in crop species has also been widely investigated (Hilu 1980).

Ruppia maritima can colonize new habitat by seeds, turions, post-reproductive shoots, and rhizomes (Verhoeven 1979, Rosenzweig 1994 in review). Recent monitoring of SAV populations in the Chesapeake Bay has shown that Ruppia maritima (widgeon grass) is very abundant, and in some areas occurs in large monospecific stands (Orth et al. 1989; Orth and Nowak 1990). More recently, natural re-vegetation has been observed in many areas Bay-wide, with widgeon grass being the primary colonizer (Orth and Nowak 1990). Environmental characteristics such as light, temperature, and salinity have been shown to affect the growth and reproduction of Ruppia maritima (Verhoeven 1975, 1979; Richardson 1980; Brock 1982; Evans et al. 1986; Koch and Dawes 1991). Sediment and water column nutrient dynamics have also been shown to affect its physiology and biology (Thursby and Harlin 1984; Thursby 1984a, 1984b). In addition, germination and the seed bank have been investigated as important factors influencing the colonization and distribution of this plant in suitable habitats (Seeliger and Koch 1984, Van Vierssen et al. 1984, McMillan 1988, Koch and Seeliger 1988). Zostera marina and Ruppia maritima coexist in many areas of the lower Chesapeake Bay. Zostera tends to grow in deeper and cooler waters, especially when it coexists with Ruppia. During the

warmer summer months, Ruppia often dominates as Zostera plants die back, increasing the available light for Ruppia. During the cooler spring months, Ruppia grows as a short understory plant in what can be described as a Zostera forest. In areas with a gradual depth gradient, Ruppia often grows in shallow, warmer waters while Zostera grows in deeper and cooler waters. Zostera seeds are protected by a thin seed coat. The seed coat of Ruppia is much thicker and hence may be better adapted to forming a dormant seed bank and may be better adapted to establishing new populations. Since macrophyte communities are valuable as shelter, grazing areas, and breeding habitat in Chesapeake Bay, the conservation of these plants is extremely important.

The seed bank of Ruppia maritima was characterized for five sites in lower Chesapeake Bay. Seeds were tested for viability. Each site was profiled for depth, distribution, and abundance of Ruppia maritima and Zostera marina. Our objectives in this study were to investigate the possible establishment and maintenance of macrophyte beds by Ruppia seed banks.

Methods and Materials

Site Descriptions

Five 200 m transects were investigated during Spring, Summer, and Fall of 1991 and 1992. The transects were located at the following sites (Fig. 1.12):

1. Rappahannock River near Weems, Virginia
2. Corrotoman River near its confluence with the Rappahannock River
3. Piankatank River off the western shore of Gwynn Island
4. York River on the north shore of Goodwin Islands
5. Chesapeake Bay off the south-east shore of Goodwin Islands

Seed Bank

We took sediment core samples along transects at each site. Cores were taken at 20 m intervals and were 10 cm deep with an inside diameter of 9.5 cm. To check for differences between near surface and deep sediments, we split each core into surface and deep cores at 5 cm. Each split core was sieved through a 1 mm sieve. The sieved samples were stored in a ziplock bag (Glad-Lock) and stored in a cooler on board the boat. At the laboratory the samples were stored in a dark refrigerator at 8°C. No differences were found between deep and shallow sediments. Samples were examined under a stereo-microscope. Whole seeds were removed and stored for subsequent analysis for viability. Seed fragments were counted and discarded.

Seed Viability

Seed coats were removed and the embryo was crushed in the presence of 2% tetrazolium dye. Viable embryos stained pink because of the reaction between the dye and dehydrogenases.

Germination

Seeds were stored in fresh distilled water in a dark 10° C incubator then transfered to enriched agar plates and placed in a 12D : 12L, 15° C incubator.

Plates: to 0.5l distilled water

5g agarose

0.38g KNO_3

0.13g $NaSiO_2 + 9H_2O$

0.03g NaH_2PO_4

Plates were checked once a week for newly germinated seeds and measurements were recorded for leaf and root growth.

Cover and Depth Profiles

Each transect was marked off with a metric transect line. At 10 m intervals a 1 m^2 patch was measured for percent plant cover as defined by bottom area displaced by vegetation (Orth and Moore 1983b). Depth at each 10 m interval was measured by using a 2 m graduated rule.

Results

Raw data tables for this study can be found in Appendix 3. Figures 4.1-4.5 characterize each site. All data are means for the year. The figures contain information for plant distribution and percent cover indicated by the graph at the top of each figure. The horizontal axis (meters from shore) applies to this graph as well as for the bottom graph. Fractions of viable seeds (annual mean) are inside the balls. Pins indicate sediment cores. Number of fragments and viable seeds are indicated at the bottoms of the pins. These numbers are displayed graphically as well to indicate their relationship to plant cover. Depth profiles were converted to mean low water using tidal data obtained from the Virginia Institute of Marine Science.

Table 4.1 shows the results of analysis of variance for seed bank distribution by date for each site. There was a significant difference in the number of seeds in the sediments for every site. The Bay transect had the lowest F value (.06). This was due to the small number of seeds sieved from the sediment. When ANOVAs were performed between sites, no significant relationship could be found.

The seed bank distribution in relation to percent plant cover (arcsin transformed) was analyzed for the five sites. There was a high standard deviation (STDEV = 22.01) in relation to the mean (MEAN = 35.11). However, upon regression analysis, all sites showed significantly similar trends in plant distribution and abundance (Table 4.2,

Fig. 4.6) as well as for seed number in relation to distance from shore (Table 4.3, Fig. 4.7). The trend in the number of seeds declining as distance from shore increases is depicted in a boxplot graph (fig. 4.8). This boxblot also depicts the variation in the number of seeds between sites. This variation is significantly different and is summarized in

Table 4.4.

Finally, the number of viable seeds in the sediment was a small fraction of the total number of viable seeds and seed coat fragments sieved from the sediment cores (Table 4.5). The number of seeds was significantly different between sampling times only at the Corratomman site (Table 4.1).

Discussion

There were a number of factors influencing the seed bank at the study sites. Season, plant cover, depth (indirectly, affecting plant cover), and also the presense of Zostera marina. We did not figure Zostera into our analysis directly. However, Zostera has a shading effect on Ruppia that affects seasonal distribution and abundance of Ruppia. The distribution and abundance of Ruppia was a factor in the analysis of the data.

The number of viable seeds in the sediments varied during the year and was not related to season. Only the Corratomman site had significantly different numbers of seeds in the sediments between sampling dates. This may have been due to the overall growth of that population during the past two seasons. Cow nosed rays (Rhinoptera bonasus) decimated that population in 1990 while foraging for soft shelled clams (Macoma arenaria). Data for the other sites indicates that there is a constant supply of viable seeds in the sediments during the year and that these seeds could germinate upon stimulation and/or genetic timing. Although all sites had different depth and cover

profiles, the general pattern of the seed bank distribution was similar for all sites. This was a significant finding in relation to maintenance and management of Ruppia beds in Chesapeake Bay. Transplant or re-seeding projects can now take place with a better knowlege of the seed bank distribution at these sites.

The timing of seed germination may be an important factor in Ruppia populations. Seed germination in seagrasses has been observed to occur due to factors such as temperature and salinity. However, environmental stimuli may not be the only factors in seed germination of seagrasses. Whether or not genetic factors such as a seasonal "clock" influence germination and, therefore, recruitment in Ruppia populations is still unknown. Population dynamics such as recruitment, birth and death rates, and interspecific competition with Zostera are areas for further study. The seed ecology of Ruppia maritima may be of great importance in understanding the population and community dynamics of submerged angiosperm ecosystems in Chesapeake Bay.

Table 4.1. Summary statistics of one way ANOVA for number of seeds vs. date for each study site.

SOURCE	DF	SS	MS	F	p
Corratomman	2	622.4	311.2	4.27	0.023
Rappahannock	2	99.5	49.8	0.76	0.476
Piankatank	2	118.1	59.1	1.68	0.199
Goodwin	2	2.32	1.16	0.45	0.643
Goodwin Bay	2	0.067	0.033	0.06	0.946

Table 4.2. Regression analysis for Ruppia cover in relation to distance from shore comparing the five sites. There was a significant negative relationship. That is, plant cover decreased as the distance from shore increased. The plot of residuals showed no odd variation in the regression.

Predictor	Coef	Stdev	t-ratio	p
Constant	50.770	3.867	13.13	0.000
Meters	-0.15027	0.03292	-4.56	0.000

s = 20.16 R-sq = 17.0% R-sq(adj) = 16.1%

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	8465.7	8465.7	20.83	0.000
Error	102	41445.4	406.3		
Total	103	49911.1			

Table 4.3. Regression analysis for Ruppia seed bank distribution (seeds in relation to distance from shore). There was a significant negative relationship. The number of seeds decreased as the distance from shore increased. The plot of residuals showed no odd variation in the regression.

Predictor	Coef	Stdev	t-ratio	p
Constant	8.905	1.733	5.14	0.000
Dist	-0.03536	0.01396	-2.53	0.015

s = 5.672 R-sq = 11.8% R-sq(adj) = 9.9%

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	206.28	206.28	6.41	0.015
Error	48	1544.15	32.17		
Total	49	1750.43			

Table 4.4. ANOVA of the number of seeds between sites. The analysis compares the number of seeds along the transect at each site.

SOURCE	DF	SS	MS	F	p
Site	4	990.8	247.7	14.67	0.000
ERROR	45	759.6	16.9		
TOTAL	49	1750.4			

```
                                                INDIVIDUAL 95 PCT CI'S FOR
                                                MEAN BASED ON POOLED
                                                STDEV
LEVEL   N    MEAN     STDEV ----+---------+---------+---------+--
1      10   12.960    4.720                 (----*----)
2      10    6.520    6.594          (----*----)
3      10    3.490    4.043      (----*----)
4      10    1.100    1.394  (----*----)
5      10    1.010    0.595  (----*----)
                        ----+---------+---------+---------+-
POOLED STDEV =          4.109    0.0     5.0     10.0    15.0
```

Table 4.5. Percent viable seeds at each site. Means for the study period.

Dist (m)	Corr	Rapp	Gwyn	York	Bay
20	34.8%	8.4%	0.0%	50.0%	0.0%
40	9.1%	10.9%	4.0%	20.0%	28.6%
60	51.4%	11.7%	0.0%	22.2%	14.3%
80	9.4%	14.0%	33.3%	40.0%	33.3%
100	11.9%	8.0%	0.0%	0.0%	0.0%
120	19.0%	17.6%	20.0%	0.0%	14.3%
140	11.9%	14.3%	0.0%	0.0%	10.0%
160	24.1%	0.0%	0.0%	0.0%	0.0%
180	15.4%	11.8%	0.0%	0.0%	100% (1 seed)
200	33.3%	0.0%	0.0%	0.0%	28.6%

Figures 4.1 - 4.5. Yearly mean seed reserve, depth profile, and plant cover for each study site.

The following profiles for each study site contain different types of information. The combination of information may help the reader envision the temporal and spatial dynamics at each site.

The figures contain information for plant distribution and percent cover as indicated by the graph at the top of each figure. The vertical axis for the top graph is 0 - 100% plant cover. The horizontal axis (meters from shore) applies to the top and bottom graphs. Fractions of viable seeds are inside each ball. Pins indicate where sediment cores were taken along the transects. mean number of fragments and viable seeds are indicated at the bottom of the pins. These numbers are displayed graphically as well to indicate their relationship to plant cover. Depth profile values are at mean low water.

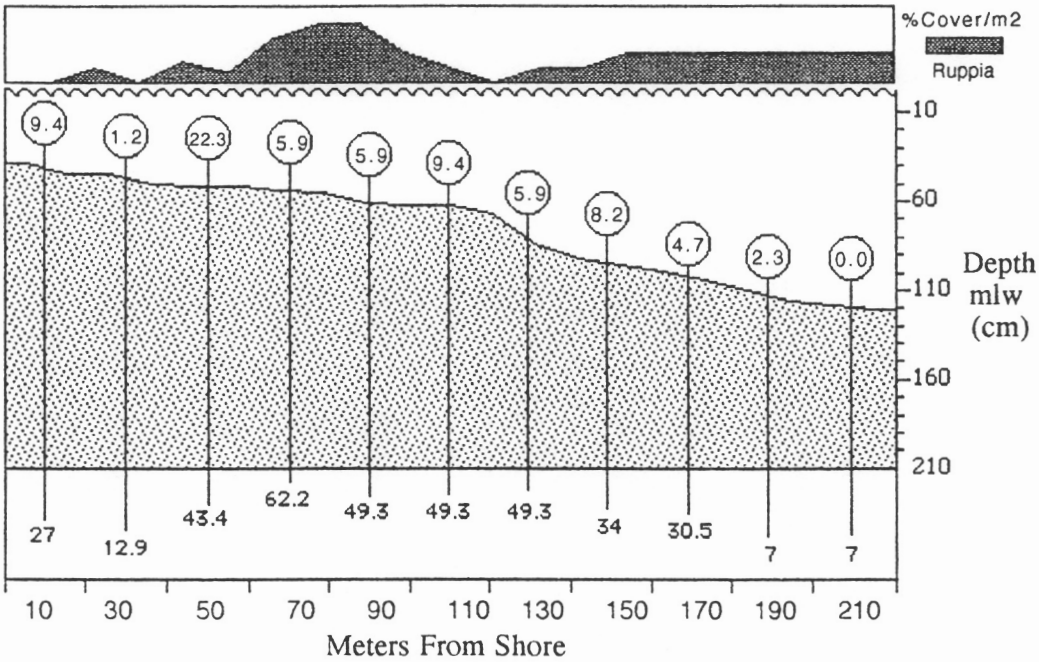

Fig. 4.1. Corrotoman River. Mean seed reserve, depth profile, and plant cover.

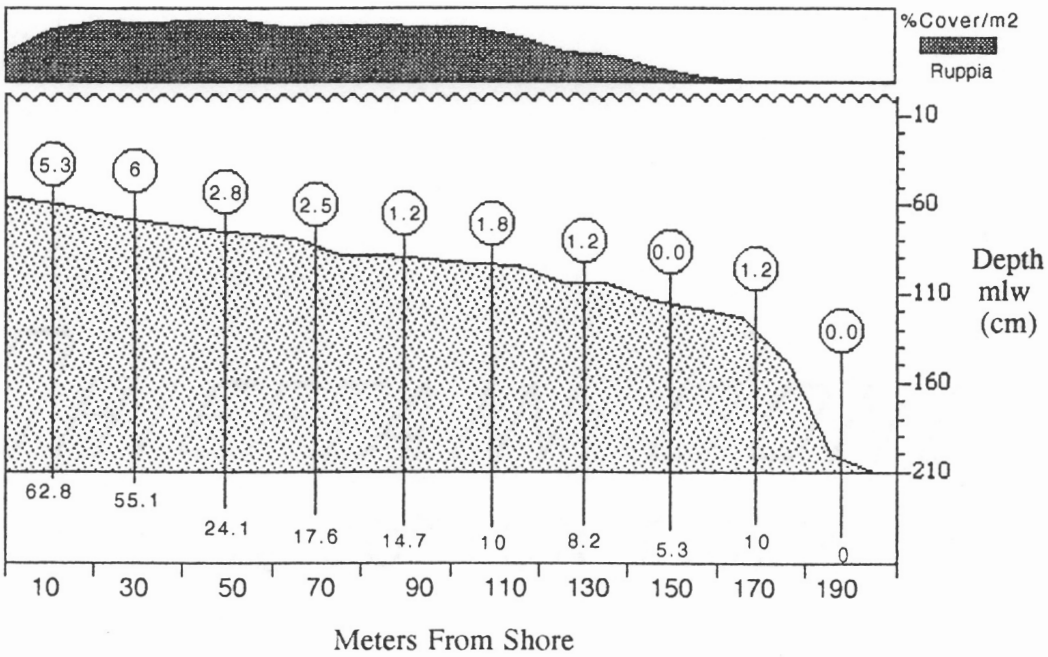

Fig. 4.2. Rappahannock River. Mean seed reserve, depth profile, and plant cover.

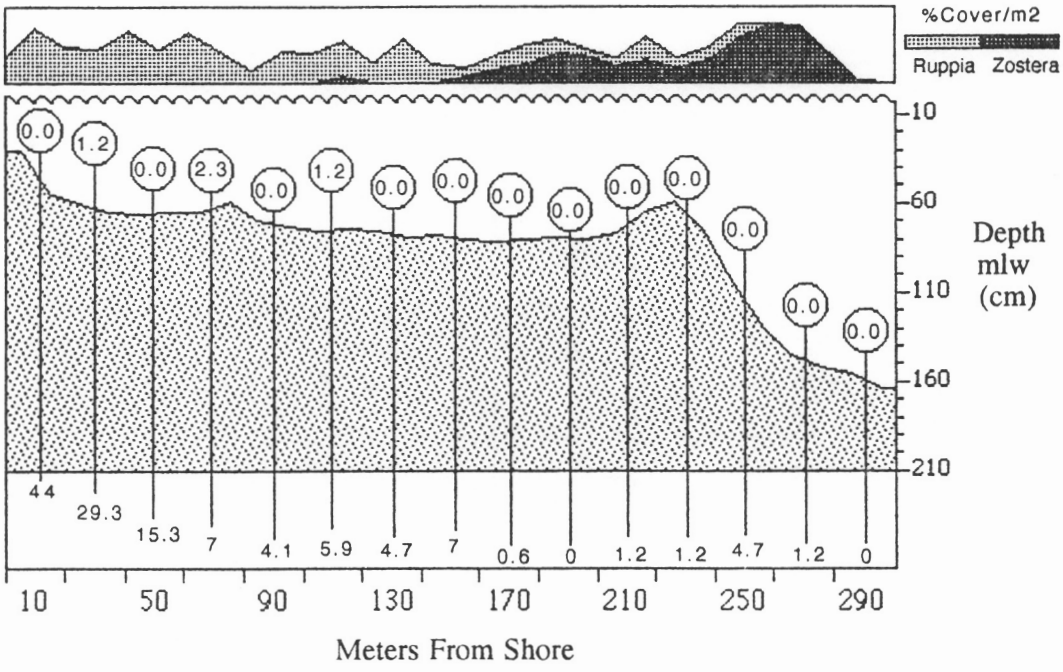

Fig. 4.3. Piankatank River. Mean seed reserve, depth profile, and plant cover.

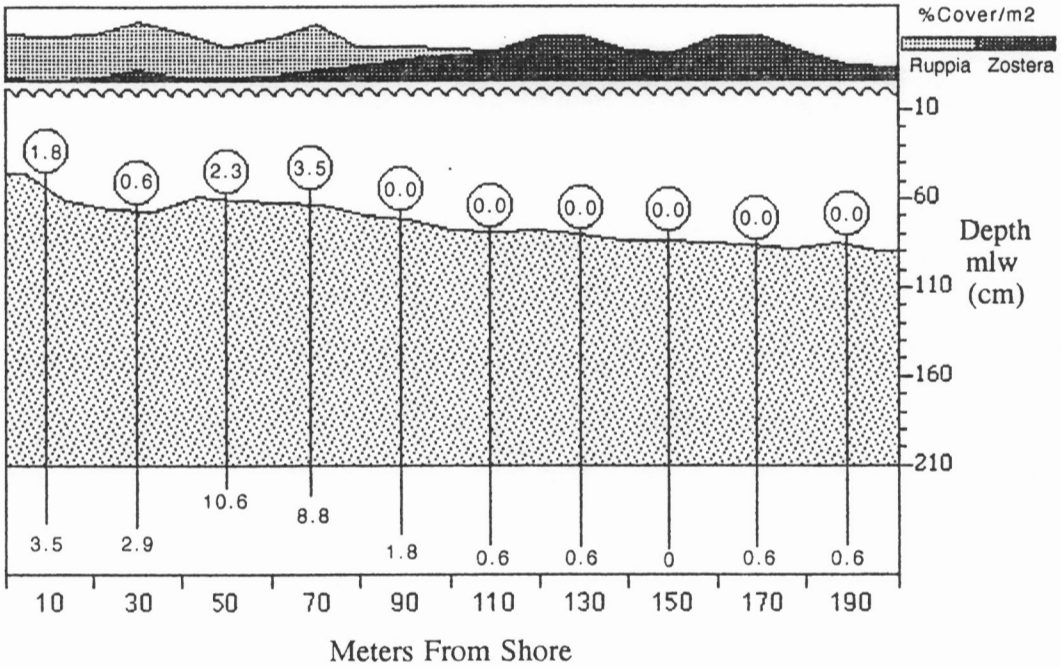

Fig. 4.4. Goodwin Islands (York River). Mean seed reserve, depth profile, and plant cover.

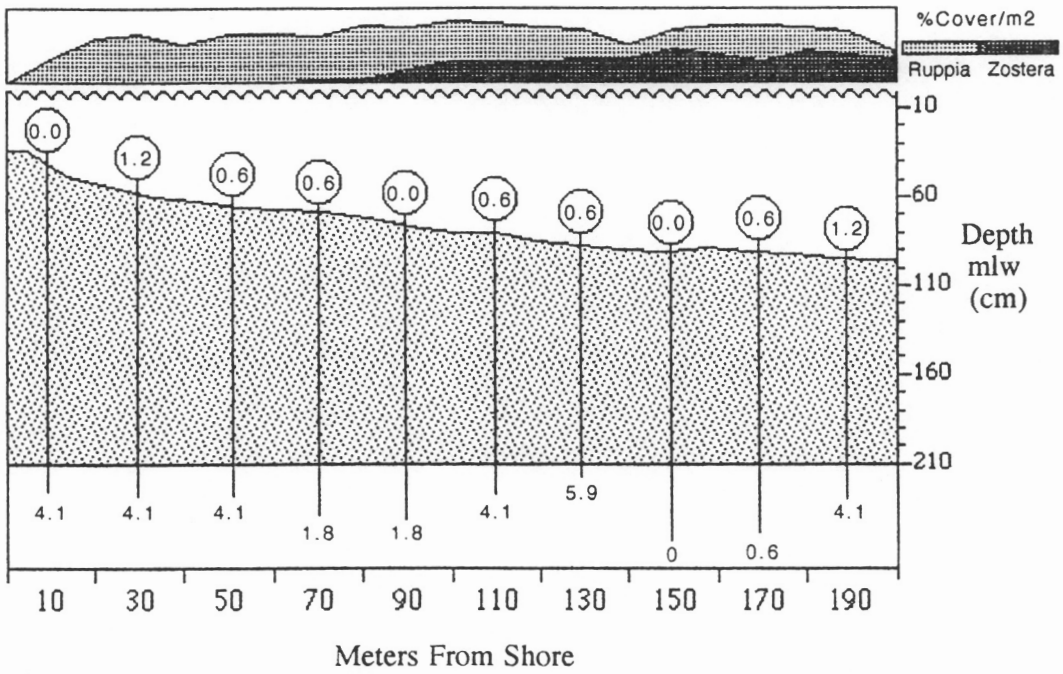

Fig. 4.5. Goodwin Islands (Chesapeake Bay). Mean seed reserve, depth profile, and plant cover.

