INTERACTIVE BIOLOGY OF TWO SEAGRASSES, *ZOSTERA MARINA* L. AND *ZOSTERA JAPONICA* ASCHERS. & GRAEBN.

by

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B.Sc., The University of British Columbia, 1978

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Botany)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

June 1989

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Date June 26 '89

ABSTRACT

The two seagrasses *Zostera marina* L. and *Zostera japonica* Aschers. and Graebn. coexist in an intertidal region of the south-west coast of British Columbia. At the Roberts Bank study area three vegetation zones were identified; a seaward monospecific zone of *Z. marina* cover, a zone of mixed *Z. marina* and *Z. japonica*, and a landward monospecific zone of *Z. japonica*. The study investigating possible interactions between the two species was undertaken in three parts. First, a descriptive component compared numerous morphological characters, phenological data, and the population dynamics for each species between monospecific and mixed populations using univariate and multivariate statistical techniques. For both species shoots in deeper intertidal waters tended to be longer and with greater biomass than shoots from shallower intertidal areas. The most pronounced difference was the suppression of lateral shoot development of *Z. japonica* under a *Z. marina* canopy. Second, transplants of monospecific adult patches indicated that vigorous lateral branching would proceed regardless of location on the intertidal gradient and confirmed that the suppression of *Z. japonica* growth was due to competition. Third, a manipulation experiment using artificial shoots to mimic shading under a *Z. marina* canopy did not directly indicate that the attenuation of light under a *Z. marina* canopy was the mechanism for suppression of *Z. japonica* population growth. The artificial shoots did not adequately mimic *Z. marina* shoots as a shading canopy. In addition the "patch" design of the manipulation experiment enhanced lateral branching while reducing shoot length. The results of the manipulation experiment were therefore considered in conjunction with the results of the descriptive study and the transplant experiments.

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ACKNOWLEDGMENTS

I would like to thank Dr. Paul G. Harrison for his guidance in developing the thesis research and for the financial assistance that he provided over the course of three years. I appreciate the flexibility of the Botany department headed by Dr. Anthony Glass, and the members of my advisory committee, Drs. Robert DeWreede and Roy Turkington, in allowing me to commence the masters program on a part-time basis and adjusting the course load accordingly.

I am greatly endebted to Cynthia Durance who tutored me in the practical aspects of seagrass field research. The field work could not have been successfully completed without the cheerful help of Farida Bishay, Patrick O'Hara and Eric Mueller. General ecological discussions with Lois Hollett driving to and from the field helped put "seagrass interactions" into a more complete perspective of seagrass community ecology.

I especially wish to thank my husband, Wayne Pledger, for his understanding and patience in my undertaking a career diversion into seagrass ecology. And finally I wish to acknowledge my three year-old son, Sean, who has come to accept that mommy is often very busy at school.

INTERACTIVE BIOLOGY OF TWO SEAGRASSES
ZOSTERA MARINA L. AND *ZOSTERA JAPONICA* ASCHERS. & GRAEBN.

1 INTRODUCTION

Temperate marine shores are characterized by zonation of vegetation and invertebrate fauna. Intertidal and subtidal plant and animal species are found to inhabit bands parallel to the shore or in patches within their "potential" habitats. The clearly visible demarcation of zones has led to the formation of hypotheses regarding the many possible forces structuring the distributional limits of the dominant members of each tidal community. Patterns of distribution have been related to the direct influence of the physical environment (Lewis, 1964; Dayton, 1971; Paine, 1979). The "potential" habitat along the land-water interface will be limited by environmental conditions along the gradient. Individuals of a species will be capable of surviving within a range of the tidal gradient only if they are able to tolerate the environmental conditions associated with the location. Environmental conditions such as the nature of substrate, angle of substrate surface, the force of wave action, and regularity of the tidal cycle may place limits on the potential range of a species. In particular the regularity of the tidal cycle and the ratio of emersion time to submersion time are aspects of the environment that are related to the degree of tolerance to desiccation and often demarcate regions beyond which survival of a species is not likely.

The actual upper limits of dominant species in marine intertidal systems is typically determined by stresses associated with physical conditions such as extensive temperature extremes associated with exposure resulting in desiccation (Dayton, 1971; Connell, 1972,1975), while the lower limit of a species' distribution is determined by biological interaction (Connell, 1961; Dayton, 1971; Paine, 1974). Competition, and predation are biological processes that may be the key in determining the ultimate community structure (Connell, 1971; Lubchenco, 1978; Menge, 1978; Underwood, 1985). But each of these biotic structuring forces is influenced by abiotic environmental conditions, disturbances, and heterogeneity of resources potentially modifying the ultimate outcome (Wiens, 1977).

On soft-sediment intertidal regions of the southern British Columbia coast the two marine angiosperms *Zostera marina* L. and *Zostera japonica* Aschers. and Graebn. co-occur. At Roberts Bank (see section 4) *Z. marina* occupies the more seaward region of the site and *Z. japonica* extends higher in the intertidal. There is, however, a relatively narrow band approximately 100 m in width in which the two species overlap. In this region of mixed vegetation *Z. japonica* occupies the understory under a canopy of *Z. marina*. The present distribution of these two seagrasses at this study site could be explained in at least three general ways: 1) as the result of the abiotic conditions that exist along the intertidal gradient, 2) as the result of an interaction between either of the two species with grazers, invertebrate fauna or between themselves or 3) as the result of a combination of these factors.

2 OBJECTIVES

The general objective of this study is to describe *Zostera marina* and *Zostera japonica* vegetation that occurs in three zones of the Roberts Bank sand flat, and to investigate the processes determining the observed zonation. The specific objectives of the study are:

1. to describe (a) population dynamics, (b) morphology, (c) phenology, and (d) biomass distribution of monospecific and mixed populations of *Zostera marina* and *Zostera japonica*, and to identify differences between the monospecific and mixed populations of each species,

2. to determine whether differences are due to abiotic conditions or species interactions,

3. to identify and test probable mechanisms of interspecific interaction between *Zostera marina* and *Zostera japonica*.

Each of these three objectives will be pursued in separate sections of this thesis (sections 5, 6, and 7, respectively) following an overview of theoretical considerations (section 3) and a description of the species, study sites and vegetation zones (section 4). Finally in section 8, an overview of the findings of this research will be presented.

3 THEORETICAL ASPECTS OF INTERSPECIFIC INTERACTION

3.1 Competition

Interspecific plant competition is the interaction between individuals of different species while acquiring adequate supplies of nutrients, light, water, and space. Increases in the population density of one species will lead to a decrease in the per capita growth rate and population density of the other species. The process of competition may be expressed by differential mortality of the competing organisms and be manifest at the level of the population but it is also possible that the stress imposed by competition will be expressed by differences in morphology or resource allocation within individuals. Plants may also respond to the presence of a neighbour with a variation in growth habit and size, photosynthetic rate and growth rate, and phenology (Sultan, 1987). Harper (1977) presented several cases of plasticity in plant size in response to density stress. Adjustments in branching patterns, leaf turnover rate and biomass allocation to reproduction have also been attributed to competitive success of some plant species (Bazzaz, 1984). Titus and Adams (1979) demonstrated how two coexisting submerged macrophytes compensated for the restrictions imposed by the other species through morphological variation and physiological modifications. Therefore interspecific interactions may result not in changing population numbers but in adjustments in morphological or physiological characters that may compensate for interactive stress (Harper, 1961; Donald, 1963).

When one individual consumes, removes or reduces the availability of a limited resource to another the competition is termed "exploitation" (Begon et al., 1986). The removal of limited supplies of water and nutrients from the substrate would be a form of exploitative competition. Hall (1974) demonstrated competitive interactions between the grass *Setaria anaps* and the legume

Desmodium intortum. The presence of *Setaria* severly reduced the growth of *Desmodium* which also showed signs of potassium deficiency. He concluded, after further tests, that both species were limited by a common pool of nutrients. Tilman's model of competitive interactions, based on the differential utilization of limited resources, could be used to describe the competitive interaction of these two species (Tilman, 1986; see section 3.4).