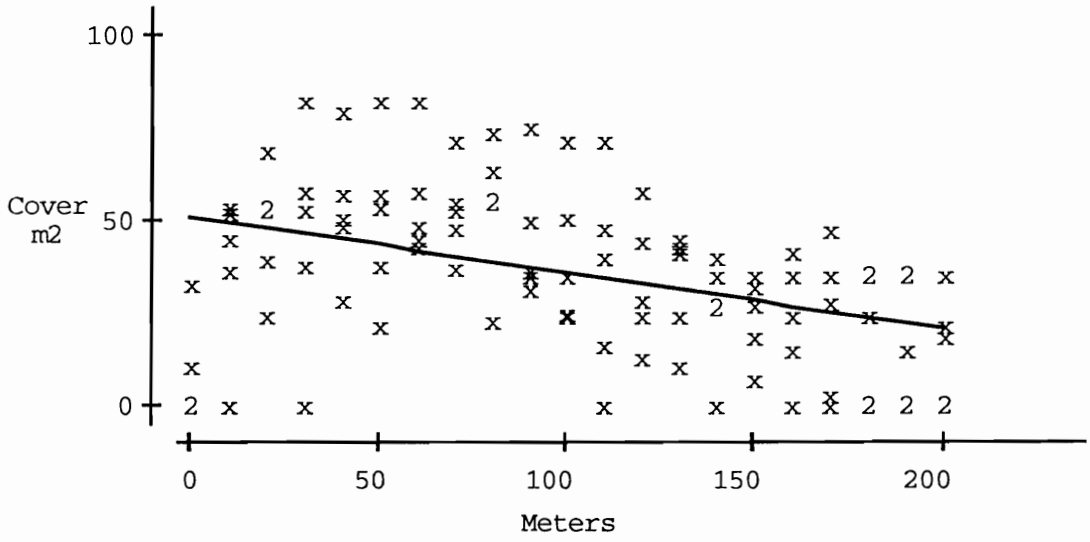

Fig 4.6. Relationship between Ruppia cover/m^2 and distance from shore. A 2 indicates overlapping data points.

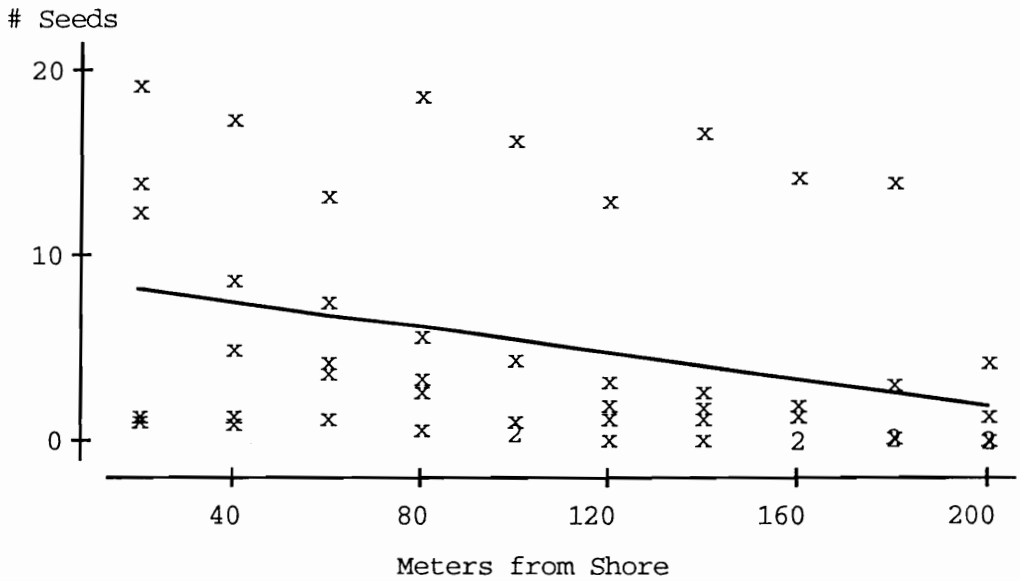

Fig 4.7. Relationship between number of seeds and distance from shore. A 2 indicates overlapping data points.

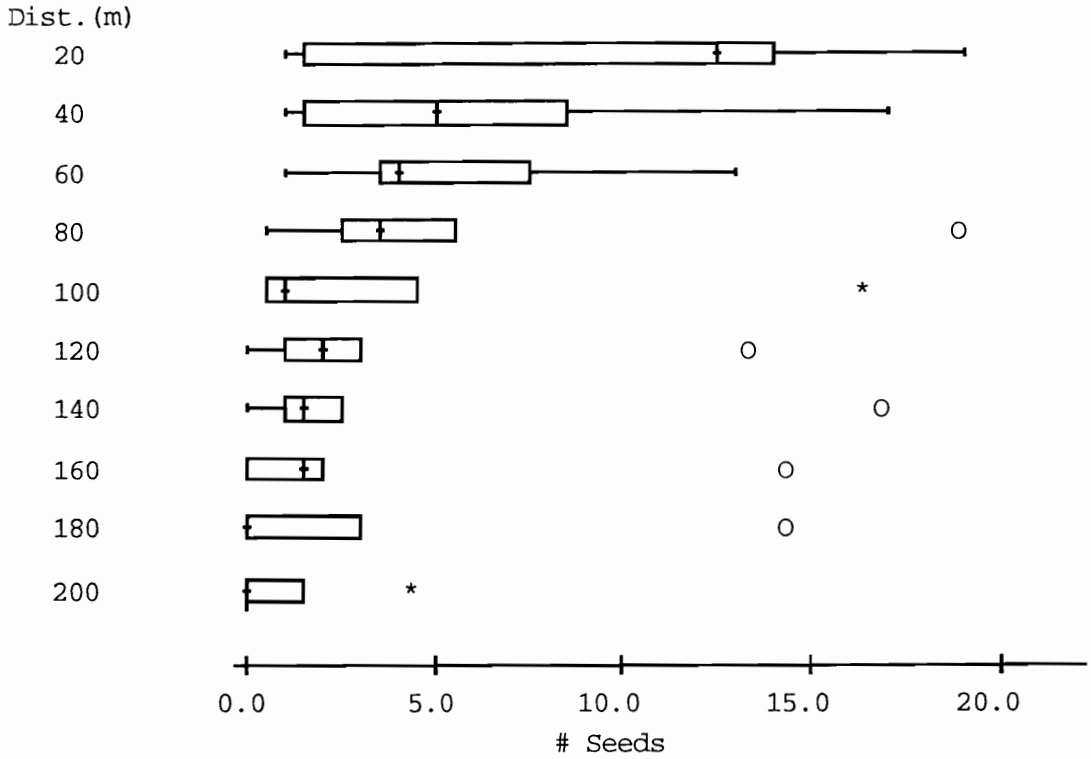

Fig. 4.8. Boxplot of the number of seeds at each station (lumped sites). The graph shows the number of seeds declining as the distance from shore increases. Zeros represent outliers and asterisks represent potential outliers.

Chapter IV.

Dispersal of Ruppia Maritima sensu lato by turions and post-reproductive shoots in Chesapeake Bay.*

* Manuscript of this chapter by Michael S. Rosenzweig and Robert J. Orth in review by Aquatic Botany.

Abstract

The predominant mode of asexual reproduction reported for Ruppia maritima is by vegetative propagation by rhizomes. Two previously unreported modes of vegetative dispersal for this species are reported: turions and post-reproductive shoots. Turions have not been reported previously for this taxon in North America. Post-reproductive shoots have not been reported previously for this taxon. This paper describes these two newly discovered modes of vegetatve propagation and discusses their significance to populations of Ruppia maritima in Chesapeake Bay and elsewhere.

Introduction

The reproductive ecology of Ruppia maritima has been the focus of several studies in South America, Europe, United States, and Australia (Verhoeven 1975, 1979; Richardson 1980; Brock 1982a, 1982b; Evans et al. 1986; Koch and Dawes 1991; Seeliger and Koch 1984; Van Vierssen et al. 1984; McMillan 1988; Koch and Seeliger 1988).

Vegetative dispersal is an important means of colonization for aquatic plants in general (Sculthorpe 1967). In particular, it is possible for one species to have predominantly one form of dispersal. Spreading by rhizomes and fragmentation of rhizomes, stolons, and tubers all contribute to the large clonal populations found at some sites. Turions are asexual propagules that form during autumn when the meristematic tips of rhizomes form a bulb-like structure composed of leaf tissue (Sculthorpe 1967). During spring, new leaves grow from the turions and the entire structure can break off the parent rhizome and disperse to new habitats. Post-reproductive shoots are the stems on which seeds have been produced. These shoots remain viable once they have detached from the rhizome and have not been described previously for Ruppia maritima. This

paper describes both turions and post-reproductive shoots as being important in the dispersal of Ruppia maritima in Chesapeake Bay.

Turions

Turions are similar to rhizomes, stolons, and tubers, in that they function as hibernacula (Sculthorpe 1967). Turions have been described for other macrophytes, such as Hydrocharis, Myriophyllum, and Utricularia. Brock (1982b) describes turions for the two austral species, Ruppia tubersoa and Ruppia polycarpa. Those turions acted as perennating agents for populations of both taxa. Turions for Ruppia maritima have not previously been described and were first observed in June, 1991, at several locations along a transect across a Ruppia maritima bed in lower Chesapeake Bay (Fig. 5.1). These transects were part of a seed reserve study currently under investigation by the authors. Turions were discovered while digging sediment cores along the Rappahannock River transect. Water temperature was 19°C. The turions were not incorporated in the sediment core itself, but floated up to the surface while the substrate was being disturbed. Turions floated to the surface at four locations along this transect. A total of only ten turions was observed. No turions were found at any other location during the course of this study. Upon dissection and microscopic inspection, the turions appeared to be comprised of leafy aerenchyma, which explains why they floated to the surface after being detached from the rhizomes. The dissected tissue stained dark for starch with potassium iodide (IKI). The turions were all between 1 - 2 cm in diameter and had new leaves growing from them. Three specimens were collected, dried and mounted on herbarium sheets (Fig. 5.2).

Post-reproductive shoots

During a field study of seagrass beds at Tangier Island (mid Chesapeake Bay, as indicated on Fig. 5.1). Late in May of 1991, post reproductive shoots of Ruppia maritima were observed with new root and leaf growth (Fig. 5.3). Ruppia maritima begins its reproductive cycle as the water warms over 20°C. This shoot was discovered floating over a dense seagrass bed of Zostera marina where the water temperature was no higher than 15°C. No Ruppia maritima was observed in the vicinity of this bed. Since Ruppia maritima was found only flowering in protected warm inlets at Tangier Island during this study, it is assumed that the post-reproductive shoot floated from one of those protected beds. During subsequent field expeditions in lower Chesapeake Bay post-reproductive shoots were found at all sites (including the transects listed above). These post-reproductive shoots also were found colonzing 1.0 m^2 experimental plots along the Goodwin Island transects in July and September, 1992. All vegetation had been removed from these plots in March, 1992.

Discussion

Verhoeven (1979) described the growth habit of Ruppia maritima as including horizontal rhizomes and vertical stems. He described vegetative dispersal by fragmented vertical stems that occurred during the growing season. Plants could overwinter as rhizomes, and rhizomes or seeds could reestablish habitats. In Chesapeake Bay, Ruppia maritima persists in some areas and in others it is ephemeral (unpublished data). Factors influencing the presence of Ruppia maritima from year to year include water quality, habitat quality, inter-specific competition for resources (primarily with Zostera marina), and the life-stage of plants in relation to the above. First year plants may not become reproductive at some sites (Chapter III). If this is the case, then the same site may be partially or completely devoid of plants the following growing season if water quality or

habitat quality stresses the plants. Perennial persistence of Ruppia maritima depends on a combination of environmental, ecological, and specific biological factors of the plant. In Chesapeake Bay, turions and post-reproductive shoots combine features of both sexual and asexual reproduction and shed light on why this plant shows a remarkable ability to rapidly colonize suitable habitats. Turions take advantage of their high starch content to nourish new plant growth at the beginning of the growing season. More research is necessary to determine why turions were found only at the one site. Because turion production has a distinct seasonal component (Sculthorpe 1967), sampling at our sites, except for the Rappahannock River site, may have been too late to detect the presence of turions. If turions are being produced only at certain sites, then it may be a combination of biological and ecological factors that influence the develoment of turions in this species, rather than any ecotypic variation in the plants themselves. The ability of this species to spread asexually by rhizomes and post-reproductive shoots, as well as its ability to produce turions, may be a primary reason that Ruppia maritima has spread so rapidly in some areas of Chesapeake Bay (Orth et al. 1986, 1989, 1992). The combination of sexual and asexual reproduction makes Ruppia maritima very efficient as a primary colonizer and a perennial member of estuarine habitats of Chesapeake Bay.

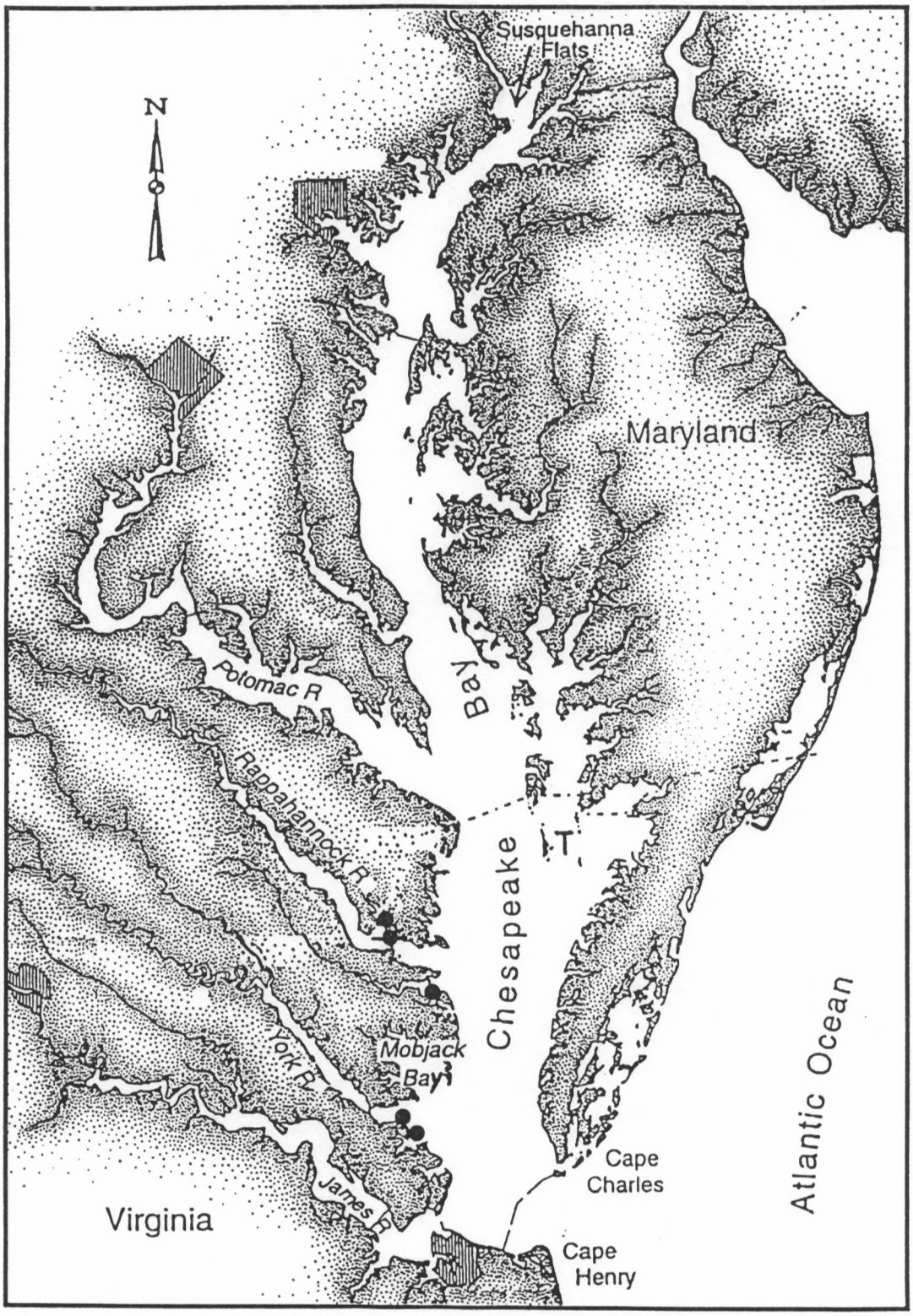

Fig. 5.1. Study Sites. The Rappahannock River site is marked with a cross-hatched dot. Tangier Island is to the west of the "T".

VIRGINIA POLYTECHNIC INSTITUTE AND STATE UNIVERSITY HERBARIUM

Flora of: Rappahannock River
Lancaster County, VA Near Weems

Turions of Ruppia maritima L.

Floated to surface after bottom was disturbed. Original diameter of about two cm.

Coll: M.S. Rosenzweig No:
Date: 8 June 1992 Det: Rosenzweig

Fig. 5.2. Turions mounted on a herbarium sheet. Collected in the Rappahannock River (Site 2). These turions all have sprouted new leaves.

Fig. 5.3. Post-reproductive shoot collected at Tangier Island. New roots were growing at the lower left. New leaves also were growing along the stem.

Chapter V.

Colonization of *Ruppia maritima* in lower Chesapeake Bay*

* In preparation as a manuscript to be submitted to Conservation Biology.

Abstract

Ruppia maritima grows in monospecific stands or with Zostera marina in the lower part of Chesapeake Bay. Some populations are ephemeral and others are more permanent. The effect of water quality on the establishment and survival of vegetation is not fully understood, but poor water quality does have a known effect on the survival of vegetation transplanted into experimental plots. Colonization of habitats by Ruppia can be by both sexual and asexual propagules. In this study, colonization strategies of Ruppia were investigated at two nearby sites at Goodwin Islands, located at the mouth of the York River. These sites contained monospecific stands of Ruppia as well as mixed Ruppia and Zostera. Colonization and subsequent survival in plots was related to propagule type, seasonal timing, and plot location relative to the surrounding vegetation. A tropical storm affected the sites by causing many of the plants to be torn up.

Introduction

Chesapeake Bay is the largest estuary in the continental United States and is one of the most productive bodies of water in the world (National Oceanic and Atmospheric Administration and Virginia Institute of Marine Science 1991 p. 6). Its 64,000 square mile watershed encompasses parts of New York, Pennsylvania, Maryland, Delaware, Virginia, and West Virginia. Five major rivers are tributaries of Chesapeake Bay: The Susquehanna, Potomac, Rappahannock, York, and James. In addition, hundreds of smaller rivers and streams are part of the Chesapeake Bay watershed. Chesapeake Bay with its extensive littoral zone and broad salinity range (0 to 33 0/00), supports many different species of organisms including submerged aquatic vegetation (SAV) (Orth and Moore 1983a). A major decline in the distribution and abundance of SAV has been occurring in the Bay since the 1960s (Kemp et al. 1983, Orth and Moore 1983a). This decline accelerated during the 1970s most notably after 1972, the year of Tropical Storm

Agnes. In addition to reducing salinities bay-wide for up to four weeks, the storm catalyzed the transport of large quantities of suspended sediment into the watershed (Orth and Moore 1983a). By 1974, the distribution and abundance of the submerged "grasses" Zostera marina and Ruppia maritima had been drastically altered throughout the bay; and by 1980, many areas contained sparse beds or lacked vegetation completely (Orth and Moore 1983a).

Conservation and management of SAV in The Bay has focused mostly on Zostera marina . Presumably, mapping of grass beds has included distributions of both Zostera marina and Ruppia maritima, but individual species have not been distinguished. The Virginia Institute of Marine Science conducts seed collection and re-seeding mainly of Zostera marina. Studies on the effects of decreased photosynthetically active radiation (PAR) on Zostera marina seed dispersal and germination and on the nutrient dynamics of Zostera communities have been conducted by Bay-area scientists (Wetzel and Penhale 1981, Orth and Moore 1988, Dennison et al. 1992). Few studies have been conducted on Ruppia maritima in these Zostera/Ruppia communities in Chesapeake Bay.

The National Estuarine Research and Reserve System (NERRS) was established through the Federal Coastal Zone Management Act of 1972 to provide opportunities for long-term estuarine research and monitoring; and for estuarine education and interpretation; to provide a basis for more informed coastal management decisions; and to promote public awareness, understanding, and appreciation of estuarine ecosystems and their relationships to the environment as a whole (National Oceanic and Atmospheric Administration and Virginia Institute of Marine Science 1991, p. XI). In the Virginia portion of Chesapeake Bay, the York River was chosen as the first tributary for the NERRS sites (National Oceanic and Atmospheric Administration and Virginia Institute of Marine Science 1991 p. 7). Four sites were chosen as the first components of the York River NERRS-VA sites representing the different ecological zones of the York

River. They were (National Oceanic and Atmospheric Administration and Virginia Institute of Marine Science 1991):

1. Goodwin Islands; representing polyhaline conditions at the York River mouth.
2. Catlett Islands; representing mesohaline conditions in the lower estuary of the York River.
3. Taskinas Creek; representing oligohaline conditions in the transitional zone of the York River.
4. Sweet Hall Marsh; representing freshwater conditions in the tidal portion of the Pamunkey River tributary of the York River.

The present study was situated at the Goodwin Islands so as to incorporate the results into the larger research and educational goals of the NERRS.