Interference competition (sensu Miller, 1967) refers to an active hindrance to access of the resource. Allelopathy (Miller, 1967; Rice, 1974, 1979) may be described as a form of interference. The resources are not removed but toxic substances introduced by one species to the substrate are thought to deter other organisms from establishing. Competition for light between plants involves the reduction of light beneath the canopy layer, a reduction in an essential and possibly limiting resource for green plants. Competing plants may be active in shoot elongation in order to place the primary photosynthetic organs into a better position, higher into the canopy. Vance (1984) considers the reduction of sunlight encountered by one plant because of shading by another to be a form of interference. Harper (1961) defines interference as "any change in the environment created by the proximity of individuals that may alter the growth rate or form of neighbouring individuals". This is a more general definition of competition that encompasses both exploitive and interference competition as those terms are used here.

Whether plants simply remove resources by consumption or actively interfere with resource availability is a philosophical argument. Plants do compete for resources often to the exclusion or at least to the detriment of one species. Implicit in the concept of competition is the existence of "winners" and "losers". The losers will be diminished in numbers and/or reduced in stature, if not excluded from the habitat completely. In contrast, Hunter and Aarssen (1988) contend that neighbouring plants may be competing for limiting resources and yet benefiting from the association simultaneously. The negative aspects of competitive interactions may be moderated by beneficial interactions such as: improving soil or microclimate, providing physical support, transfering nutrients, distracting or detering predators or parasites, reducing the impact of other competitors, encouraging beneficial rhizosphere components and attracting pollinators or dispersal agents. Although the losers may suffer a degree of population reduction or morphological modifications they may also benefit from association with the winner.

3.2 Measurement of plant interactions

The effects of interactions between plant species can be measured at the population level or at the level of the individual. Population parameters such as the immigration rate, population density and mortality rate are often used when investigating interspecific interactions. The outcome of competition for a single resource can be described using the Lotka-Volterra model (Lotka, 1925; Volterra, 1926). If the initial size of each population, their carrying capacities and intrinsic rates of increase are known the model will indicate which species is excluded or if a stable coexistence is possible.

Since interactions between individuals of the same or another species may manifest themselves in subtle plastic responses rather than a shift in the dynamics of the population, other experimental approaches have also been used. Experimental designs such as the additive and de Wit replacement series utilize a measure of relative yield either at a fixed density or a range of densities. The ratios of relative yield can then be used as indicators of competitive interaction or mutual enhancement (Harper, 1977; Fowler and Antonovics, 1981; McCreary et al., 1983). The relative yield of a species is calculated by dividing the yield of the species in mixture by the yield of the species in pure stand at the same density.

Since the relative yield total is a measure of biomass accumulated by each interacting component, it is a measure of plastic response. The use of discrete measures of morphological features in response to interaction is a more sensitive indicator of interaction than the aggregate measurements such as total biomass (McCreary et al., 1983).

The detailed measurement of morphological and phenological variation of interacting plants provides additional indicators of possible interactive mechanisms. Tilman (1987) suggested that for species to coexist stably, compromises must be made in physiological, morphological or behavioural traits. These compromises or apparent changes in the interacting plants provide direct clues as to the mechanisms involved. The mechanistic approach can then be used to predict the outcome of between-species interactions.

3.3 Coexistence

Two or more similar species are said to coexist when they have similar resource requirements and are found in close proximity to one another, sharing the same habitat. Several explanations have been proposed to explain how two similar species can coexist. Competing organisms limited by a single resource will co-occur for a short period of time before competitive interactions lead to exclusion (Miller, 1967; Diamond, 1978) or a modification in growth form or fecundity becomes evident. What appears to be coexistence of two species may be the period between initiation of competitive interaction and eventual exclusion of one competitor. The process of competition may be prolonged by unpredictable perturbations which open gaps in the habitat where space is limiting, allowing reestablishment of one of the competitors. Factors external to the competing organisms such as selective herbivory (predation) or unpredictable disturbance may reduce or even eliminate interspecific competition by significantly reducing the numbers of one species (Menge, 1979; Hunter and

Aarssen, 1988). In these situations, competition is in progress and the outcome of exclusion is delayed or obscured by the changing nature of the environment.