Submerged grass communities have been recently identified by the governors of Pennsylvania, Maryland, Delaware, and Virginia as species that are important indicators of water quality and Bay biointegrity in general (Dennison et al. 1992). Restoration and protection of aquatic ecosystems is now a national priority (National Research Council 1991). Ecological restoration and protection of estuarine systems such as the Bay have been complicated by the introduction of exotic species such as Hydrilla verticillata. Management of such aquatic weeds has focused on mechanical or chemical extermination from choked vessel channels and piers. Restoration and management of areas not yet infested with exotics must include life-history and ecological data on native species (Simberloff 1990). As a result of ever increasing human impacts in the Bay, this research is essential for the realistic prediction and management of "cornerstone" seagrass communities in Chesapeake Bay.

After Tropical Storm Agnes further disturbed the bay-wide ecological balance in 1972, water quality (in terms of photosynthetically active radiation [PAR]) was greatly reduced. This reduction had been occurring at least since the 1960s (Orth and Moore

1983a) and has been attributed to a reduction in seagrass community populations greater than that which occurred during the eelgrass blight of the 1930s (Orth and Moore 1983a). That blight in which plants were killed by the saprophyte Labrynthula (Pokorny 1967), may have been the result of larger scale climatic changes (Parker, pers comm). The world-wide reduction in seagrass beds occurred concurrently with a global temperature drop of about 1° C, which also may have been a cause of the "Dust Bowl" in the midwest region of the United States that occurred during the same time period.

Although the decrease in SAV populations during the 1930's was world wide, the decline of SAV from the 1960's to the present is restricted to Chesapeake Bay (Orth and Moore 1983a). Synergistic effects of poor land use planning, run-off, reduction of riparian areas, the conversion of forests and farmland to pavement, and the Bay-wide perturbation caused by Tropical Storm Agnes, probably have been a major causes of the loss of SAV in Chesapeake Bay. Since the most recent die-back, many areas that once were populated by Zostera marina or both Zostera and Ruppia maritima, have been re-populated by monospecific populations of Ruppia maritima. The causes of this phenomenon are largely known by conjecture alone. The distribution, abundance, and zonation of Ruppia and Zostera in Chesapeake Bay are probably controlled by underwater light penetration (available PAR), temperature, and possibly salinity (Wetzel and Penhale 1981, 1983). Wetzel et al. (1981) compared the photosynthetic parameters of the two species. Ruppia had a higher light and temperature optimum and a shorter growing season, and was photosynthetically less efficient than Zostera in low levels of underwater light. Ruppia was thus considered a high light plant. In addition, the relatively high ratio of Chlorophyll a to b in Ruppia compared with other seagrasses also suggests that Ruppia is less adapted to low light environments than some of the seagrasses (Evans et al. 1986). In addition to light, nutrients may also contribute to SAV community dynamics. Studies have revealed that root absorption of oxygen, phosphate,

ammonia, and nitrate by Ruppia may influence its ability to compete with other taxa in multispecific communities (Thursby 1984a; Thursby and Harlin 1982, 1984).

Many sites in Chesapeake Bay that once had extensive beds of Zostera marina have since grown back with extensive monospecifc beds of Ruppia maritima (Orth and Moore 1988). Other sites contain mixed beds of Ruppia and Zostera. The ability of Ruppia to colonize these habitats and maximize its growth at times when it will not compete with Zostera is similar to that in other SAV communities. In Southern Texas, Ruppia coexists with Halodule wrightii. Halodule out-shades Ruppia during the warmer months, whereas Ruppia dominates during cooler months (Pulich 1985). Although this is opposite (in terms of temperature and dominance) to what occurs in Chesapeake Bay, Ruppia occupies a vegetative niche in both habitats, making SAV communities more desirable habitat for other organisms for an extended period of time. Similar replacement dynamics involving Ruppia species have been found at other sites in Europe (Verhoeven and van Vierssen 1978) and in Canada (Bigley and Harrison 1986).

In Chesapeake Bay, Ruppia maritima reproduces by sexual as well as asexual propagules. Under optimal conditions and age of the plants, prodigious numbers of seeds are produced. Spreading by rhizomes also occurs and is probably the dominant form of propagation. Asexual dispersal also occurs as a result of "post-reproductive shoots", which remain viable after seed production, break off the parent rhizome, and colonize new habitat. Lastly, turions have been found at one site and are presumably another strategy that has enabled Ruppia to colonize many sparsely populated or bare habitats in Chesapeake Bay. Turions are bulb-like structures that grow around the meristematic tips of rhizomes. They can overwinter and then can sprout new shoots and roots the following Spring. It is possible for them to be dispersed if they are dislodged from the sediments.

The object of this study was the colonization strategies of Ruppia at the mouth of the York River at Goodwin Islands. Concurrently two other studies investigated pollination and the seed bank of Ruppia maritima in lower Chesapeake Bay. Information from these studies will also appear in the text to augment the results of this colonization study and its importance on the conservation and management of submerged seagrass communities in Chesapeake Bay.

Methods and Materials

During Spring, Summer, and Fall of 1991, I took investigative trips around the plant beds surrounding Goodwin Islands. Using VIMS aerial photographs as a reference, I did underwater surveys of many of the plant beds and chose two sites that fit all three criteria:

1. Mixed bed sites on the river (north) and bay (east) sides of the islands.
2. Proximity to distribution and abundance transects previously studied by Orth and Moore and others at VIMS.
3. Proximity to my own transects which were used in a seed reserve study.

One site extended from the north side of Goodwin Islands near the mouth of the York River (37°13'12" Latitude, 76°23'90" Longitude). The second site extended from the south-east side of Goodwin Islands into the Bay (37°13'15" Latitude, 76°22'94" Longitude) (Fig. 1.10, 1.11).

A nylon transect line marked every meter was used to measure the distances to the colonization patches. In addition, the transect line could later be used to help locate the patches. Fifteen 1 m^2 patches were selected at each site. The selection of patches was based on distribution and abundance of plants in the beds and on the overall topography

of the sites. The patch size was based on the size of plots used in previous work in these plant beds; and also on plot size of terrestrial studies at Goodwin Islands. At site one, the patches were dug in series. Patches were located on linear transect at both sites except for three off shore locations at site 2, because of sand bars, consequently there were no plants, so pairs of patches were selected between sand bars. This topography probably affected the colonization of plants and also was important in how the site was affected by severe storms.

In March, 1992, the patches were cleared of all vegetation, roots, and rhizomes. They were dug down to 20 cm, and the sediments returned to the patches after sieving through a 1 cm sieve. Thus, seeds were left in the sediments. Monthly evaluations were conducted from April through October and then one evaluation was made in March, 1993. The following data were gathered during each patch evaluation:

- Seedling germination.
- Rhizome growth into the patches from the surrounding bed (enumerated as the number of nodes).
- Number of plant shoots.
- Number of rooted post-reproductive shoots.

These data were collected for both Ruppia maritima and Zostera marina. Colonization of the patches by shoots (rhizomes), seedlings, and Ruppia post-reproductive shoots was measured for seven consecutive months beginning in April, 1992, and again in March, 1993 to track colonization after one year. In addition, the distribution and abundance of plants in the beds surrounding the colonization patches were also measured (percent plant cover) as a reference.

Results

Raw data tables for this study can be found in Appendix 2. In addition, percent cover of plants was compared between the colonization plots and the surrounding plant beds for the same time period (Fig. 3.1a-3.1h, Fig. 3.2a-3.2h).

Table 3.1 shows the data on total Ruppia and Zostera shoots, seedlings, and Ruppia post-reproductive shoots for each date at each of the two sites. Two way t-test analysis was performed to examine for colonization differences between sites. Table 3.2 displays these results when comparing data between the two sites. Colonization by Ruppia post-reproductive shoots was not significantly different between sites. Two way t-tests were also performed to test for shoot colonization differences between the two species (Table 3.3). Differences in colonization by seedlings between the two species were not examined as they germinate in different environmental conditions.

Discussion

It has been observed that boat propeller scars made through vegetation beds of Ruppia and Zostera are first colonized by Ruppia (K. Moore, pers comm). Similarly, in the colonization patches that I created at Goodwin Islands, Ruppia was the predominant and rapid colonist, especially during the warm water months of late spring and summer (Fig. 3.1a-3.1h, Fig. 3.2a-3.2h). Although this was the trend for both sites, significant differences resulted, possibly due, in part, to storms that occurred in October, 1992, that severely disturbed the Bay site. The March, 1993, data for the York river site show that the plant cover of the patches was similar to that of the surrounding beds (Fig. 3.1h). This was not the case for the Bay site (Fig. 3.2h). The colonization patches were devoid of plant cover except for a very few shoots and seedlings as compared to the York River site (Table 3.1 and Fig. 3.2a-3.2h). When colonization at the two sites was compared, significant differences occurred for Ruppia shoots and seedlings (Table 3.2). The Bay

site had significantly more colonizing shoots and the York River site had significantly more seedlings (Table 3.1). Differences were not significant for Zostera shoots or seedlings. Although colonization by post-reproductive shoots was not significantly different between the sites, there were no post-reproductive shoots found at the York River site as compared with a total of 13 at the Bay site (Table 3.1).

During relatively calm weather, the York River site generally had more turbid water than the Bay site. In addition, during low tides, the sand bars at the Bay site acted as a boundary that may have kept many of the floating post-reproductive shoots in the area. The dynamics of these two sites drastically changed during storms. The Bay site's exposure to Chesapeake Bay wave action exposed the plants to severe disturbance and the depth profile and location of sand bars shifted after the two tropical storms that passed throughout the area during October, 1992. The York River site remained relatively sheltered by Goodwin Islands during these storms and the plant beds were relatively unaffected.

The Bay site had significantly more Ruppia shoots than Zostera shoots (Table 3.3). This was not the case for the York River site (Table 3.3). A combination of disturbance followed by calm, clear water may have contributed to these differences. Ruppia is a warm water high light species that remains suppressed as an understory plant until Zostera dies back during late Spring and Summer. In the Bay site, Ruppia received more days of clear warm water than in the York River site. This may explain the larger proportion of shoots (faster rhizome growth) in the plots. Seed germination was greater at the York River site, even though disturbance was more intense at the Bay site. Reproductive shoots were produced in abundance at both sites during the study. Exact figures were not established during this study. However, in a previous study at a nearby site mean reproductive shoot density was measured at 1700 shoots/m^2 (Silberhorn, unpublished manuscript). If each shoot produced an average of six seeds, then a mean of

10,200 fruits/m^2 production is possible. This is an enormous number of sexual propagules relative to the few that colonized the plots (Table 3.1). This and the absence of post-reproductive shoot colonization at the York River site may be explained by some life history information about Ruppia. I observed that no reproductive shoots were produced by any plants colonizing the plots during the study period. Perennial forms of Zostera do not produce reproductive
shoots until their second year of growth. If this is also the case with Ruppia then a faster growing, population may predominate at the Bay site. This would explain the faster growing rhizomes (with access to more days of better light penetration) with less energy allocated to producing sexual shoots/propagules than at the York River site. The final factor that may have contributed to the faster asexual propagation of Ruppia at the Bay site is temperature. At every visit, temperature averaged from 0.5° C to 1.0° C higher at the Bay site. This may have had some contributing effect during Summer when the water temperature increased above 25° C to 31° C at the Bay site in August, 1992.

Conclusions

The community structure and population interactions of Ruppia and Zostera dominated habitats is more complex than is easily explained by factors such as light and temperature. This study suggests that community structure is affected by age of plants, energy allocation towards reproductive or vegetative propagation, photosynthetically active radiation (PAR) related or unrelated to shading by Zostera, and habitat disturbance. Data for shoot density are within the ranges reported in the literature (Kantrud 1991).

Some predictions can be made as a result of this study that could affect conservation efforts: (1) establishing the approximate age of plant populations is important in predicting energy allocation (asexual vs. sexual); (2) measuring changes in species densities is valuable in establishing zonation and light-related interactions

(overstory, understory and seasonal effects); (3) mapping changes in depth profile in relation to disturbance by current, wave action, and relative susceptibility to storms is important in predicting population changes and community structure.

Ruppia can conserve energy allocation by having reproductive shoots that remain viable and could colonize open habitat. Although they may mostly wash ashore or out to deep water, at least some may be able to disperse or remain in the same population. Lastly, a knowledge of the presence and position of a potential seed bank could be valuable in assessing management of existing beds and establishment of new communities. This has been investigated in a separate study (Rosenzweig, in review). The position of the seed reserve is related to both depth and to plant density. Colonization by seeds may be important in establishing beds decimated by storms or by Cow-nosed Rays (Rhinoptera bonasas) foraging for Soft-shelled Clams (Macoma arenaria) in plant beds. Seeds may also be important in maintaining annual plant populations.

Clearly, these plant communities require continued detailed assessment. In addition, modeling the physical and biological interactions occurring in these habitats may provide an ability to better serve future conservation efforts in Chesapeake Bay.

Table 3.1. Ruppia (Rup), and Zostera (Zos) Shoots (Shts), Seedlings (Sds), and Ruppia Reproductive Shoots (Rep Shts). Total colonization by date for both sites.

Date	Rup Shts York	Rup Shts Bay	Zos Shts York	Zos Shts Bay	Rup Sds York	Rup Sds Bay	Zos Sds York	Zos Sds Bay	Rep Shts York	Rep Shts Bay
Apr-92	0	0	19	0	0	0	0	0	0	0
May-92	115	3887	34	382	3	0	0	0	0	0
Jun-92 183	4152	79	382	4	0	0	0	0	0	
Jul-92	249	4258	70	293	4	0	0	0	0	5
Aug-92	630	4433	119	61	4	0	0	0	0	5
Sep-92	504	3808	116	61	4	0	0	0	0	3
Oct-92	626	3446	116	93	4	0	0	2	0	0
Mar-93		512	125	1032	217	5	2	5	0	0
0										

Table 3.2. t-Test comparisons; York River site vs. Bay site. DF = 7.

	Ruppia		Zostera	
	Shoots	Seedlings	Shoots	Seedlings
t =	4.04	5.51	0.09	0.56
P =	0.0051	0.0004	0.93	0.59

Table 3.3 t-Test comparisons; Ruppia vs. Zostera Shoots for both sites. DF = 7.

	York River (Site 1)	Bay (Site 2)
t =	1.04	4.32
P =	0.32	0.0036

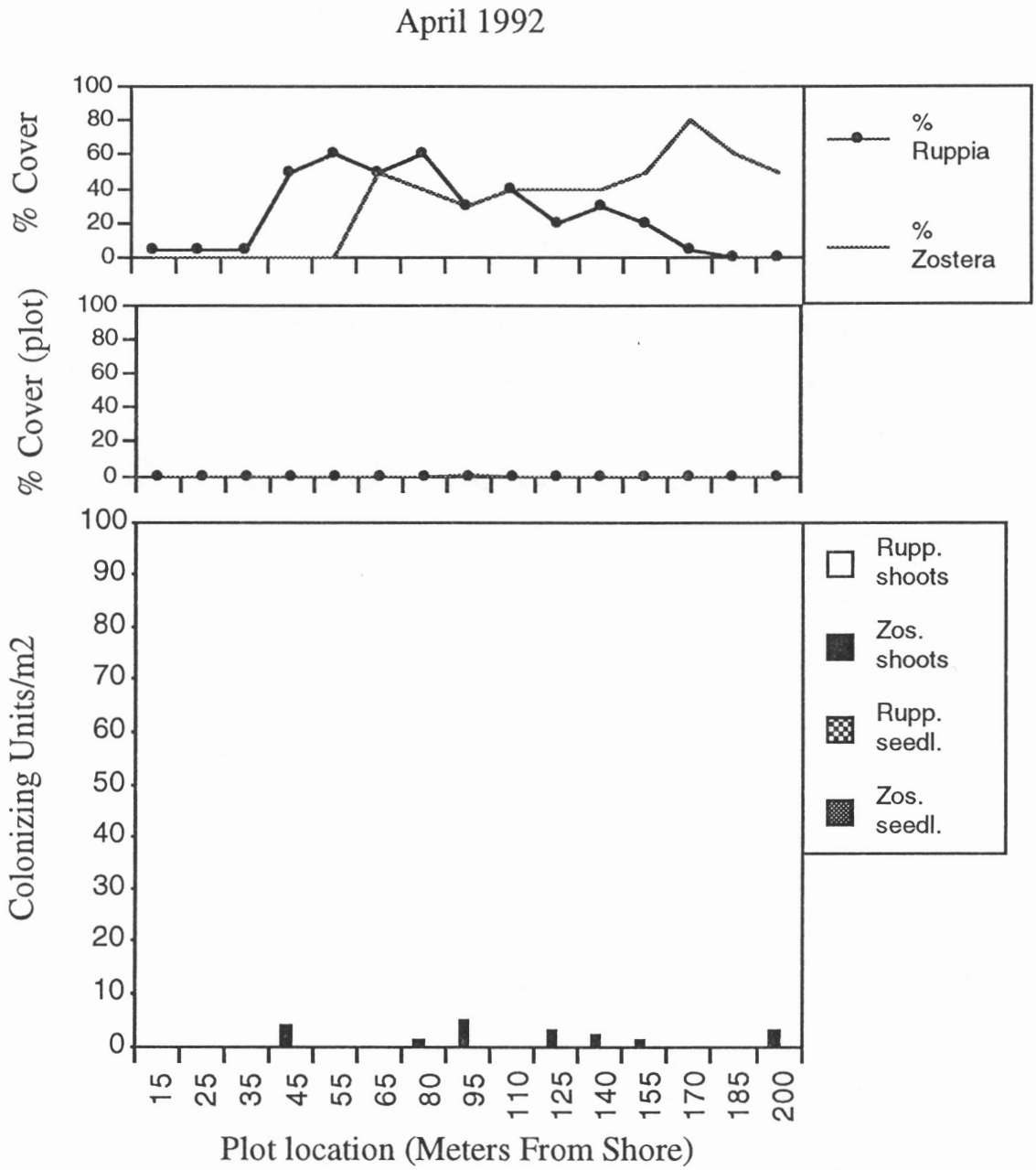

Fig. 3.1a Goodwin Islands, York River site colonization plot, April 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

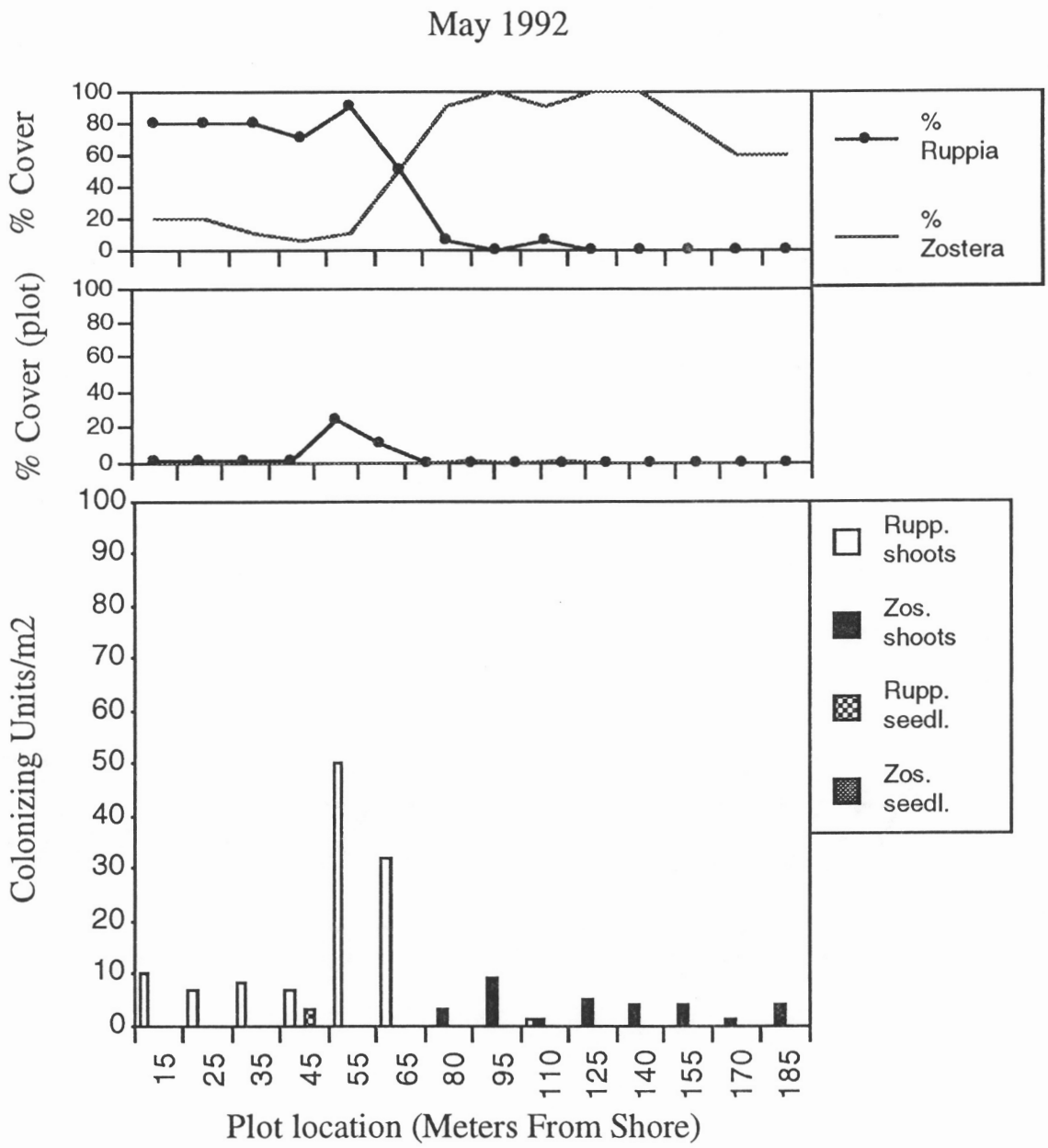

Fig. 3.1b Goodwin Islands, York River site colonization plot, May 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

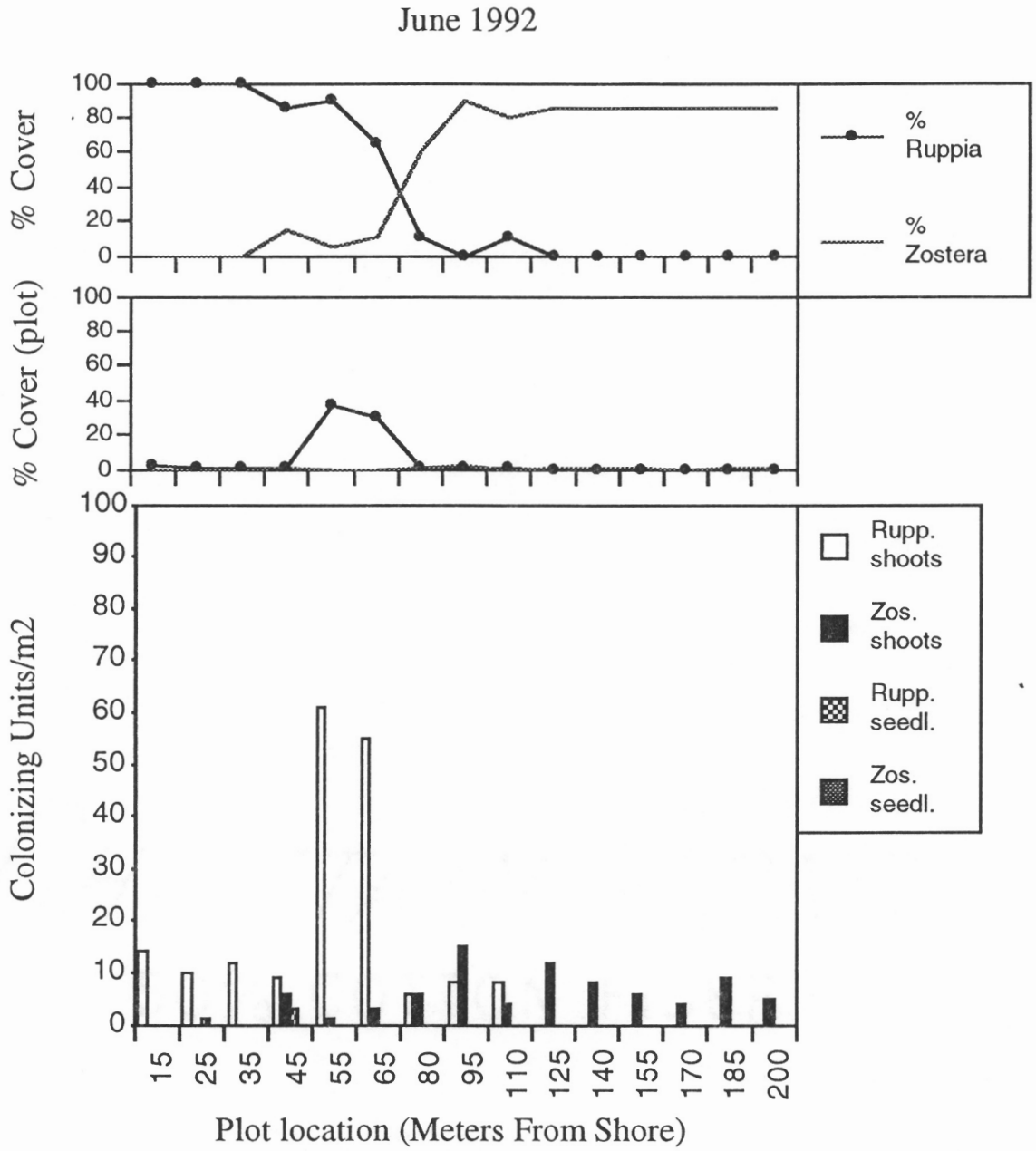

Fig. 3.1c Goodwin Islands, York River site colonization plot, June 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

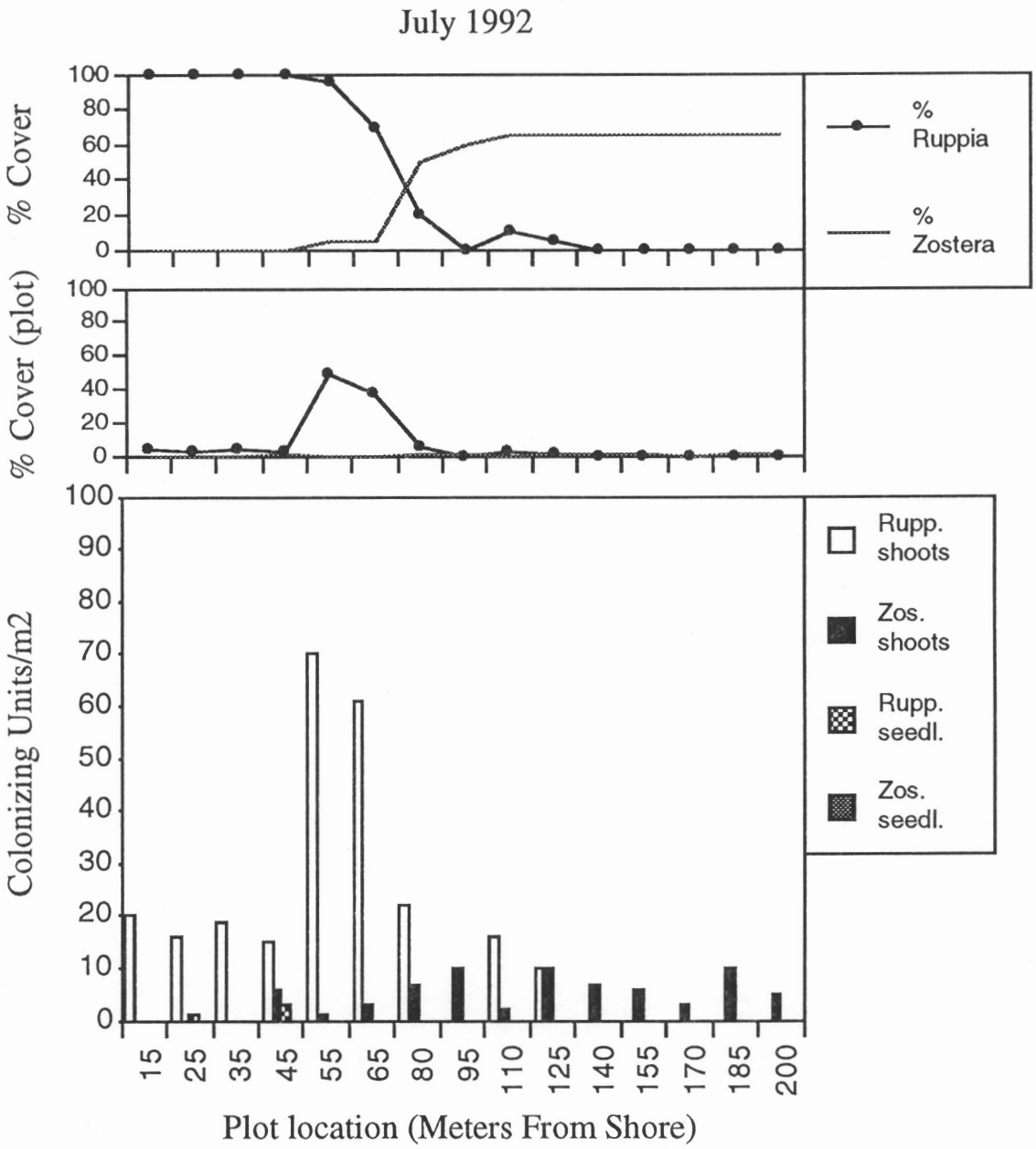

Fig. 3.1d Goodwin Islands, York River site colonization plot, July 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

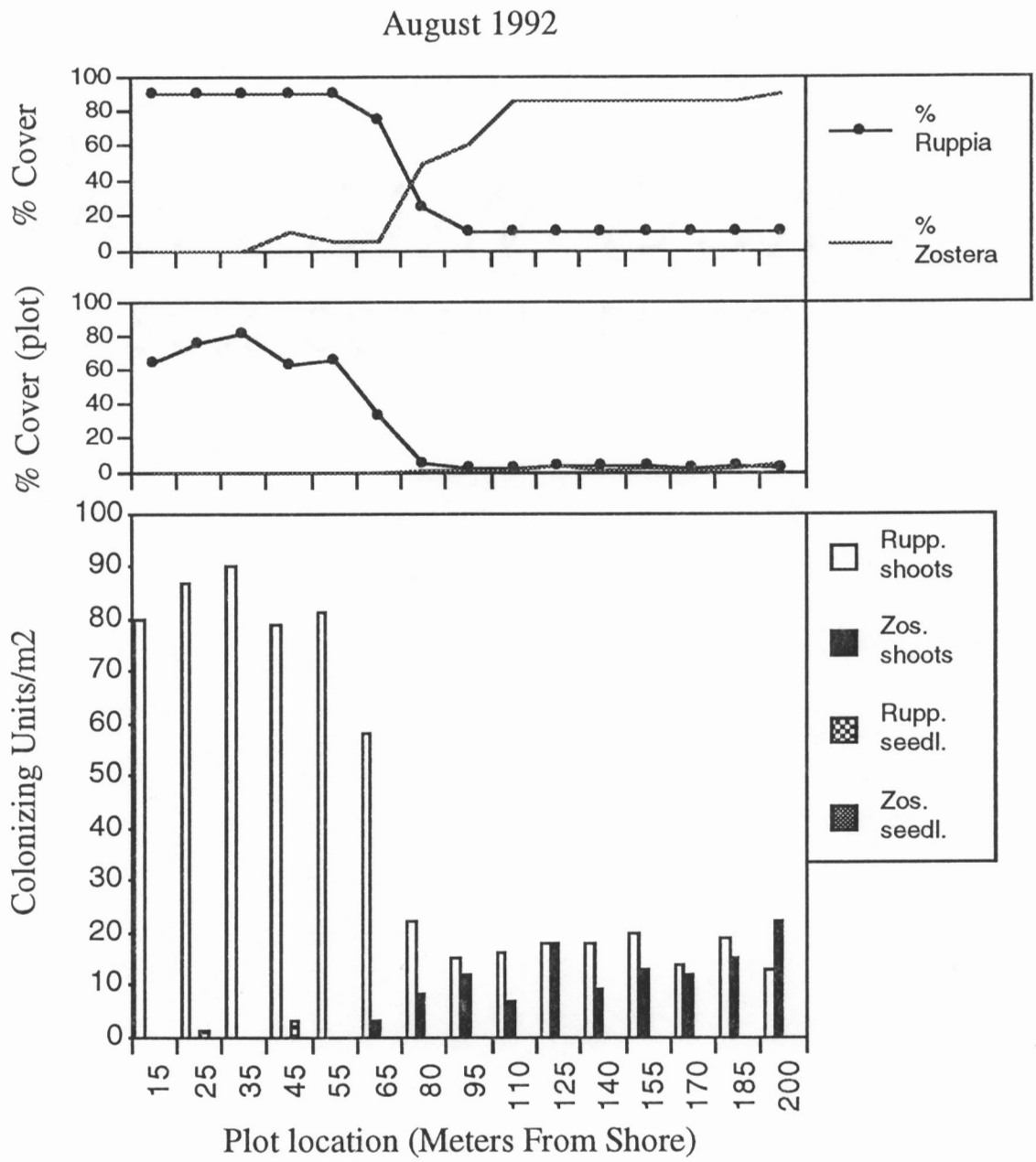

Fig. 3.1e Goodwin Islands, York River site colonization plot, Aug. 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

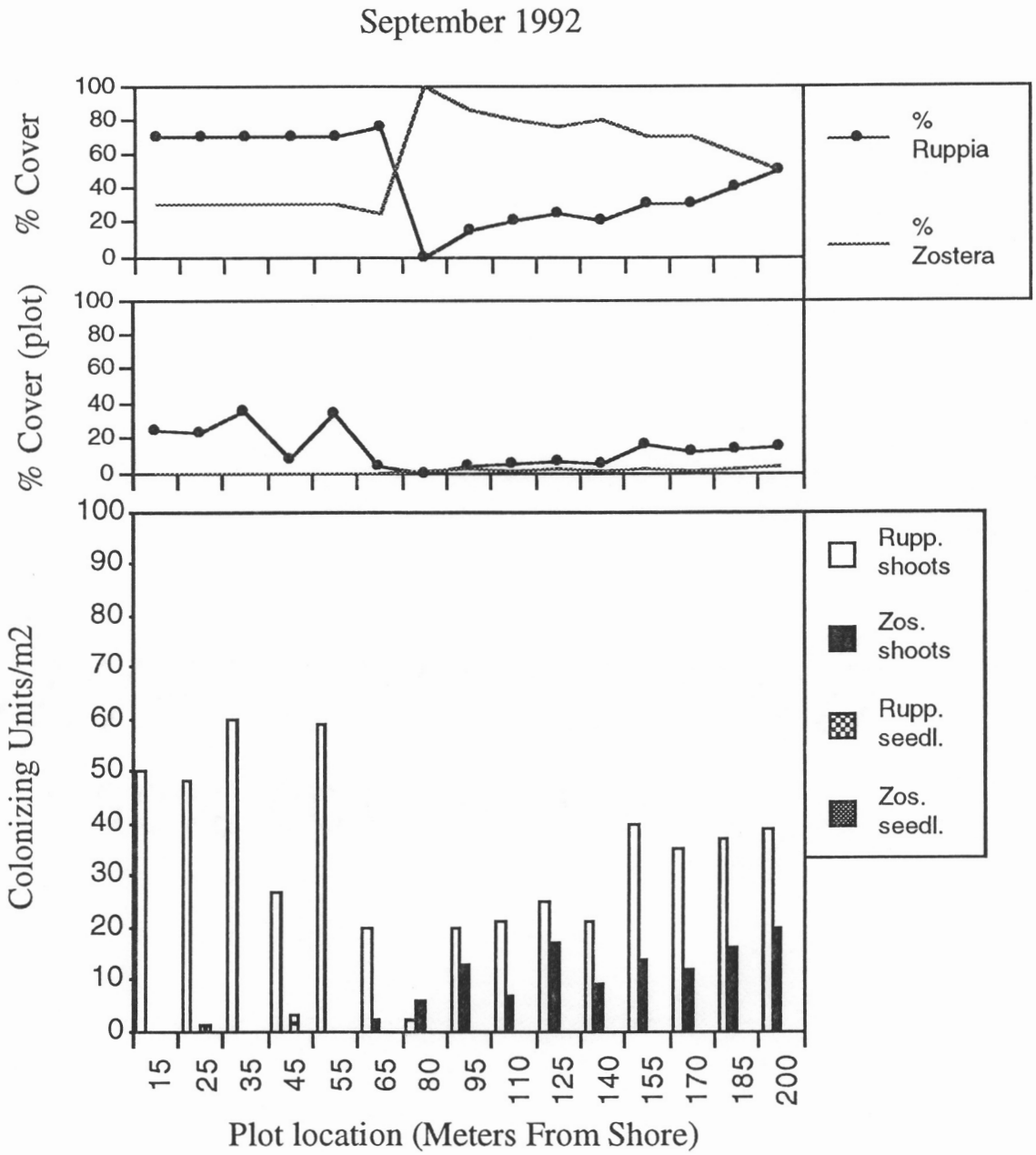

Fig. 3.1f Goodwin Islands, York River site colonization plot, Sept. 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

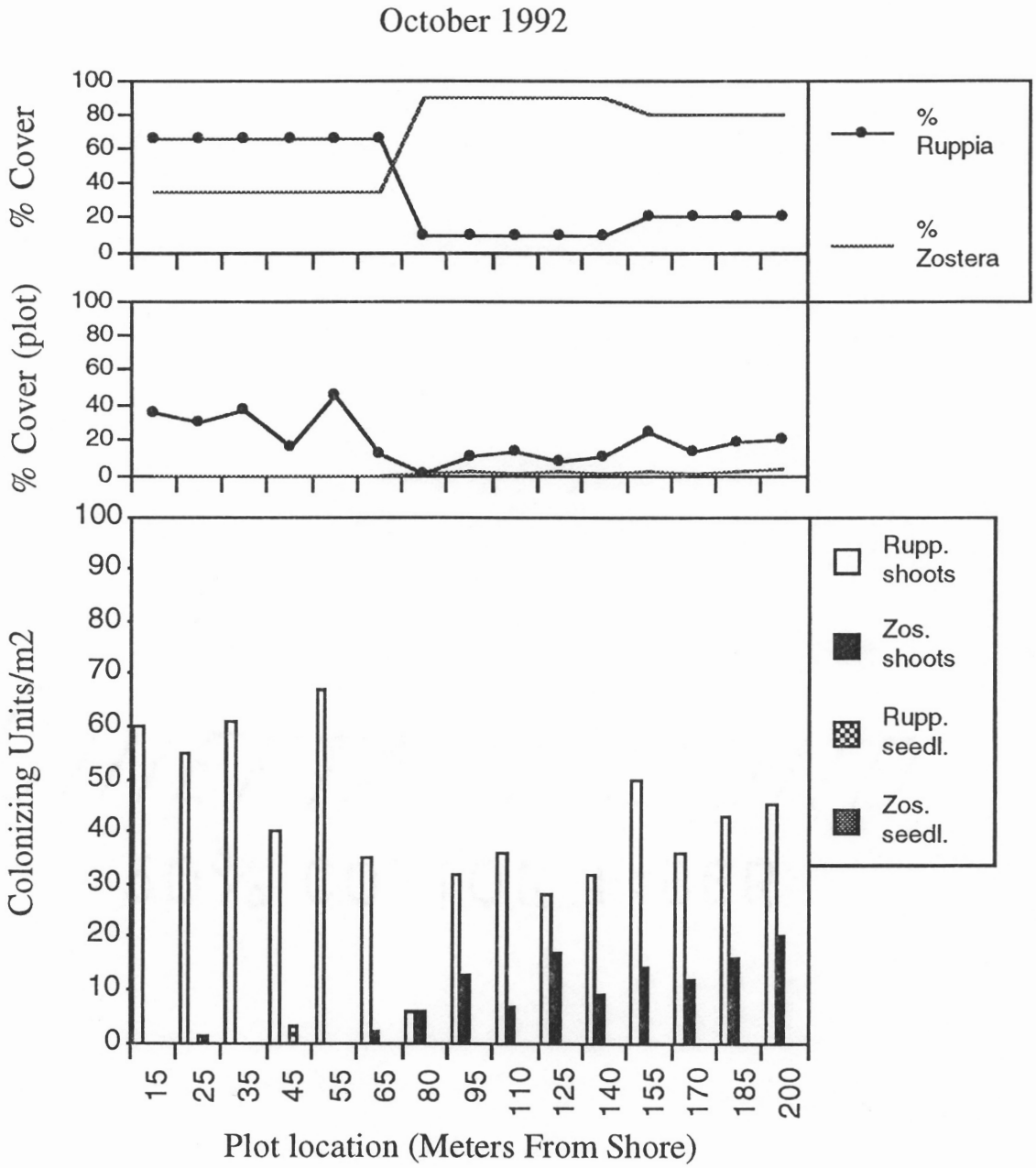

Fig. 3.1g Goodwin Islands, York River site colonization plot, Oct. 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

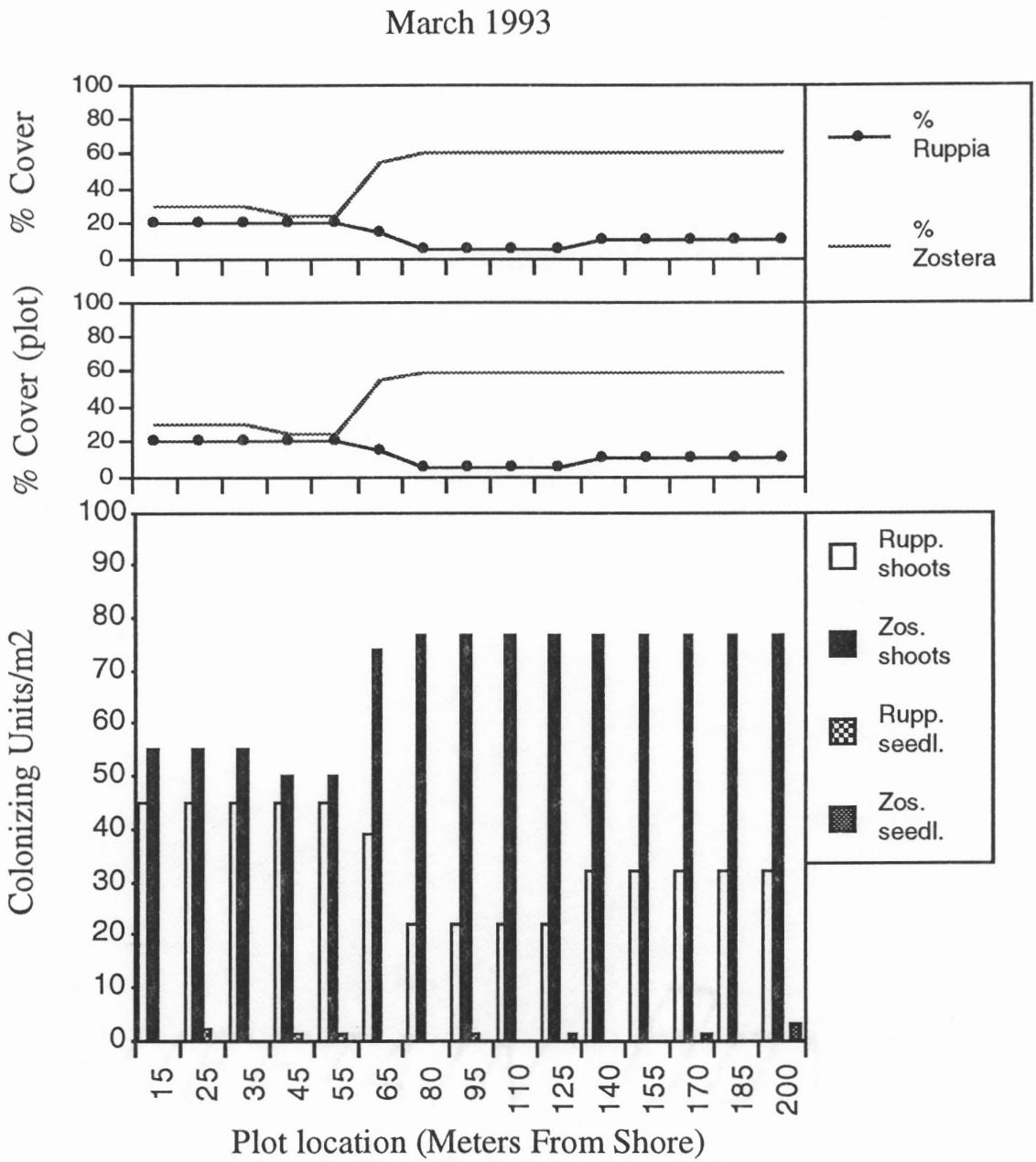

Fig. 3.1h Goodwin Islands, York River site colonization plot, March 1993. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