A second explanation for the coexistence of two similar species that are suited to the same habitat takes into account that they are likely to be competing for more than a single resource. The two similar species will also have similar requirements for a number of resources. Tilman (1986, 1987) describes differential resource utilization not as a separation of resource consumption in time or space but as a partitioning of the amount consumed by each species when a second limiting resource is involved. The two species must compete for at least two resources and they will coexist as long as one species is more limited by one resource and the other species is more limited by the other resource. A second stipulation is that each species must consume more of the resource that is more limiting to its own growth than the second limiting resource. The competing species will then appear to be sharing two limiting resources. This explanation implies an immediate response to competitive interaction not an evolutionary adaptation.

A third explanation suggests that in a stable environment with a limited supply of resources, co-occuring individuals may respond to competitive interactions with a subtle variation in resource utilization. The change in resources available due to the presence of a competitor results in plastic modifications of morphology, growth pattern, or phenology. This shift in habitat useage or temporary niche differentiation permits the coexistence of two similar species (Schoener, 1974). While the individuals of the species have modified their niche in response to the presence of another species, they may retain the ability to reestablish their fundamental niche in the absence of the competitor.

A fourth explanation involves the natural selection of individuals from competing populations for divergent resource requirements leading to a permanent differentiation of the fundamental niches of the competitors. The coexistence of the two species may then the result of competition in the past (Connell, 1980). The populations of coexisting species will have avoided competitive interactions through an evolutionary process of divergence in resource requirements (Schoener, 1974).

A fifth explanation suggests that although two similar species at present occur in a common habitat, they may have evolved separately the sets of characters that enable them to coexist. The two species may never have competed, but have responded to different and isolated forces of natural selection. When the two species do co-occur, such as in the introduction of a non-native species, their differences allow them to coexist.

3.4 Seagrass interactions

Interactions between seagrass species have been studied by Poiner (1984), Turner (1985), and Williams (1987). Poiner investigated the population dynamics of two tropical seagrasses, *Cymodocea* sp. and *Zostera capricorni* Ashers., and concluded that while physical factors may be limiting the distribution of one species, the presence of this species in turn limits the distribution of the other by some unknown mechanism. Competitive interactions between seagrasses has been mostly inferred in such studies. Turner (1985) proposed several possible mechanisms by which the seagrass *Phyllospadix scouleri* Hook preempts space from algal and invertebrate species. The list of possible mechanisms includes whiplash of blades, physical barriers that blades present to spores, shading, sand accumulation and allelopathy.

Williams (1987) alone has tested a possible mechanism for interspecific competition between two tropical seagrass species. In a Caribbean lagoon, Williams performed experimental manipulations to test for competition for light and sediment nutrients. Clear plastic strips that mimicked the size and density of the dominant seagrass species *Thalassia testudinum* Banks ex König were implanted in combination with and without time-release fertilizer stakes. The results indicated that the plastic canopy did not affect the growth rate of *Syringodium filiforme* Kützing leaves but the leaves achieved a greater length because they were protected from breakage by the larger artificial leaves. In this tropical system, however, belowground competition for nutrients was more important than competition among leaves for light.

An obvious mechanism by which terrestrial as well as aquatic plants interact is the aboveground shading of understory species. A second more difficult area to study is the belowground interactions where root systems may compete for space, water and nutrients. In marine systems preemption of substrate space and interference in colonization by another species have been documented for benthic algae and infauna (Lubchenco, 1978, 1986; Peterson, 1978; Paine, 1979; Backman, 1984). In contrast the provision of physical support and protection from either biotic or abiotic factors have been suggested as beneficial interactions between competitors (Williams, 1987; Hunter and Aarssen, 1988). In the seagrass ecosystem a limited supply of nutrients or light filtered through a canopy of taller plants or epiphytes may be the resource dimensions along which the plants compete (Orth, 1977; Wetzel and Neckles, 1986; Short, 1987). The limitation of available substrate or interference in seed germination and seedling establishment is another possible avenue of interspecific interaction between seagrasses.