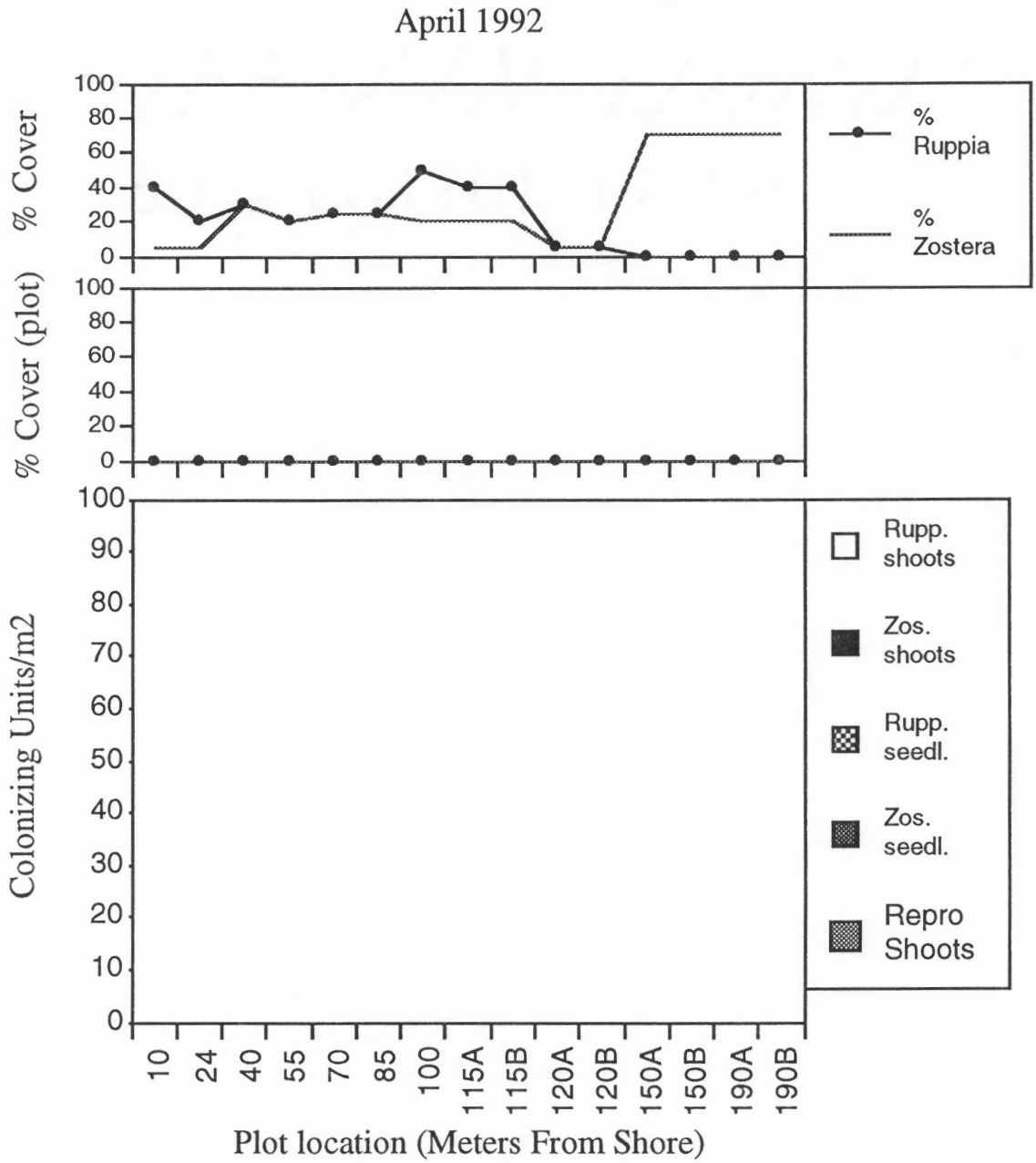

Fig. 3.2a Goodwin Islands, Bay site colonization plot, April, 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

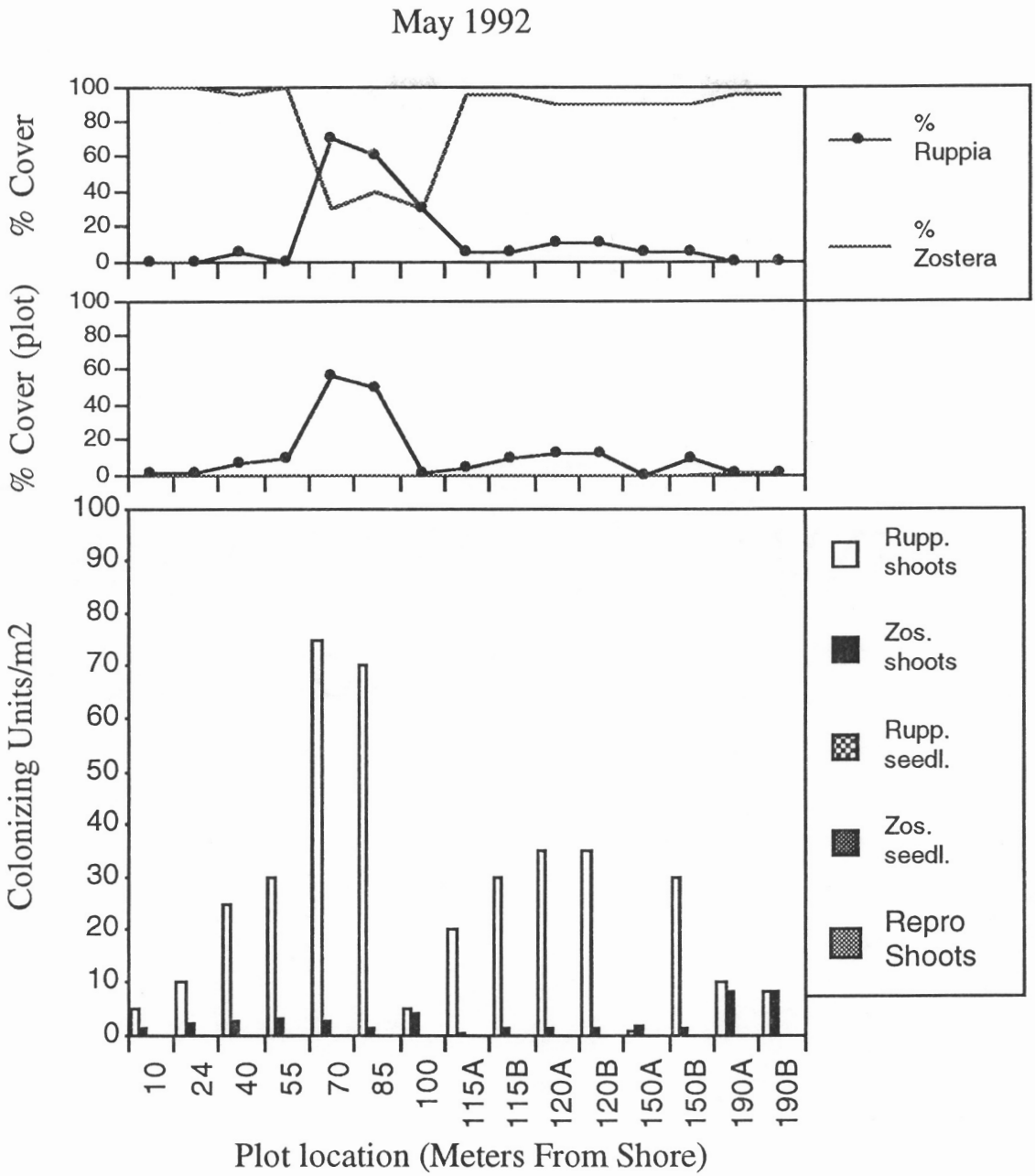

Fig. 3.2b Goodwin Islands, Bay site colonization plot, May, 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

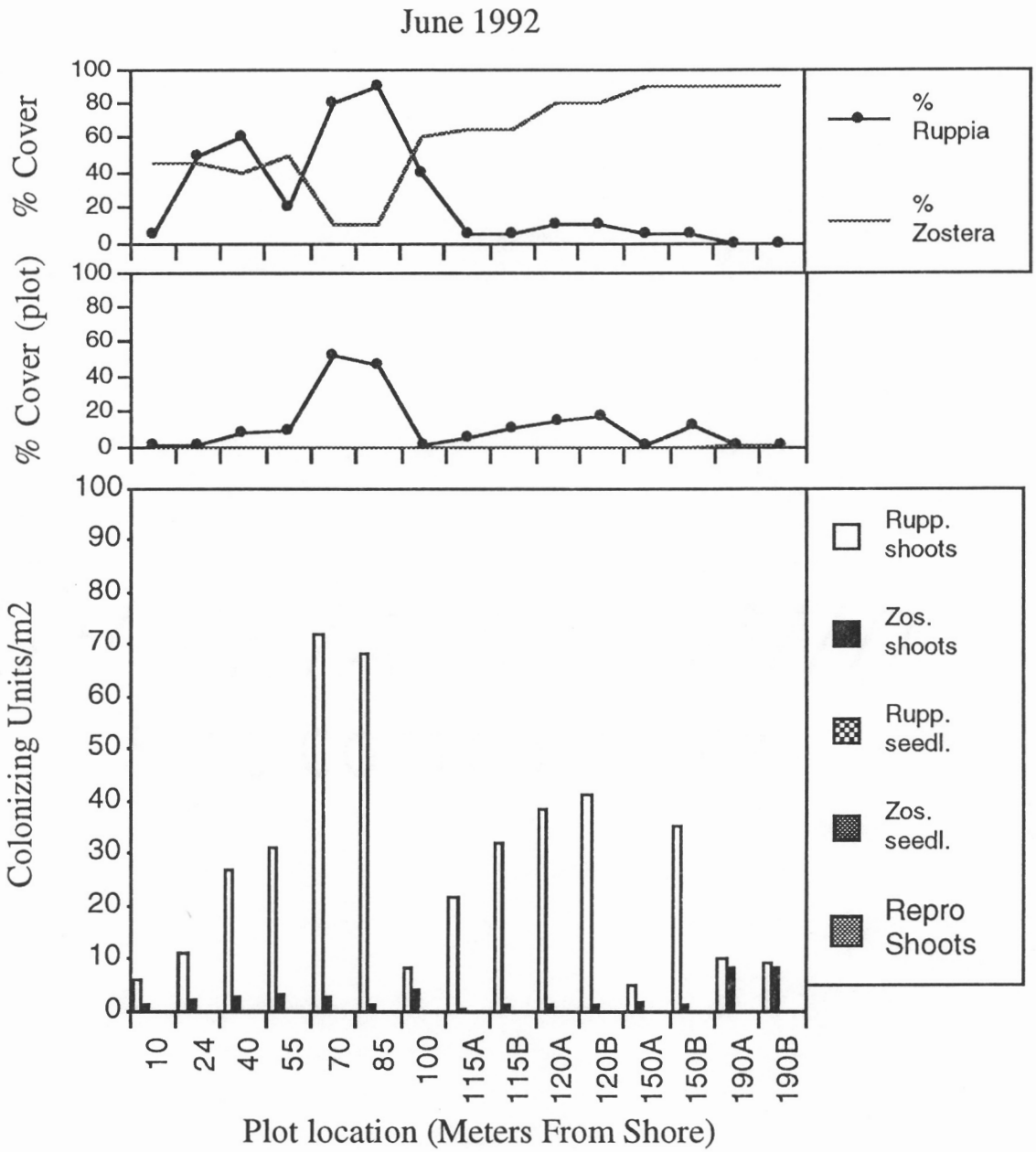

Fig. 3.2c Goodwin Islands, Bay site colonization plot, June, 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

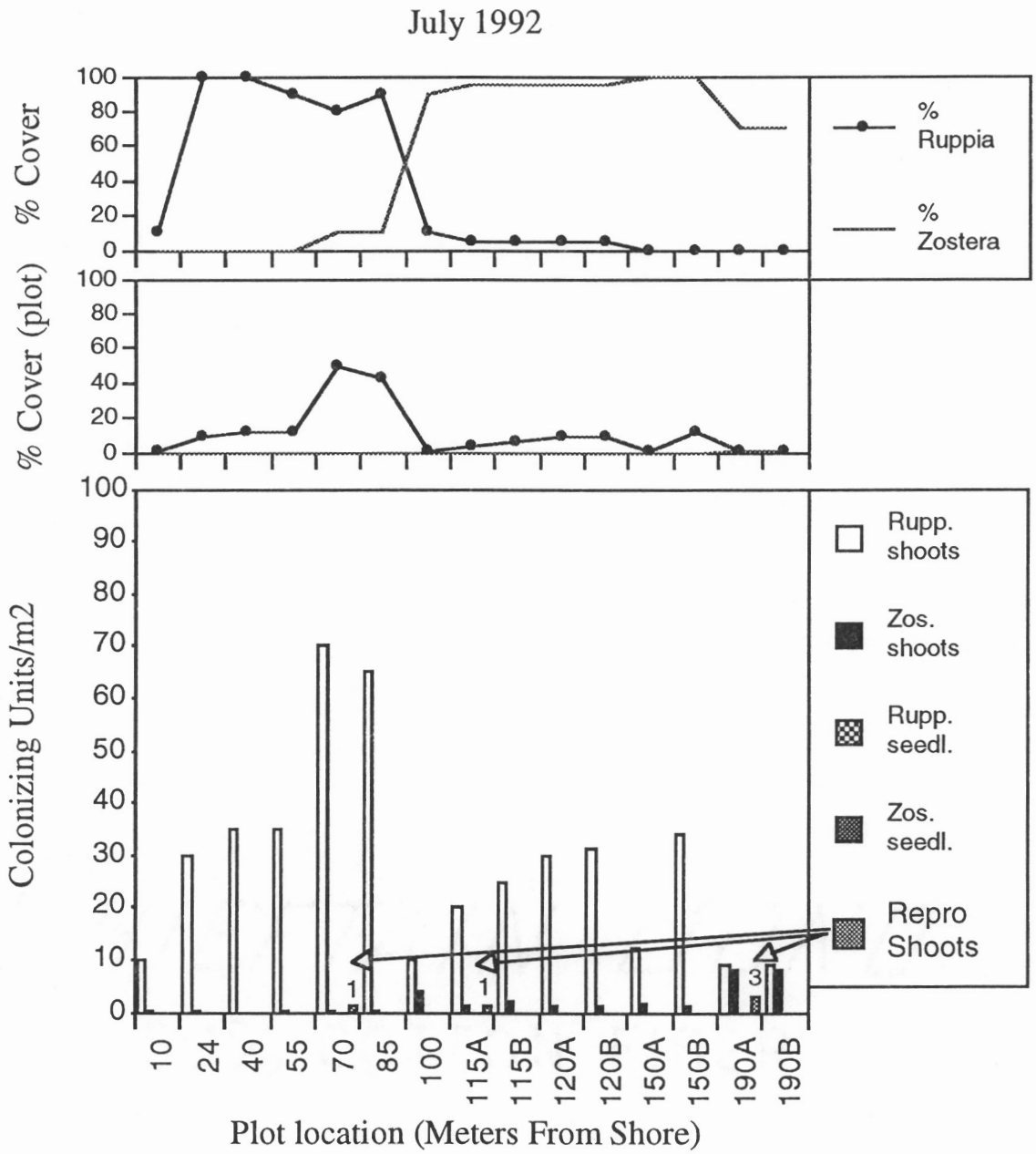

Fig. 3.2d Goodwin Islands, Bay site colonization plot, July, 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

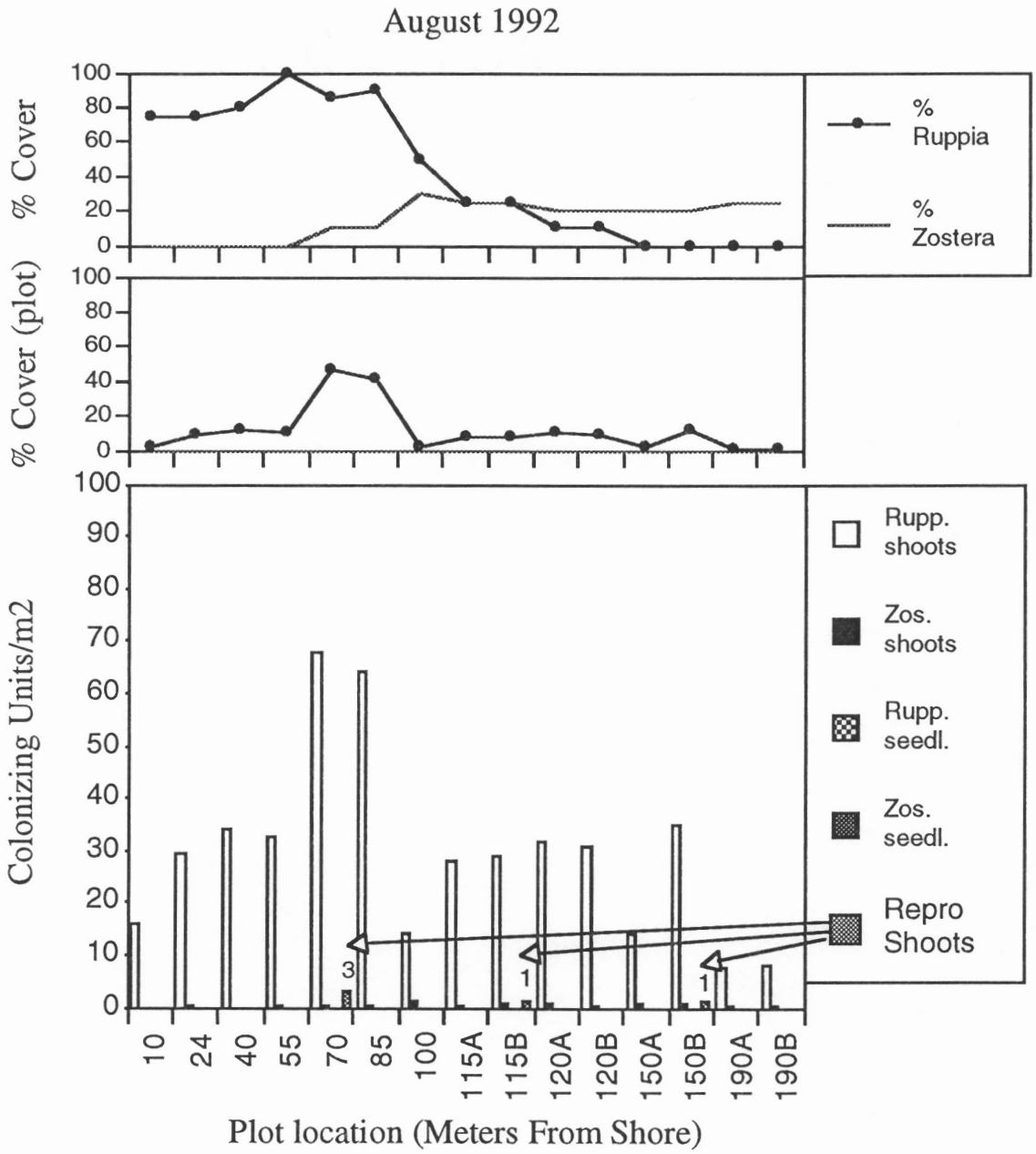

Fig. 3.2e Goodwin Islands, Bay site colonization plot, Aug., 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

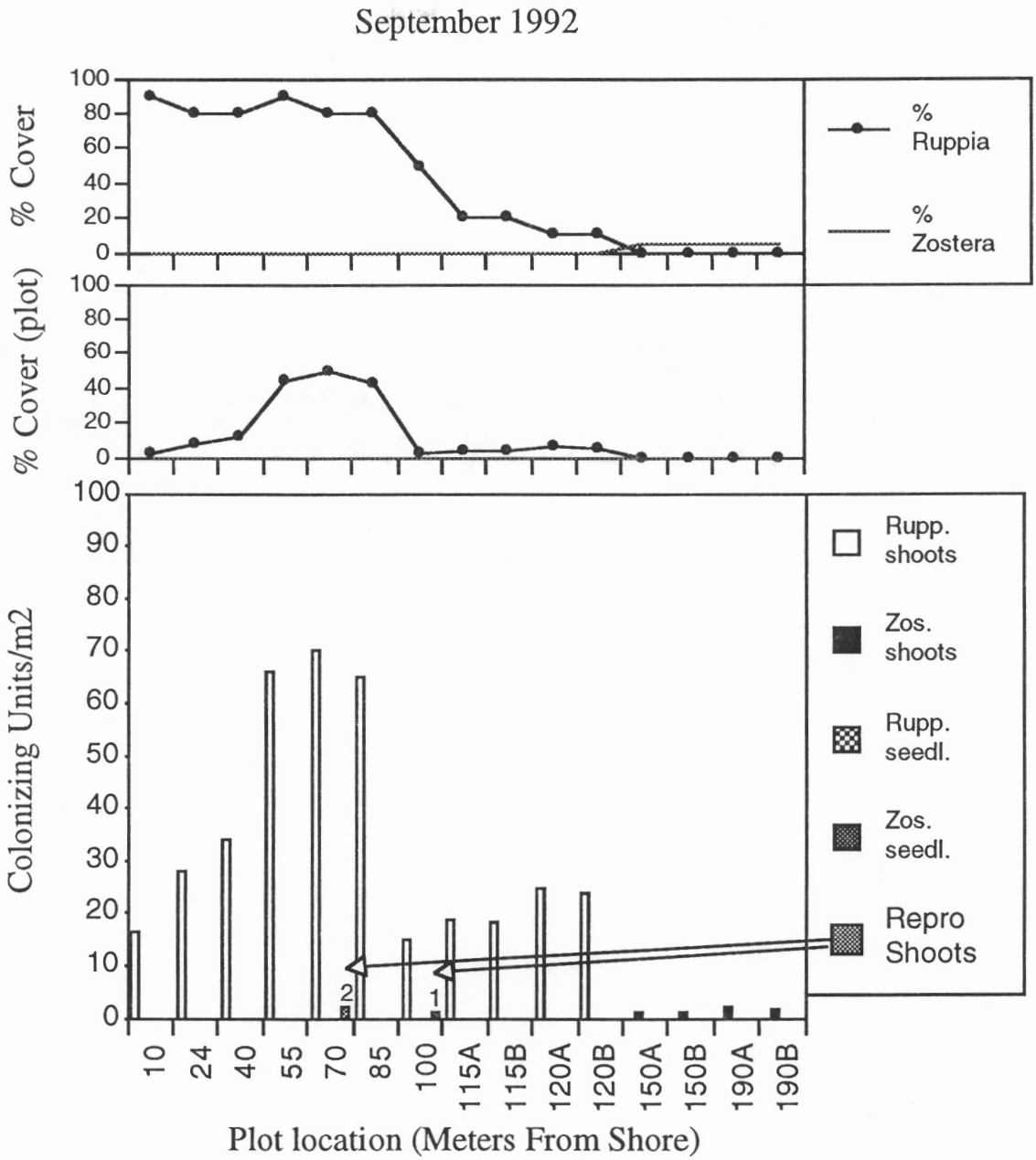

Fig. 3.2f Goodwin Islands, Bay site colonization plot, Sept., 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

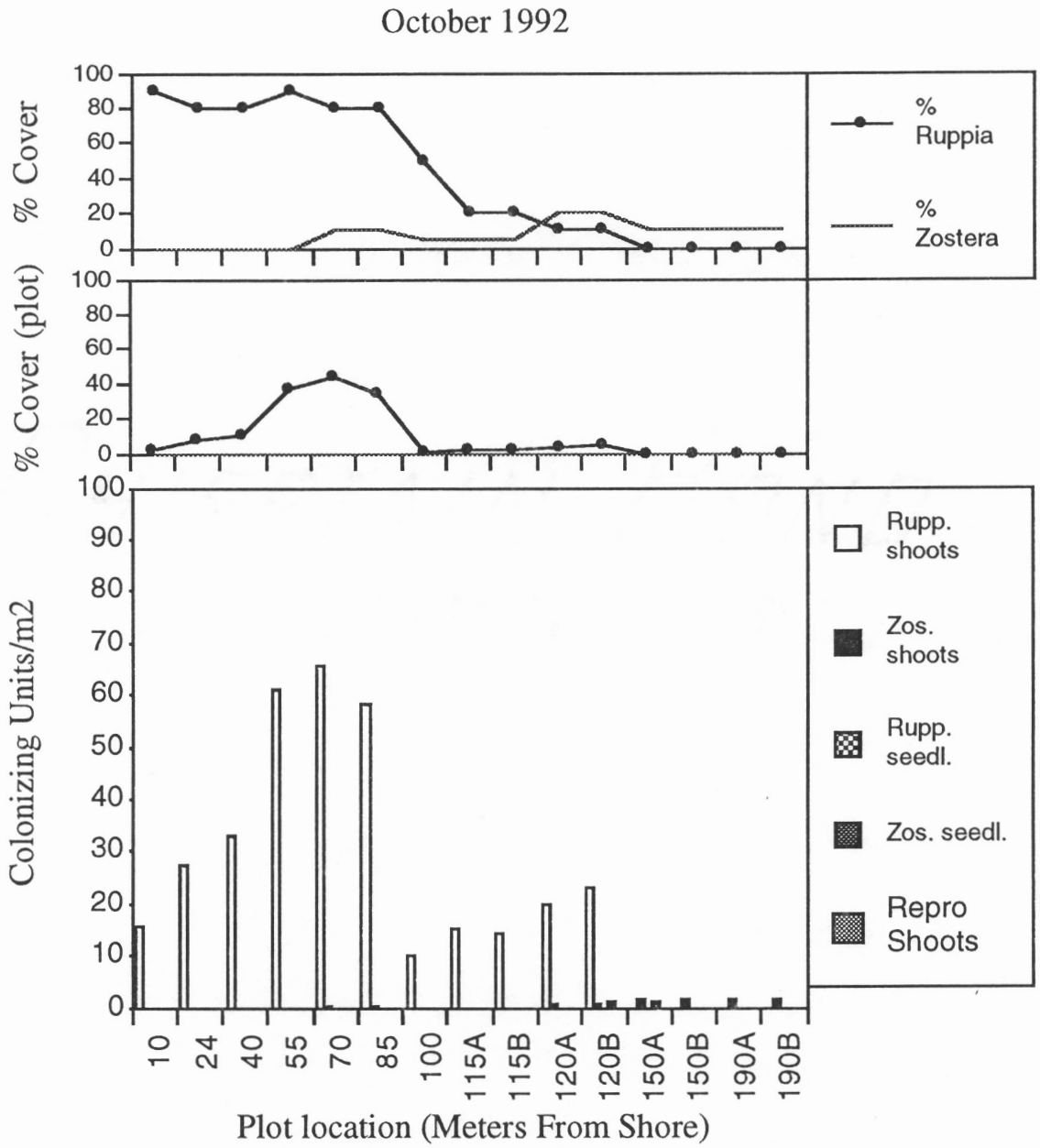

Fig. 3.2g Goodwin Islands, Bay site colonization plot, Oct., 1992. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

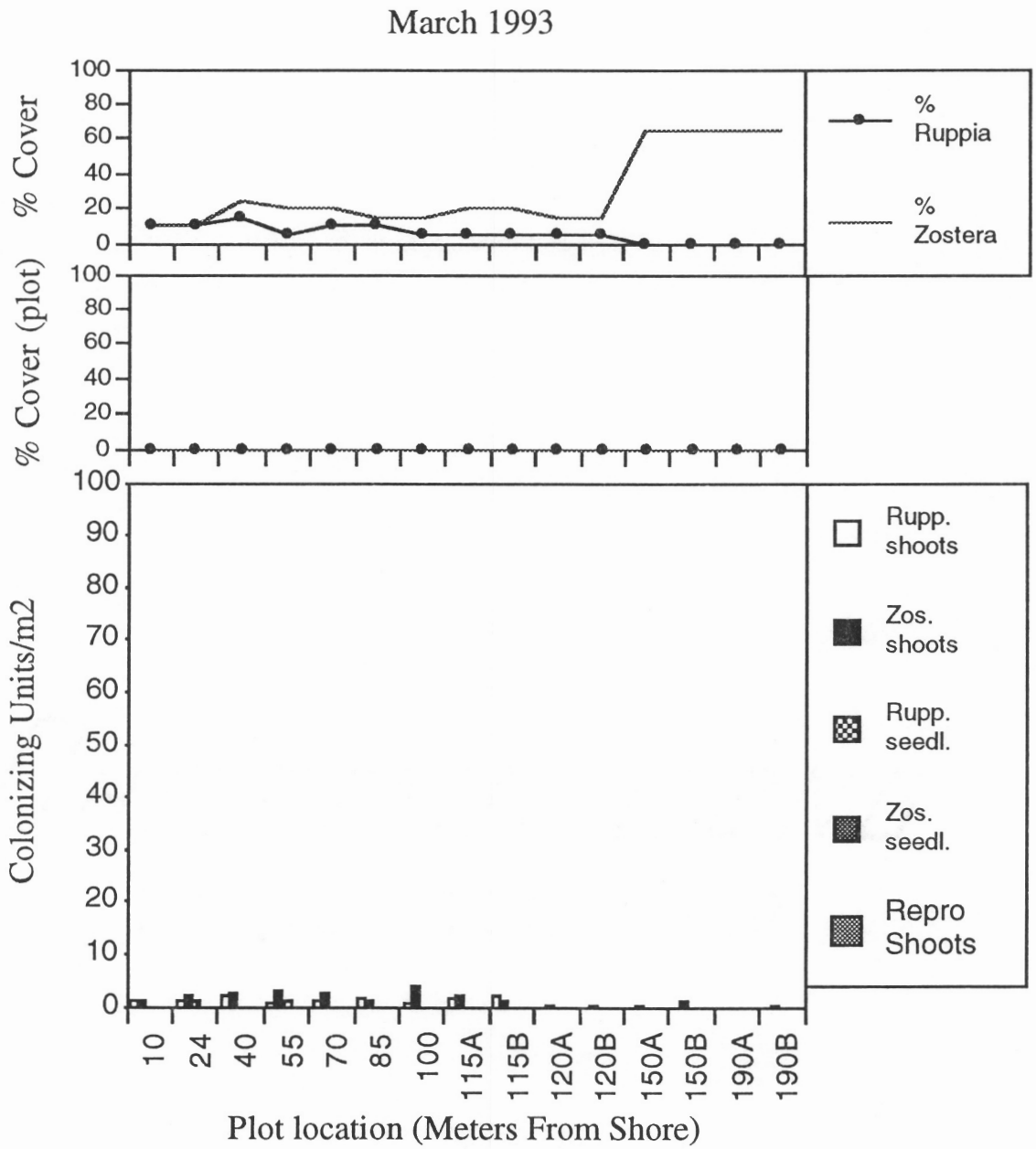

Fig. 3.2h Goodwin Islands, Bay site colonization plot, March, 1993. Percent cover surrounding the plot is compared to percent cover inside the plot and to the numbers of colonizing units/m^2 that accrued for the month.

Summary and Conclusions

The community structure and population interactions of Ruppia and Zostera habitats are more complex than is easily explained by factors such as light and temperature. This study suggests that community structure is affected by age of plants, energy allocation towards roproductive or vegetative propagules, photosynthetically active radiation related or unrelated to shading by Zostera, and habitat disturbance. Data for shoot density are within the ranges reported in the literature (Kantrud 1991). Other factors such as oxygen, nitrogen, and phosphorus availability in the sediments were not measured in this study, but have been addressed in the literature (Thursby and Harilin 1982; Thursby 1984a, 1984b). Since both Ruppia and Zostera can both absorb and can transport nutrients directly from the water through their leaves and can both transport oxygen to their roots, then nutrient availability may not have been a factor affecting the results of this study.

The results of this study could affect conservation efforts in the following ways:

1. Establishing the approximate age of plant populations is important in predicting energy allocation towards asexual versus sexual reproduction.
2. Measuring changes in species densities is valuable in establishing zonation and light related interactions (seasonal overstory and understory zonation) and in predicting cyclical and successional changes.
3. Mapping changes in depth profile in relation to disturbance by currents, wave action, and relative susceptibility to storms is impoortant in predicting population changes and community structure.

Ruppia maritima can conserve energy allocation by having reproductive shoots that remain viable and can also be potential colonists. Although they may mostly wash

ashore or out to deep water, at least some may be able to disperse or remain in the same population.

A knowlege of the presence and position of a potential seed bank could be valuable in assessing existing beds and establishment of new communities. In this study, the seed reserve was related to both depth and plant density. Colonization by seeds may be important in establishing populations decimated by storms or by animals such as Rhinoptera bonasas that forage for Soft-shelled clams (Macoma arenaria) in plant beds. Seeds may also be important in maintaining annual plant populations. The pollination biology of Ruppia is much like that of other species in the Potamogetonaceae. Further study as to the occurrence of apomixis is still needed. This study indicates that plants can both cross and self pollinate. In addition, the peduncle of inflorescences displays a downward growth into the water column after pollen is released and before seeds develop. This may be to prevent desiccation of developing seeds and also to hide seeds beneath the water from potential water fowl predators.

Clearly these plant communities require continued detailed assessment. In addition, modeling the physical and biological interactions occurring in these communities may provide an ability to better serve future conservation efforts in Chesapeake Bay.

Literature Cited

Bigley, R.E. and P.G. Harrison, 1986. Shoot demography and morphology of Zostera japonica and Ruppia maritima from British Columbia, Canada. *Aquatic Botany*, 24:69-82.

Bristow, Alec 1978. The sex life of plants. Holt, Rinehart and Winston, New York, p. 59.

Brock, M.A. 1982a. Biology of the salinity tolerant genus Ruppia L. in saline lakes in South Australia. I. Morphology variation within and between species and ecophysiology. *Aquatic Botany*, 13:219-248.

Brock, M.A. 1982b. Biology of the salinity tolerant genus Ruppia L. in saline lakes in South Australia. II. Population ecology and reproductive biology. *Aquatic Botany*, 13:249-268.

Cambridge, M.L. and A.J. McComb 1984. The loss of seagrass from Cockburn Sound, western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany*, 20:229-243.

Charlton, W.A. and U. Posluszny. 1991. Meristic variation in Potamogeton flowers. *Botanical Journal of the Linnean Society*, 106:265-293.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. The New York Botanical Garden, Bronx, New York, 555 pp.

Dennison, W.C., R.J. Orth, K.A. Moore, J.C. Stevenson, V. Carter, S. Kollar, P.W. Bergstrom, and R.A. Batiuk. 1992. Assessing water quality with submersed aquatic vegetation. *Bioscience*, 43(2):86-94.

Daumann, E. 1963. Zur Frage Nach dem Ursprung der Hydrogamie, Zugleich ein Beitrag zur Blutenokologie von Potamogeton. Preslia 35:23-30.

Endler, J. A. 1989. Conceptual and other problems in speciation. In. Otte, D. and J.A. Endler [eds.]. Speciation and its Consequences. Sinauer Associates, Inc. Sunderland, MA.

Environmental Protection Agency. 1980. Environmental Protection Agency Research Summary: Chesapeake Bay. Office of Research and Development. EPA-600/8-80-019, May 1980, pp. 10-16.

Evans, A.S., K.L. Webb, and P.A. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, Zostera marina L. and Ruppia maritima L. *Aquatic Botany*, 24:185-197.

Faegri, K., Van der Pijl. 1966. The Principles of Pollination Ecology. 1st Edition. Pergamon Press, Oxford, p. 37.

Gibbons, A. 1991. Systematics goes molecular, *Science*, 251:872-874.

Gregory, P.H., 1951. Deposition of airborne Lycopodium spores on cylinders. Ann. *Applied Biology*, 38, pp. 357-376.

Hartog, den C. 1977. Structure, function, and classification in seagrass communities. pp. 89-121. In C. P. McRoy and C. Helfferich [eds.], Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, Inc., New York.

Helfferich, C. and C. P. McRoy, 1980. Introduction: The spaces in the pattern. pp. 1-5. In R. C. Phillips and C. P. McRoy [eds.]. Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, New York.

Heywood, V.H.. 1985. Flowering plants of the world. Croom Helm, London, pp. 43-45.

Hilu, K.W. and J.M.J. De Wet. 1980. Effect of artificial selection on grain dormancy in Eleusine (Gramineae). Systematic Botany, 5(1):54-60.

Kantrud, H.A. 1991. Wigeongrass (Ruppia maritiima L.): A literature review. United States Department of the Interior, Fish and Wildlife Service, Washington, D.C. 58 pages.

Kemp, W.M., W.R. Boyton, R.R. Twilley, J.C. Stevenson, and J.C. Means 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. Mar. Tech. Soc. J. 17:78-89.

Koch, E.W. and C.J. Dawes 1991. Influence of salinity and temperature on the germination of Ruppia maritima L. from the North Atlantic and Gulf of Mexico. *Aquatic Botany*, 40:387-391.

Koch, E.W. and U. Seeliger 1988. Germination ecology of two Ruppia maritima L. populations in southern Brazil. *Aquatic Botany*, 31:321-327.

Kuo, F., R.W. Ridge, and S.V. Lewis. 1990. The leaf internal morphology and ultrastructure of Zostera muelleri Irmisch ex Aschers. (Zosteraceae): a comparative study of the intertidal and subtidal forms. *Aquatic Botany*, 36:217-236.

Larkum, A.W.D., A.J. McComb, S.A. Shepherd, 1989. Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Oxford. 678pp.

Larkum, A.W.D. and R.J. West. 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. *Aquatic Botany*, 37:55-70.

Leck M.A, V. Thomas Parker, R.L. Simpson [eds.], Ecology of Soil Seed Banks. Academic Press, San Diego, 1989, 462pp.

Les, D.H. and E. Schneider. 1993. Putative evolutionary linkage between Nymphiflorae and Alismatiflorae - molecular and morphological perspectives. Lecture presented at the Monocot Symposium, Royal BotanicGardens, Kew, U.K., 18-23 July 1993.

Mayr, E. 1954. Change of genetic environment and evolution. pp. 157-180. In J. Huxley, A.C. Hardy, and E.B. Ford [eds.], Evolution as a Process. George Allen and Unwin Ltd., London.

Mazzella, L., G.F. Russo, 1989. Grazing effect of two Gibbula species (Mollusca, Archaeogastropoda) on the epiphytic community of Posidonia oceanica leaves. *Aquatic Botany*, 35:357-373.

McCann, C. 1945. Notes on the genus Ruppia (Ruppiaceae). *Journal of the Bombay Natural History Society*, 45:396-402.

McMillan, C. 1982. Reproductive physiology of tropical seagrasses. *Aquatic Botany*, 14:245-258.

McMillan, C. 1983. Seed germination in Halodule wrightii and Syringodium filiforme from Texas and the U.S. Virgin Islands. *Aquatic Botany*, 15:217-220.

McMillan, C. 1988. Seed germination and seedling development of Halophila decipiens Ostenfeld (Hydrocharitaceae) from Panama. *Aquatic Botany*, 31:169-176.

Meacham, C.A. 1980. Phylogeny of the Berberidaceae with an evaluation of classification. Systematic Botany 5(2): pp. 149-172.

National Oceanic and Atmospheric Administration, and Virginia Institute of Marine Science. 1991. Chesapeake Bay National Estuarine Research Reserve System in Virginia: Final environmental impact statement and final management plan. U.S. Department of Commerce, National Ocean Service, Washington, D.C., and Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia.

National Research Council, Committee on Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy Water Science and Technology Board Commission on Geosciences, Environment, and Resources. 1991. Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy. Prepublication Copy, National Academy Press, Washington, D.C. 11 pp.

Orth, R.J. and K.A. Moore. 1981. Submerged Aquatic Vegetation of the Chesapeake Bay: Past, Present, and Future. Transactions of the 46th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C. pp. 271-283.

Orth, R.J. and K.A. Moore. 1983a. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science*, 222:51-53.

Orth, R.J. and K.A. Moore. 1983b. Submersed vascular plants: Techniques for analyzing their distribution and abundance. *Marine Technology Society Journal*, 17(2):38-52.

Orth, R.J. and K.A. Moore. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: An historical perspective. *Estuaries*, 7(4B):531-540.

Orth, R.J. and K.A. Moore. 1986. Seasonal and year-to-year variation in the growth of Zostera marina L. (Eelgrass) in the lower Chesapeake Bay. *Aquatic Botany*, 24:335-341.

Orth, R.J. and K.A. Moore. 1988. Distribution of Zostera marina L. and Ruppia maritima L. sensu lato along depth gradients in the lower Chesapeake Bay, U.S.A. *Aquatic Botany*, 32:291-305.

Orth, R.J., A.A. Frisch, J.F. Nowak, and K.A. Moore 1989. Distribution of submerged aquatic vegetation in the Chesapeake Bay and Tributaries and Chincoteaque Bay - 1987. Final Rep. U.S. EPA, Washington, DC 247 pp.

Orth, R.J. and J.F. Nowak 1990. Distribution of submerged aquatic vegetation in the Chesapeake Bay and tributaries and Chincoteaque Bay - 1989. Final Rep. U.S. EPA, Washington, DC, 249pp.

Palmer, J.D., 1985. Evolution of chloroplast and mitochondrial DNA in plants and algae. pp. 131-240. In Ross J. MacIntyre [ed.], Molecular Evolutionary Genetics. Plenum Press, New York.

Palmer, J.D. 1986. Isolation and structural analysis of Chloroplast DNA. *Methods in Enzymology*, 118:167-186.

Philbrick, C.T. 1991. Hydrophily: Phylogenetic and evolutionary considerations. *Rhodora*, 93:36-50.

Phillips, R.C., C.P. McRoy, 1980. Handbook of Seagrass Biology: An Ecosystem Perspective, Garland STPM Press, New York.

Phillips, R.C., Ernani G. Meñez. 1988. Seagrasses. Smithsonian Contributions to the Marine Sciences, Washington, D.C. No. 34, 48pp.

Pokorny, K.S. 1967. Labrinthula. *Protozoology*, 14:697-708.

Procter, M., P. Yeo. 1978. Pollination of Flowers. Collins Ltd., London, pp. 277-285.

Pulich, W.M., Jr. 1985. Seasonal growth dynamics of Ruppia maritima L. s.l. and Halodule wrightii Aschers. in southern Texas and evaluation of sediment fertility status. *Aquatic Botany*, 23:53-66.

Rasmussen, Erik, 1977. The wasting disease of eelgrass (Zostera marina) and its effects on environmental factors and fauna. pp. 1-51. In C. Peter McRoy & Carla Helfferich [eds.], Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, Inc., New York. 487pp.

Richardson, F.D. 1980. Ecology of Ruppia maritima L. in New Hampshire (U.S.A.) tidal marshes. *Rhodora*, 82:403-439.

Rosenzweig, M.S.R. 1994. On the Life History, Systematics, and Ecology of Ruppia maritima L. (Potamogetonaceae) in lower Chesapeake Bay. Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061. pp. 75-82.

Sculthorpe, C.D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold Publishers Ltd., London, 1985 reprint by Koeltz Scientific Books, D-6240 Könisgstein, West Germany, 610 pp.

Seeliger, U. and E.W. Koch. 1984. Germination and algal - free laboratory culture of Widgeon Grass, Ruppia maritima. *Estuaries*, 7(2):176-178.

Setchell, W.A. 1922. Zostera marina in its relation to temperature. *Science*, 56(1455):1-4.

Setchell, W.A. 1929. Morphological and phenological notes on Zostera marina L. *University of California Publications in Botany*, 14(19):389-452.

Shaffer-Fehre, M. 1991a. The endotegmen tuberculae: an account of little - known strucures from the seed coat of the Hydrocharitoideae (Hydrocharitaceae) and Najas (Najadaceae). *Botanical Journal of the Linnean Society*, 107:169-188.

Shaffer-Fehre, M. 1991b. The position of Najas within the subclass Alismatidae (Monocotyledones) in the light of new evidence from seed coat structures in the Hydrocharitoideae (Hydrocharitales). *Botanical Journal of the Linnean Society*., 107:189-209.

Silberhorn, G.M., R.J. Orth, and K.A. Moore. 1983. Anthesis and seed production in Zostera marina L. (Eelgrass) from the Chesapeake Bay. *Aquatic Botany*, 15:133-144.