In a temperate, soft-sediment seagrass ecosystem a possible mechanism of competitive interaction is through modification of light attenuation. Reduction of available light results in a decrease in shoot density in monospecific populations (Backman and Barilotti, 1976; Dennison and Alberte, 1982). This result suggests that the canopy cover formed by one species may also regulate the shoot density of an understory species. The possible advantage of maintaining longer leaf lengths under the canopy of another species has not been explored in a temperate system. The focus of this research is to determine whether competitive interactions are occurring between two seagrass species and test if a reduction in available light is the means by which the interaction occurs.

4 DESCRIPTION OF SPECIES, STUDY SITES, AND VEGETATION ZONES

4.1 Description of species

Zostera marina L. and *Zostera japonica* Aschers. & Graebn. are marine angiosperms that belong to the family Zosteraceae. As a group these plants are referred to as seagrasses. They occur in shallow coastal water, sometimes penetrating into brackish water habitats (den Hartog, 1967; Tomlinson, 1982; Phillips and Meñez, 1988). Seagrasses may form discrete patches of vegetation in newly colonized sites or continuous meadows in well established sites (Orth and Moore, 1981).

4.1.1 *Zostera marina*

Zostera marina is the larger of the two *Zostera* species found in British Columbia waters. Typically the plant has a perennial rhizome buried in sediments composed of sand and mud. A terminal shoot of three to eight strap-like leaves arises from the growing tip (Fig. 1a). New leaves are formed at the apical meristem nested within the leaf bundle. Youngest leaves are in the center of the bundle, with progressively older leaves on alternate sides. The length of leaves and hence the length of the shoot is a function of meristematic activity at the base of each leaf. The two or three innermost leaves demonstrate growth, whereas the outer older leaves, having achieved their maximum length for the given environmental conditions, are colonized by epiphytes or senesce and break off with wave action. Leaves are lost and new leaves are produced throughout the year.

Branches may arise from the terminal meristem at irregular intervals (Tomlinson, 1974). The new lateral shoot is initially enclosed within the bundle sheath of the terminal shoot. With continued development of new leaves and rhizome internode extension the two shoots become separated in space. The vegetative shoots that appear discrete above the sediments are connected by