Silberhorn, G.M., S. Dewing, R.J. Orth, and K.A. Moore. Unpublished manuscript. Anthesis, seed production and changes in distribution and abundance in populations of Ruppia maritima L. from the Chesapeake Bay, Virginia, USA. 12 pp.

Simberloff, D. 1990. Reconstructing the ambiguous: Can island ecosystems be restored? In D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson [Eds], 1990, Ecological restoration of New Zealand Islands. Conservation Sciences Publication No. 2, Department of Coservation, Wellington, pp 37-50.

Stevens, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Syst. 11:333-358.

Stuessy, T. 1990. Plant Taxonomy: The systematic evaluation of comparative data. Columbia University Press, New York, NY.

Sytsma, K.J. and J.F. Smith. 1990. Phylogenetics in Clarkia (Onagraceae): Restriction site mapping of Chloroplast DNA. *Systematic Botany*, 15(2):280-295.

Templeton, A. R. 1989. The meaning of species and speciation: A genetic perspective. In Otte, D. and J.A. Endler [eds.]. Speciation and its Consequences. Sinauer Associates, Inc. Sunderland, MA.

Thursby, G.B. 1984a. Nutritional requirements of the submerged angiosperm Ruppia maritima in algae - free culture. *Marine Biology*, 16:45-50.

Thursby, G.B. 1984b. Root - exuded oxygen in the aquatic angiosperm Ruppia maritima. *Marine Biology*, 16:303-305.

Thursby, G.B. and M.M. Harlin. 1982. Leaf - Root interactions in the uptake of ammonia by Zostera marina. *Marine Biology*, 72:109-112.

Thursby, G.B. and M.M. Harlin. 1984. Interactions of leaves and roots of Ruppia maritima in the uptake of phosphate, ammonia and nitrate. *Marine Biology*, 83:61-67.

Tomlinson, P.B. 1980. Leaf morphology and anatomy in seagrasses. pp. 7-28. In R.C. Phillips & C.P. McRoy [eds.], Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, New York.

Van Vierssen, W., R.J. Van Wijk, and J.R. Van der Zee. 1978. Some additional notes on the cytotaxonomy of Ruppia taxa in Western Europe. *Aquatic Botany*, 11:297-301.

Van Vierssen, W. 1982. Some notes on the germination of seeds of Najas marina L. *Aquatic Botany*, 12:201-203.

Van Vierssen, W., C.M. Van Kessel, and J.R. Van Der Zee. 1984. On the germination of Ruppia taxa in western Europe. *Aquatic Botany*, 19:381-393.

Verhoeven, J.T.A. 1975. Ruppia - dominated communities in the Camargue, France. Distribution and structure in relation to salinity and salinity fluctuations. *Aquatic Botany*, 1:197-268.

Verhoeven, J.T.A. 1978. Natural regulation of plant biomass in a Ruppia - dominated system. Proceedings EWRS 5th Symposium on Aquatic Weeds. pp. 53-61.

Verhoeven, J.T.A. 1979. The ecology of Ruppia - dominated communities in western Europe: I. Distribution of Ruppia representatives in relation to their autecology. *Aquatic Botany*, 6:197-268.

Verhoeven, J.T.A., R.P.W.M. Jacobs, and W. Van Vierssen. 1982. Life - strategies of aquatic plants: Some critical notes and recommendations for further research. In J.J. Symoens, S.S. Hooper and P. Compère [Eds.], 1982, Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels, pp. 158-164.

Verhoeven, J.T.A., and W. Van Vierssen. 1978. Distribution and structure of communities dominated by Ruppia, Zostera, and Potamogeton species in the inland waters of "De Bol", Texel, The Netherlands. *Estuarine and Coastal Marine Science*, 6:417-428.

Waldron, K.W., E.A.H. Baydoun, C.T. Brett, 1989. Comparison of cell wall composition of tissues from the seagrasses Halophila and Halodule. *Aquatic Botany*, 35:209-218.

Walker, D.I. and A.J. McComb. 1990. Salinity response of the seagrass Amphibolis antarctica (Labill.) Sonder et Aschers.: An experimental validation of field results. *Aquatic Botany*, 36:359-366.

Whitehead, D. 1983. Wind Pollination: Some Ecological and Evolutionary Perspectives. In L. Real [ed.], Pollination Biology. Academic Press, pp. 93-110.

Wetzel, R.L., P.A. Penhale. 1981. Photosynthesis, light response and metabolism of submerged macrophyte communities in the lower Chesapeake Bay, Virginia. pp. 50-107 In R.L. Wetzel [ed.], Final Report. Structural and functional aspects of the ecology of submerged aquatic macrophyte communities in the lower Chesapeake Bay. Virginia Institute of Marine Science. Applied Marine Science Ocean Engineering Special Report, No. 267.

Wetzel, R.L., P.A. Penhale. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Tech. Soc. J.*, 17(2):22-31.

Wetzel, R.L., P.A. Penhale, K.L. Webb. 1981. Plant community structure, elemental composition and sediment characteristics of a temperate, estuarine seagrass ecosystem; Vacluse Shores, lower Chesapeake Bay, Virginia. pp. 9-49, In R.L. Wetzel [ed.], Final Report. Structural and functional aspects of the ecology of submerged aquatic macrophyte communities in the lower Chesapeake Bay. Virginia Institute of Marine Science. Applied Marine Science Ocean Engineering Special Report, No. 267.

Zieman, Joseph C., R. Orth, R.C. Phillips, A. Thorhaug. 1984. The effects of oil on seagrass ecosystems. pp. 37-64. In J.C. Cairns Jr. & A.L. Buikema Jr. [eds.], Restoration of Habitats Impacted By Oil Spills. Butterworth Publishers, Boston.

Appendix 1. Pollination of Ruppia maritima L. from Chesapeake Bay in a flow-through mesocosm system.

Data from Pollination study:

Treatment 1 (T1) = 1 Reproductive shoot, 1 Flower.

Treatment 2 (T2) = 1 Reproductive shoot, 2 Flowers.

Treatment 3 (T3) = 2 Reproductive shoots, 1 Flower, Same Ramet.

Treatment 4 (T4) = 2 Reproductive shoots, 1 Flower, Same Ramets.

Collections for T1, T2, T3, at Goodwin Islands.

Collections for T4, at Goodwin Islands and Sandy Point (York River).

Data from Peduncle growth study:

Lists chamber and measurements (cm) for the downward growth of inflorescence peduncles.

N/A indicates an unused chamber

Appendix 1.0. Pollination data. Number of seeds produced for each treatment.

Seeds T1	Seeds T2	Seeds T3	Seeds T4
2	2	5	5
2	2	1	3
3	5	3	3
5	1	3	4
1	0	4	4
4	3	1	6
0	1	3	2
2	4	2	5
6	1	3	5
4	4	2	2
1	4	2	5
1	0	4	5
2	3	8	3
3	1	5	7
1	5	4	6
3	6	4	3
1	5	4	5
2	1	8	2
2	2	4	2
4	3	4	3
5	3	4	0
0	4	3	2
3	2	3	3
0	6	3	3
2	0	2	4
6	2	5	5
5	3	2	2
1	3	3	1
5	7	3	0
2	4	5	0
5	2	2	6
4	0	3	3
1	2	7	0
3	5	0	2
3	0	3	4
5	1	4	0
3	4	3	4
6	4	3	3
2	1	2	N/A
N/A	0	2	N/A
N/A	0	2	N/A
N/A	0	1	N/A
N/A	3	4	N/A

Appendix 1.0. Pollination data, continued

Seeds T1	Seeds T2	Seeds T3	Seeds T4
N/A	4	4	N/A
N/A	4	3	N/A
N/A	0	3	N/A
N/A	5	1	N/A
N/A	0	2	N/A
N/A	1	3	N/A
N/A	1	2	N/A
N/A	5	5	N/A
N/A	2	5	N/A
N/A	1	3	N/A
N/A	N/A	4	N/A
N/A	N/A	1	N/A
N/A	N/A	1	N/A
N/A	N/A	1	N/A
N/A	N/A	1	N/A
N/A	N/A	2	N/A
N/A	N/A	2	N/A
N/A	N/A	1	N/A
N/A	5	3	N/A
N/A	1	0	N/A
N/A	4	1	N/A
N/A	1	3	N/A
N/A	0	2	N/A
N/A	5	1	N/A
N/A	2	5	N/A

Appendix 1.1. Peduncle data. The downward growth measurements (cm) of peduncles is listed for 81 inflorescences using the pollination chambers.

Chamber	Peduncle Length
A1	2
A2	1.4
A3	1.7
A4	1.1
A5	1.7
A6	0.9
A7	0
A8	1
A9	0.85
B1	0.95
B2	0.97
B3	1.3
B4	1.6
B5	1.4
B6	0.94
B7	0.96
B8	1.5
B9	1.7
C1	2
C2	2.3
C3	1.4
C4	1
C5	0.98
C6	0.97
C7	1.6
C8	1.1
C9	1.6
D1	0.98
D2	1.3
D3	2.3
D4	0.97
D5	0.96
D6	1.7
D7	1.1
D8	1.2
D9	0.94
E1	0.92
E2	1.5
E3	1
E4	1
E5	1.3

Appendix 1.1. Peduncle data, continued.

F4	0.95
F5	0.99
F6	1.5
F7	1
F8	1.9
F9	0.97
G1	2.3
G2	1.9
G3	1.7
G4	0.99
G5	0.97
G6	1.1
G7	1.5
G8	1.4
G9	0.96
H1	0.93
H2	0.85
H3	1.6
H4	1.9
H5	1.4
H6	0.98
H7	0.99
H8	1.6
H9	2
I1	1.3
I2	1.4
I3	1
I4	0.96
I5	0.99
I6	1.4
I7	1.5
I8	1
I9	1.1
E6	0.95
E7	2
E8	0.98
E9	0.97
F1	1.6
F2	1.5
F3	1.2
Mean length	1.29 cm

Appendix 2. Colonization and seasonal succession of Ruppia maritima and Zostera marina on experimental plots at Goodwin Islands, Chesapeake Bay.

Site 1 = North side of Goodwin Islands (York River).

Site 2 = East side of Goodwin Islands (Bay).

Appendix 2.1. Colonization data, Site 1, April 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Apr-92	5	0	0	0	0	0	0	0
25	Apr-92	5	0	0	0	0	0	0	0
35	Apr-92	5	0	0	0	0	0	0	0
45	Apr-92	50	0	0	4	0	1	0	0
55	Apr-92	60	1	0	0	0	0	0	0
65	Apr-92	50	50	0	0	0	0	0	0
80	Apr-92	60	40	0	1	0	1	0	0
95	Apr-92	30	30	0	5	0	1	0	0
110	Apr-92	40	40	0	0	0	0	0	0
125	Apr-92	20	40	0	3	0	1	0	0
140	Apr-92	30	40	0	2	0	1	0	0
155	Apr-92	20	50	0	1	0	1	0	0
170	Apr-92	5	80	0	0	0	0	0	0
185	Apr-92	1	60	0	0	0	0	0	0
200	Apr-92	0	50	0	3	0	1	0	0
			Totals >	0	19	0	7	0	0

Appendix 2.2. Colonization data, Site 1, May 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	May-92	80	20	10	0	1	0	0	0
25	May-92	80	20	7	0	1	0	0	0
35	May-92	80	10	8	0	1	0	0	0
45	May-92	70	5	7	0	1	0	3	0
55	May-92	90	10	50	0	3	0	0	0
65	May-92	50	50	32	0	1	0	0	0
80	May-92	5	90	0	3	0	1	0	0
95	May-92	0	100	0	9	0	2	0	0
110	May-92	5	90	1	1	1	1	0	0
125	May-92	0	100	0	5	0	2	0	0
140	May-92	0	100	0	4	0	1	0	0
155	May-92	0	80	0	4	0	1	0	0
170	May-92	0	60	0	1	0	1	0	0
185	May-92	0	60	0	4	0	1	0	0
200	May-92	0	60	0	3	0	1	0	0
			Totals >	115	34	9	11	3	0

Appendix 2.3. Colonization data, Site 1, June 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Jun-92	100	0	14	0	1	0	0	0
25	Jun-92	100	0	10	0	2	0	1	0
35	Jun-92	100	0	12	0	1	0	0	0
45	Jun-92	85	15	9	6	1	1	3	0
55	Jun-92	90	5	61	1	3	1	0	0
65	Jun-92	65	10	55	3	1	1	0	0
80	Jun-92	10	60	6	6	1	1	0	0
95	Jun-92	0	90	8	15	1	3	0	0
110	Jun-92	10	80	8	4	1	1	0	0
125	Jun-92	0	85	0	12	0	3	0	0
140	Jun-92	0	85	0	8	0	2	0	0
155	Jun-92	0	85	0	6	0	1	0	0
170	Jun-92	0	85	0	4	0	1	0	0
185	Jun-92	0	85	0	9	0	3	0	0
200	Jun-92	0	85	0	5	0	1	0	0
			Totals >	183	79	12	19	4	0

Appendix 2.4. Colonization data, Site 1, July 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Jul-92	100	0	20	0	3	0	0	0
25	Jul-92	100	0	16	0	2	0	1	0
35	Jul-92	100	0	19	0	2	0	0	0
45	Jul-92	100	0	15	6	2	1	3	0
55	Jul-92	95	5	70	1	3	1	0	0
65	Jul-92	70	5	61	3	1	1	0	0
80	Jul-92	20	50	22	7	1	1	0	0
95	Jul-92	0	60	0	10	1	3	0	0
110	Jul-92	10	65	16	2	1	1	0	0
125	Jul-92	5	65	10	10	0	3	0	0
140	Jul-92	0	65	0	7	0	2	0	0
155	Jul-92	0	65	0	6	0	1	0	0
170	Jul-92	0	65	0	3	0	1	0	0
185	Jul-92	0	65	0	10	0	3	0	0
200	Jul-92	0	65	0	5	0	1	0	0
			Totals >	249	70	16	19	4	0

Appendix 2.5. Colonization data, Site 1, August 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Aug-92	90	0	80	0	5	0	0	0
25	Aug-92	90	0	87	0	6	0	1	0
35	Aug-92	90	0	90	0	6	0	0	0
45	Aug-92	90	10	79	0	4	1	3	0
55	Aug-92	90	5	81	0	5	1	0	0
65	Aug-92	75	5	58	3	3	1	0	0
80	Aug-92	25	50	22	8	2	1	0	0
95	Aug-92	10	60	15	12	1	3	0	0
110	Aug-92	10	85	16	7	2	1	0	0
125	Aug-92	10	85	18	18	1	3	0	0
140	Aug-92	10	85	18	9	2	2	0	0
155	Aug-92	10	85	20	13	3	1	0	0
170	Aug-92	10	85	14	12	2	1	0	0
185	Aug-92	10	85	19	15	2	3	0	0
200	Aug-92	10	90	13	22	1	1	0	0
			Totals >	630	119	45	19	4	0

Appendix 2.6. Colonization data, Site 1, September 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Sep-92	70	30	50	0	5	0	0	0
25	Sep-92	70	30	48	0	6	0	1	0
35	Sep-92	70	30	60	0	6	0	0	0
45	Sep-92	70	30	27	0	4	1	3	0
55	Sep-92	70	30	59	0	5	1	0	0
65	Sep-92	75	25	20	2	3	1	0	0
80	Sep-92	0	100	2	6	2	1	0	0
95	Sep-92	15	85	20	13	1	3	0	0
110	Sep-92	20	80	21	7	2	1	0	0
125	Sep-92	25	75	25	17	1	3	0	0
140	Sep-92	20	80	21	9	2	2	0	0
155	Sep-92	30	70	40	14	3	1	0	0
170	Sep-92	30	70	35	12	2	1	0	0
185	Sep-92	40	60	37	16	2	3	0	0
200	Sep-92	50	50	39	20	1	1	0	0
			Totals >	504	116	45	19	4	0

Appendix 2.7. Colonization data, Site 1, October 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Oct-92	65	35	60	0	5	0	0	0
25	Oct-92	65	35	55	0	6	0	1	0
35	Oct-92	65	35	61	0	6	0	0	0
45	Oct-92	65	35	40	0	4	1	3	0
55	Oct-92	65	35	67	0	5	1	0	0
65	Oct-92	65	35	35	2	3	1	0	0
80	Oct-92	10	90	6	6	2	1	0	0
95	Oct-92	10	90	32	13	1	3	0	0
110	Oct-92	10	90	36	7	2	1	0	0
125	Oct-92	10	90	28	17	1	3	0	0
140	Oct-92	10	90	32	9	2	2	0	0
155	Oct-92	20	80	50	14	3	1	0	0
170	Oct-92	20	80	36	12	2	1	0	0
185	Oct-92	20	80	43	16	2	3	0	0
200	Oct-92	20	80	45	20	2	1	0	0
			Totals >	626	116	46	19	4	0

Appendix 2.8. Colonization data, Site 1, March 1993 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.
15	Mar-93	20	30	45	55	5	4	0	0
25	Mar-93	20	30	45	55	4	7	2	0
35	Mar-93	20	30	45	55	6	6	0	0
45	Mar-93	20	25	45	50	4	2	1	0
55	Mar-93	20	25	45	50	5	3	1	0
65	Mar-93	15	55	39	74	3	4	0	0
80	Mar-93	5	60	22	77	3	10	0	0
95	Mar-93	5	60	22	77	2	8	1	0
110	Mar-93	5	60	22	77	3	9	0	0
125	Mar-93	5	60	22	77	3	10	0	1
140	Mar-93	10	60	32	77	4	7	0	0
155	Mar-93	10	60	32	77	4	10	0	0
170	Mar-93	10	60	32	77	3	8	0	1
185	Mar-93	10	60	32	77	4	10	0	0
200	Mar-93	10	60	32	77	4	9	0	3
			Totals >	512	1032	57	107	5	5

Appendix 2.9. Colonization data, Site 2, April 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Apr-92	40	5	0	0	0	0	0	0	0
24	Apr-92	20	5	0	0	0	0	0	0	0
40	Apr-92	30	30	0	0	0	0	0	0	0
55	Apr-92	20	20	0	0	0	0	0	0	0
70	Apr-92	25	25	0	0	0	0	0	0	0
85	Apr-92	25	25	0	0	0	0	0	0	0
100	Apr-92	50	20	0	0	0	0	0	0	0
115A	Apr-92	40	20	0	0	0	0	0	0	0
115B	Apr-92	40	20	0	0	0	0	0	0	0
120A	Apr-92	5	5	0	0	0	0	0	0	0
120B	Apr-92	5	5	0	0	0	0	0	0	0
150A	Apr-92	0	70	0	0	0	0	0	0	0
150B	Apr-92	0	70	0	0	0	0	0	0	0
190A	Apr-92	0	70	0	0	0	0	0	0	0
190B	Apr-92	0	70	0	0	0	0	0	0	0
			Totals >	0	0	0	0	0	0	0

Appendix 2.10. Colonization data, Site 2, May 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	May-92	0	100	50	12	7	3	0	0	0
24	May-92	0	100	100	20	10	5	0	0	0
40	May-92	5	95	250	25	16	5	0	0	0
55	May-92	0	100	300	30	17	6	0	0	0
70	May-92	70	30	750	25	27	5	0	0	0
85	May-92	60	40	700	10	26	3	0	0	0
100	May-92	30	30	50	40	7	6	0	0	0
115A	May-92	5	95	200	5	14	2	0	0	0
115B	May-92	5	95	300	10	17	3	0	0	0
120A	May-92	10	90	350	10	19	3	0	0	0
120B	May-92	10	90	350	10	19	3	0	0	0
150A	May-92	5	90	7	15	1	3	0	0	0
150B	May-92	5	90	300	10	17	2	0	0	0
190A	May-92	0	95	100	80	2	9	0	0	0
190B	May-92	0	95	80	80	2	9	0	0	0
			Totals >	3887	382	201	67	0	0	0

Appendix 2.11. Colonization data, Site 2, June 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Jun-92	5	45	60	12	7	4	0	0	0
24	Jun-92	50	45	110	20	11	5	0	0	0
40	Jun-92	60	40	270	25	16	5	0	0	0
55	Jun-92	20	50	310	30	18	6	0	0	0
70	Jun-92	80	10	720	25	28	6	0	0	0
85	Jun-92	90	10	680	10	26	3	0	0	0
100	Jun-92	40	60	81	40	8	6	0	0	0
115A	Jun-92	5	65	217	5	14	2	0	0	0
115B	Jun-92	5	65	320	10	17	3	0	0	0
120A	Jun-92	10	80	382	10	19	3	0	0	0
120B	Jun-92	10	80	412	10	19	3	0	0	0
150A	Jun-92	5	90	50	15	2	3	0	0	0
150B	Jun-92	5	90	350	10	18	2	0	0	0
190A	Jun-92	0	90	100	80	3	9	0	0	0
190B	Jun-92	0	90	90	80	3	9	0	0	0
			Totals >	4152	382	209	69	0	0	0

Appendix 2.12. Colonization data, Site 2, July 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Jul-92	10	0	100	2	8	4	0	0	0
24	Jul-92	100	0	300	5	11	5	0	0	0
40	Jul-92	100	0	350	0	16	5	0	0	0
55	Jul-92	90	0	350	4	18	6	0	0	0
70	Jul-92	80	10	700	2	28	6	0	0	1
85	Jul-92	90	10	650	5	26	3	0	0	0
100	Jul-92	10	90	100	40	10	6	0	0	0
115A	Jul-92	5	95	200	10	14	2	0	0	1
115B	Jul-92	5	95	250	20	17	3	0	0	0
120A	Jul-92	5	95	300	10	19	3	0	0	0
120B	Jul-92	5	95	312	10	19	3	0	0	0
150A	Jul-92	0	100	124	15	4	3	0	0	0
150B	Jul-92	0	100	340	10	18	2	0	0	0
190A	Jul-92	0	70	92	80	3	9	0	0	3
190B	Jul-92	0	70	90	80	3	9	0	0	0
			Totals >	4258	293	214	69	0	0	5

Appendix 2.13. Colonization data, Site 2, August 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Aug-92	75	0	160	0	9	4	0	0	0
24	Aug-92	75	0	295	1	11	5	0	0	0
40	Aug-92	80	0	340	0	16	5	0	0	0
55	Aug-92	100	0	325	1	18	6	0	0	0
70	Aug-92	85	10	681	2	28	6	0	0	3
85	Aug-92	90	10	643	1	26	3	0	0	0
100	Aug-92	50	30	140	10	10	6	0	0	0
115A	Aug-92	25	25	281	5	14	2	0	0	0
115B	Aug-92	25	25	290	6	18	3	0	0	1
120A	Aug-92	10	20	320	7	19	3	0	0	0
120B	Aug-92	10	20	309	4	19	3	0	0	0
150A	Aug-92	0	20	140	9	4	3	0	0	0
150B	Aug-92	0	20	350	7	18	2	0	0	1
190A	Aug-92	0	25	79	3	3	9	0	0	0
190B	Aug-92	0	25	80	5	3	9	0	0	0
			Totals >	4433	61	216	69	0	0	5

Appendix 2.14. Colonization data, Site 2, September 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Sep-92	90	0	165	0	9	4	0	0	0
24	Sep-92	80	0	280	0	11	5	0	0	0
40	Sep-92	80	0	342	0	16	5	0	0	0
55	Sep-92	90	0	658	0	19	6	0	0	0
70	Sep-92	80	0	701	0	31	6	0	0	2
85	Sep-92	80	0	650	0	26	3	0	0	0
100	Sep-92	50	0	150	0	10	6	0	0	1
115A	Sep-92	20	0	190	0	14	2	0	0	0
115B	Sep-92	20	0	185	0	18	3	0	0	0
120A	Sep-92	10	0	250	0	19	3	0	0	0
120B	Sep-92	10	0	237	0	19	3	0	0	0
150A	Sep-92	0	5	0	10	3	3	0	0	0
150B	Sep-92	0	5	0	13	10	1	0	0	0
190A	Sep-92	0	5	0	20	3	6	0	0	0
190B	Sep-92	0	5	0	18	3	7	0	0	0
			Totals >	3808	61	211	63	0	0	3

Appendix 2.15. Colonization data, Site 2, October 1992 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Oct-92	90	0	159	0	9	4	0	0	0
24	Oct-92	80	0	275	0	11	5	0	0	0
40	Oct-92	80	0	330	0	16	5	0	0	0
55	Oct-92	90	0	612	0	19	6	0	0	0
70	Oct-92	80	10	659	5	31	6	0	0	0
85	Oct-92	80	10	584	4	26	3	0	0	0
100	Oct-92	50	5	100	0	10	6	0	0	0
115A	Oct-92	20	5	154	0	14	2	0	0	0
115B	Oct-92	20	5	145	0	18	3	0	0	0
120A	Oct-92	10	20	198	7	19	3	0	0	0
120B	Oct-92	10	20	230	9	19	3	0	1	0
150A	Oct-92	0	10	0	15	3	3	0	1	0
150B	Oct-92	0	10	0	16	10	1	0	0	0
190A	Oct-92	0	10	0	19	3	6	0	0	0
190B	Oct-92	0	10	0	18	3	7	0	0	0
			Totals >	3446	93	211	63	0	2	0

Appendix 2.16. Colonization data, Site 2, March 1993 (R. = Ruppia, Z. = Zostera, S. = Shoots, Rh. = Rhizomes, D = Seedlings, Rep. = Ruppia Reproductive Shoots)

Dist	Date	% R.	% Z.	R.S.	Z.S.	R.Rh.	Z.Rh.	R.D.	Z.D.	Rep.
10	Mar-93	10	10	11	12	5	3	0	0	0
24	Mar-93	10	10	13	20	1	4	1	0	0
40	Mar-93	15	25	20	25	1	5	0	0	0
55	Mar-93	5	20	6	30	3	6	1	0	0
70	Mar-93	10	20	14	25	4	5	0	0	0
85	Mar-93	10	15	17	10	4	3	0	0	0
100	Mar-93	5	15	9	40	3	6	0	0	0
115A	Mar-93	5	20	15	20	1	2	0	0	0
115B	Mar-93	5	20	20	10	5	1	0	0	0
120A	Mar-93	5	15	0	2	0	1	0	0	0
120B	Mar-93	5	15	0	4	0	2	0	0	0
150A	Mar-93	0	65	0	3	0	1	0	0	0
150B	Mar-93	0	65	0	11	0	3	0	0	0
190A	Mar-93	0	65	0	0	0	1	0	0	0
190B	Mar-93	0	65	0	5	0	1	0	0	0
			Totals >	125	217	27	44	2	0	0

Appendix 3. Seed reserve data from Corratoman, Rappahannock, and Piankatank rivers, and Goodwin Islands (York River site and Bay site).

For each site there are two tables:

- One for depth and percent cover.
- One for seed data.

Appendix 3.0.0. Depth and percent cover data for Corratoman River

Dist. (m)	11 Jun 91 Depth	26 Oct 91 Depth	9 Jun 92 Depth	11 Jun 91 Zostera	26 Oct 91 Zostera	9 Jun 92 Zostera	11 Jun 91 Ruppia	26 Oct 91 Ruppia	9 Jun 92 Ruppia
0	20	0	20	0	0	0	0	0	0
10	26	75	27	0	0	0	0	0	0
20	28	78	30	0	0	0	50	0	0
30	34	78	36	0	0	0	0	0	0
40	35	80	40	0	0	0	70	0	0
50	39	80	37	0	0	0	40	0	0
60	44	80	40	0	0	0	90	30	30
70	48	78	40	0	0	0	0	100	100
80	52	76	50	0	0	0	0	100	100
90	55	81	53	0	0	0	5	50	50
100	55	81	55	0	0	0	50	0	0
110	62	78	58	0	0	0	0	0	0
120	67	81	60	0	0	0	50	0	0
130	69	124	62	0	0	0	50	0	0
140	72	145	66	0	0	0	100	0	0
150	78	150	69	0	0	0	100	0	0
160	83	151	75	0	0	0	100	0	0
180	90	160	95	0	0	0	100	0	0
190	98	163	95	0	0	0	100	0	0
200	99	163	100	0	0	0	100	0	0

Appendix 3.0.1. Seed reserve data for Corratoman River. Complete seeds, Fragments, and Viable seeds

11 Jun 91 Code (meters)	11 Jun 91Comp.	11 Jun 91Frag	11 Jun 91Viab.
30	0	3	0
45	0	0	0
60	1	15	1
75	0	18	0
100	0	16	0
120	0	27	0
140	0	24	0
160	2	15	2
180	0	5	0
26 Oct 91 Code (meters)	26 Oct 91 Com	26 Oct 91 Fr.	26 Oct 91 Via.
10	8	12	8
30	1	7	1
50	17	15	17
70	5	25	5
90	5	8	5
110	8	13	8
130	5	11	5
150	5	13	5
170	4	17	4
190	2	5	2
9 Jun 92 Code (meters)	9 Jun 92 Com	9 Jun 92 Frag	9 Jun 92 Via.
10	0	8	0
30	0	4	0
50	1	7	1
70	0	10	0
90	0	18	0
110	0	2	0
130	0	7	0
150	0	1	0
170	0	4	0
190	0	1	0
210	0	6	0

Appendix 3.1.0. Depth and percent cover data for Rappahannock River

Dist. (m)	11 Jun 91 Depth	26 Oct 91 Depth	9 Jun 92 Depth	11 Jun 91 Zostera	26 Oct 91 Zostera	9 Jun 92 Zostera	11 Jun 91 Ruppia	26 Oct 91 Ruppia	9 Jun 92 Ruppia
10	61	74.5	38	0	0	0	80	0	70
20	65	78	40	0	0	0	100	70	90
30	70	84	48	0	0	0	100	100	95
40	75	88	50	0	0	0	100	100	90
50	78	91	53	0	0	0	100	100	95
60	82	95	54	0	0	0	100	100	95
70	80	99	58	0	0	0	100	90	80
80	90	111	66	0	0	0	100	80	95
90	90	106	70	0	0	0	100	80	100
100	95	109	69	0	0	0	100	70	100
110	96	115	70	0	0	0	100	90	80
120	98	116	70	0	0	0	60	70	85
130	100	134	80	0	0	0	50	50	40
140	106	125	83	0	0	0	90	30	5
150	117	137	87	0	0	0	50	10	1
160	122	137	95	0	0	0	20	0	1
170	130	133	106	0	0	0	0	0	1
180	140	183	120	0	0	0	0	0	0
190	N/A	200	N/A	N/A	0	N/A	N/A	0	N/A
200	N/A	210	N/A	N/A	0	N/A	N/A	0	N/A

Appendix 3.1.1. Seed reserve data for Rappahannok River. Complete seeds, Fragments, and Viable seeds

11 Jun 91 Code (meters)	11 Jun 91Comp.	11 Jun 91Frag	11 Jun 91Viab.
20	2	39	2
20	2	20	2
40	1	22	1
40	1	17	1
60	0	7	0
60	0	4	0
80	2	5	2
80	0	6	0
100	0	2	0
100	2	12	2
120	0	2	0
120	0	2	0
140	1	4	1
140	0	3	0
150	0	7	0
150	0	2	0
160	0	4	0
160	0	2	0

26 Oct 91 Code (meters)	26 Oct 91 Com	26 Oct 91 Fr.	26 Oct 91 Via.
20	2	21	2
20	3	14	3
40	4	15	4
40	3	11	3
60	2	3	2
60	1	5	1
80	0	3	0
80	1	1	1
100	0	0	0
100	0	4	0
120	1	5	1
120	2	0	2

Appendix 3.1.1. Continued

26 Oct 91 Code (meters)	26 Oct 91 Com	26 Oct 91 Fr.	26 Oct 91 Via.
140	0	2	0
140	1	3	1
160	0	1	0
160	0	1	0
180	0	1	0
180	1	2	1
200	0	0	0
200	0	0	0

09 Jun 92 Code (meters)	9 Jun 92 Com	9 Jun 92 Frag	9 Jun 92 Via.
10	0	4	0
10	0	0	0
30	0	9	0
50	1	10	1
70	2	10	2
90	0	7	0
90	0	4	0
90	1	7	1
110	0	3	0
110	0	2	0
130	0	3	0
130	0	2	0
150	0	0	0
150	0	0	0
170	0	1	0
170	0	0	0
190	1	10	1
190	0	2	0

Appendix 3.2.0. Depth and percent cover data for Piankatank River

Dist. (m)	26 May 91 Depth	27 Oct 91 Depth	8 Jun 92 Depth	26 May 91 Zostera	27 Oct 91 Zostera	8 Jun 92 Zostera	26 May 91 Ruppia	27 Oct 91 Ruppia	8 Jun 92 Ruppia
0	36	10	45	0	0	0	0	0	90
10	57	59	48	0	0	0	95	0	90
20	57	73	52	0	0	0	20	10	90
30	64	77	54	0	0	0	5	20	90
40	67	78	53	0	0	0	60	20	100
50	64	82	49	0	0	0	40	5	70
60	66	80	50	0	0	0	80	20	70
70	63	64	50	0	0	1	70	10	30
80	64	90	54	0	0	0	20	5	20
90	70	88	60	0	0	5	90	0	10
100	70	93	65	0	0	1	90	0	10
110	69	93	60	0	0	20	90	5	30
120	68	96	62	0	0	5	50	0	20
130	71	96	69	0	0	0	90	0	60
140	74	95	66	0	0	5	0	0	60
150	75	96	70	0	0	20	10	0	20
160	78	98	68	0	0	45	5	0	45
170	79	96	65	30	0	35	30	0	35
180	73	100	64	30	0	70	30	0	20
190	83	100	58	25	0	70	0	0	20
200	70	103	59	20	0	40	20	0	10
210	73	N/A	56	40	N/A	40	40	N/A	40
220	62	N/A	55	10	N/A	40	30	N/A	5
230	69	N/A	79	0	N/A	80	30	N/A	10
240	88	N/A	120	50	N/A	100	50	N/A	0
250	125	N/A	134	100	N/A	100	0	N/A	0
260	140	N/A	150	100	N/A	85	0	N/A	5
267	148	N/A	156	100	N/A	1	0	N/A	1
270	156	N/A	N/A	10	N/A	N/A	0	N/A	N/A
275	164	N/A	N/A	0	N/A	N/A	0	N/A	N/A

Appendix 3.2.1. Seed reserve data for Piankatank River. Complete seeds, Fragments, and Viable seeds

26 May 91 Code (meters)	26 May 91 Comp.	26 May 91 Frag	26 May 91 Viab.
10	0	2	0
30	1	4	1
40	0	11	0
60	2	0	2
80	0	2	0
110	1	3	1
125	0	0	0
140	0	4	0
160	0	0	0
180	0	0	0
210	0	1	0
220	0	1	0
260	0	3	0
260	0	1	0
280	0	0	0
27 Oct 91 Code (meters)	27 Oct 91 Com	27 Oct 91 Fr.	27 Oct 91 Via.
10	0	0	0
10	0	0	0
30	0	0	0
30	0	2	0
50	0	1	0
50	0	0	0
70	0	1	0
70	0	2	0
90	0	1	0
90	0	0	0
110	0	0	0
110	0	0	0
130	0	0	0
130	0	0	0
150	0	0	0
150	0	1	0

Appendix 3.2.1. Continued

27 Oct 91 Code (meters)	27 Oct 91 Com	27 Oct 91 Fr.	27 Oct 91 Via.
170	0	0	0
170	0	0	0
190	0	0	0
190	0	0	0
8 Jun 92 Code (meters)	8 Jun 92 Com	8 Jun 92 Frag	8 Jun 92 Via.
10	0	40	0
10	0	31	0
30	0	20	0
30	0	18	0
50	0	2	0
50	0	0	0
70	0	4	0
70	0	2	0
90	0	0	0
90	0	1	0
110	0	3	0
110	0	1	0
130	0	3	0
130	0	5	0
150	0	2	0
150	0	0	0
170	0	0	0
170	0	1	0
190	0	0	0
190	0	0	0
210	0	0	0
210	0	0	0
230	0	0	0
230	0	0	0
250	0	2	0
250	0	0	0
270	0	0	0
270	0	0	0

Appendix 3.3.0. Depth and percent cover data for Goodwin Islands, York River site.

Dist. (m)	2 Jul 91 Depth	21 Sep 91 Depth	7 Jul 92 Depth	2 Jul 91 Zostera	21 Sep 91 Zostera	7 Jul 92 Zostera	2 Jul 91 Ruppia	21 Sep 91 Ruppia	7 Jul 92 Ruppia
0	85	33	20	0	0	10	0	0	10
10	88	71	25	0	0	5	20	80	95
20	94	76	28	10	0	5	10	90	90
30	90	76	37	35	0	10	10	90	90
40	91	61	25	5	0	10	80	50	80
50	98	61	24	0	0	10	95	50	50
60	97	61	30	0	0	20	100	10	30
70	98.5	61	31	15	0	30	85	10	70
80	109	64	35	60	0	10	30	80	90
90	117	74	26	80	5	5	5	5	70
100	121	81	30	100	10	5	0	5	50
110	124	79	33	85	5	30	0	5	20
120	121	76	37	85	10	90	0	5	10
130	124	81	37	80	20	95	0	5	5
140	134	79	39	85	40	0	0	0	0
150	130	81	40	75	40	5	0	0	5
160	130	84	40	55	40	100	0	0	0
170	131	84	43	50	40	100	0	0	0
180	133	86	45	20	50	50	0	0	0
190	137	89	30	15	50	0	0	0	0
200	140	94	35	15	40	5	0	0	0

Appendix 3.3.1. Seed reserve data for Goodwin Islands, York River site. Complete seeds, Fragments, and Viable seeds

2 Jul 91 Code (meters)	2 Jul 91 Comp.	2 Jul 91 Frag	2 Jul 91 Viab.
10	1	2	1
10	0	1	0
30	1	0	1
30	0	0	0
50	0	3	0
50	0	5	0
70	0	1	0
70	0	1	0
90	0	1	0
90	0	0	0
110	0	0	0
110	0	0	0
130	0	1	0
130	0	0	0
150	0	0	0
150	0	0	0
170	0	0	0
170	0	1	0
180	0	0	0
190	0	0	0
21 Sep 91 Code (meters)	21 Sep 91 Com	21 Sep 91 Fr.	21 Sep 91 Via.
10	0	1	0
10	0	1	0
30	0	1	0
30	0	0	0
50	1	4	1
50	3	4	3
70	1	4	1
70	3	6	3
90	0	2	0
90	0	0	0
110	0	1	0

Appendix 3.3.1. Continued

21 Sep 91 Code (meters)	21 Sep 91 Com	21 Sep 91 Fr.	21 Sep 91 Via.
110	0	0	0
130	0	0	0
130	0	0	0
150	0	0	0
150	0	0	0
170	0	0	0
170	0	0	0
190	0	1	0
190	0	0	0

7 Jul 92 Code (meters)	7 Jul 92 Com	7 Jul 92 Frag	7 Jul 92 Via.
0	0	2	0
10	1	1	1
20	1	0	1
30	0	1	0
40	0	3	0
50	0	1	0
60	0	1	0
70	0	0	0
80	2	3	2
90	0	0	0
100	0	0	0
110	0	0	0
120	0	0	0
130	0	0	0
140	0	0	0
150	0	0	0
160	0	0	0
170	0	0	0
180	0	0	0
190	0	0	0
200	0	0	0

Appendix 3.4.0. Depth and percent cover data for Goodwin Islands, Bay site.

Dist. (m)	2 Jul 91 Depth	21 Sep 91 Depth	7 Jul 92 Depth	2 Jul 91 Zostera	21 Sep 91 Zostera	7 Jul 92 Zostera	2 Jul 91 Ruppia	21 Sep 91 Ruppia	7 Jul 92 Ruppia
0	71	30	0	0	0	0	0	0	0
10	84	48	13	0	0	0	5	90	10
20	89	58	16	0	0	0	30	60	100
30	95	64	20	0	0	0	60	60	95
40	99	66	22	0	0	0	50	20	100
50	101	69	27	0	0	0	90	30	90
60	105	71	27	0	0	0	80	40	95
70	105	72	29	0	0	10	50	60	80
80	110	76	31	0	0	10	70	80	90
90	111	79	42	0	0	60	60	80	35
100	112	79	51	0	0	90	70	100	10
110	113	79	50	0	0	95	70	90	5
120	117	84	56	0	0	95	60	80	5
130	118	84	60	0	0	100	60	70	0
140	118	89	61	0	5	100	10	50	0
150	118	89	65	40	5	100	40	45	0
160	117	89	61	20	0	100	40	90	0
170	118	86	70	10	0	80	60	100	0
180	121	89	67	30	10	100	30	70	0
190	121	94	70	50	5	70	20	80	0

Appendix 3.4.0. Depth and percent cover data for Goodwin Islands, Bay site.

Dist. (m)	2 Jul 91 Depth	21 Sep 91 Depth	7 Jul 92 Depth	2 Jul 91 Zostera	21 Sep 91 Zostera	7 Jul 92 Zostera	2 Jul 91 Ruppia	21 Sep 91 Ruppia	7 Jul 92 Ruppia
200	122	91	75	50	30	20	10	30	0
210	121	N/A	N/A	50	N/A	N/A	10	N/A	N/A
220	121	N/A	N/A	70	N/A	N/A	20	N/A	N/A
230	117	N/A	N/A	70	N/A	N/A	20	N/A	N/A
240	111	N/A	N/A	90	N/A	N/A	5	N/A	N/A
250	110	N/A	N/A	100	N/A	N/A	0	N/A	N/A
260	104	N/A	N/A	90	N/A	N/A	0	N/A	N/A
280	102	N/A	N/A	5	N/A	N/A	90	N/A	N/A
300	95	N/A	N/A	5	N/A	N/A	90	N/A	N/A
320	94	N/A	N/A	0	N/A	N/A	90	N/A	N/A
340	94	N/A	N/A	5	N/A	N/A	90	N/A	N/A
360	92	N/A	N/A	0	N/A	N/A	90	N/A	N/A
380	104	N/A	N/A	30	N/A	N/A	20	N/A	N/A
400	108	N/A	N/A	30	N/A	N/A	30	N/A	N/A

Appendix 3.4.1. Seed reserve data for Goodwin Islands, Bay site. Complete seeds, Fragments, and Viable seeds

2 Jul 91 Code (meters)	2 Jul 91 Comp.	2 Jul 91 Frag	2 Jul 91 Viab.
10	0	1	0
10	0	3	0
30	0	0	0
30	0	0	0
50	0	0	0
50	1	2	1
70	0	1	0
70	0	1	0
100	0	1	0
100	0	0	0
140	0	4	0
140	0	0	0
200	0	1	0
200	0	0	0
240	0	0	0
240	0	0	0
280	0	0	0
280	0	0	0
320	2	1	2
320	0	1	0
380	0	2	0
380	0	0	0
21 Sep 91 Code (meters)	21 Sep 91 Com	21 Sep 91 Fr.	21 Sep 91 Via.
10	0	1	0
10	0	1	0
30	1	3	1
30	1	3	1
50	0	1	0
50	0	0	0
70	0	0	0
70	0	1	0
90	0	0	0

Appendix 3.4.1. Continued

21 Sep 91 Code (meters)	21 Sep 91 Com	21 Sep 91 Fr.	21 Sep 91 Via.
90	0	0	0
110	0	0	0
110	1	0	1
130	0	1	0
130	1	3	1
150	0	0	0
150	0	0	0
170	0	1	0
170	0	0	0
190	0	0	0
190	0	1	0
7 Jul 92 Code (meters)	**7 Jul 92 Com**	**7 Jul 92 Frag**	**7 Jul 92 Via.**
0	0	1	0
10	0	0	0
20	0	0	0
30	0	1	0
40	0	0	0
50	0	4	0
60	1	0	1
70	0	0	0
80	0	2	0
90	0	0	0
100	0	3	0
110	0	0	0
120	0	1	0
130	0	4	0
140	0	0	0
150	0	0	0
160	0	0	0
170	1	0	1
180	0	3	0
190	0	0	0
200	0	0	0

Vita

I was born in New York City in 1963. After growing up in New York state, Florida, and Pennsylvania I attended Clark University in Worcester, Ma. I graduated in May, 1985 with a Bachelor of Arts with high honors in Biology. My honors research investigated population dynamics of Aedes triseriatus mosquitoes. I began studies at Virginia Tech in 1987 and graduated in 1990 with a Master of Science in Biology. My thesis title is "Phytoplankton Colonization and Seasonal Succession in New Experimental Ponds". My dissertation topic was born during field trips to the experimental ponds as I observed aquatic plants colonize the ponds by the soil seed bank. My subsequent discussions with Dr. Porter on the subject of aquatic plant pollination, dispersal, and colonization focused those ideas into this dissertation.