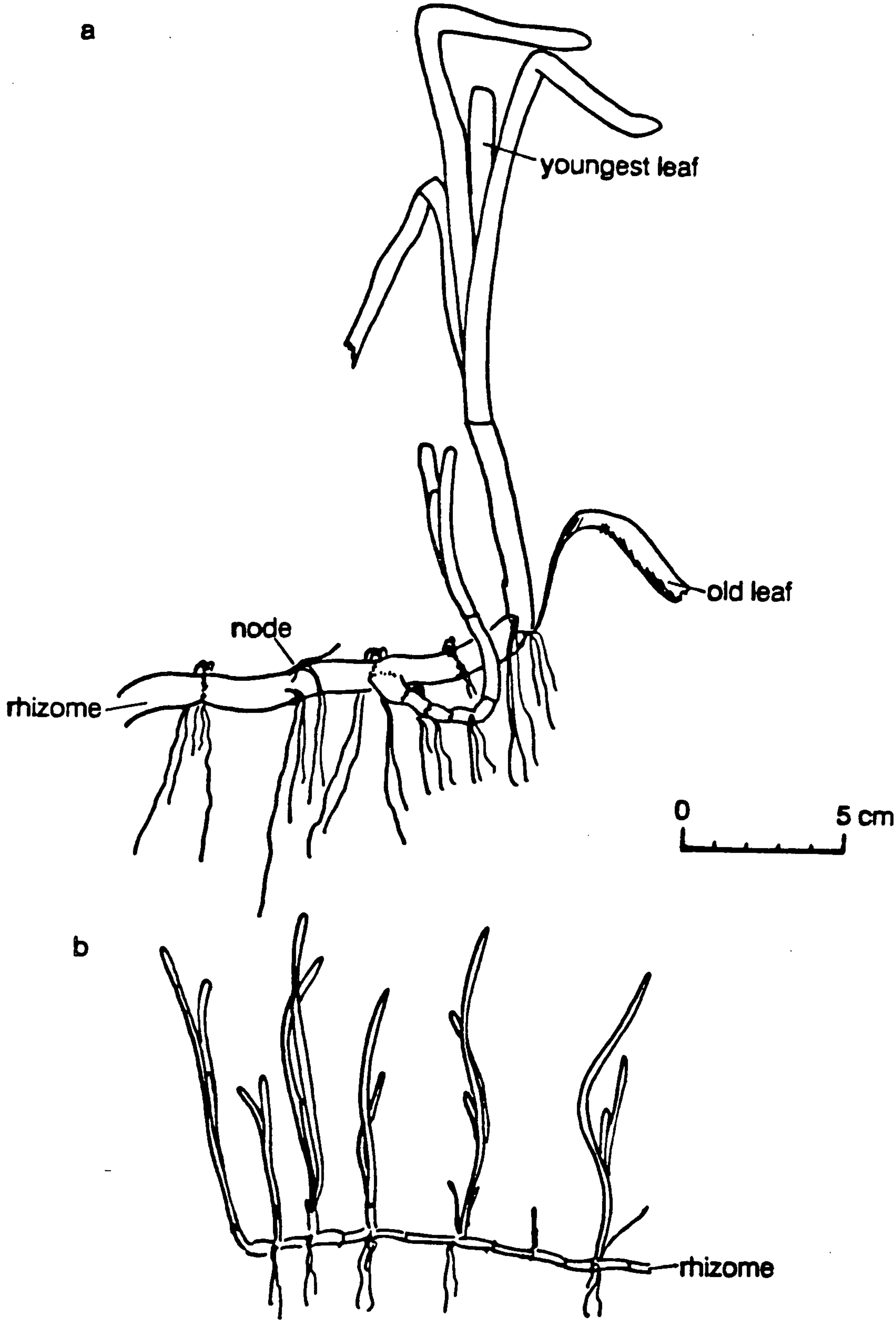

Fig. 1 Vegetative growth forms of *Zostera marina* (a) and *Zostera japonica* (b).

rhizome beneath the sediments, and hence are ramets of the same clone. As the plant "creeps" through the sediment connections between ramets eventually degenerate. A more complete description of *Z. marina* growth and morphology can be found in Setchell (1929), Arasaki (1950), and Tomlinson (1974).

Because *Zostera marina*, and seagrasses in general, have been identified as important structuring components of productive coastal ecosystems, their productivity and population dynamics have been extensively studied. McRoy (1970) in Alaska, Harrison (1979, 1982) in British Columbia, Phillips (1972) in Washington state, Kentula (1983) in Oregon, Sand-Jensen (1975) in Denmark, Nienhuis and de Bree (1977) in the Netherlands, Jacobs (1979) in France, and Aioi (1980) and Mukai et al. (1979) in Japan, provide a comprehensive description of *Z. marina* growth, phenology and productivity from various parts of the world.

Physiological and morphological differences characterize seagrasses in particular habitats. McMillan (1978) and McMillan and Phillips (1979) have investigated the variation in shoot morphology in response to controlled environments with standardized culture methods and diverse natural habitats. Morphological features of *Z. marina* showed seasonal patterns of phenotypic within-site variation as well as between-site variation. In addition changes in leaf width and chlorophyll content have been shown to correspond with environmental conditions such as temperature, light attenuation and salinity (McMillan, 1978; Dennison and Alberte, 1986). Transplant experiments performed by Phillips (1972) indicated that within a given location transplanted individuals will produce leaves that are typical of the indigenous plants. He concluded that phenotypic plasticity could account for variation in leaf characters. McMillan (1978) and Backman (1984) further established that populations of *Z. marina* have genetically different limits of plasticity for morphological features.

4.1.2 *Zostera japonica*

In contrast, very little research has been reported on *Zostera japonica*. In the literature *Z. japonica* has been referred to as *Z. nana*, *Z. americana*, and sometimes *Z. noltii*. Description of population dynamics, phenology, and growth form are included in the works of Miki (1933), Arasake (1950), Harrison (1979,1982), Bigley (1981) and Bigley and Harrison (1986).

Zostera japonica is a much smaller plant than *Z. marina*. Shoots consist of a bundle of 2-3 leaves, attaining an average length of 20 cm (Fig. 1b). Primarily an annual in the study habitat, *Z. japonica* germinates from seed in spring (March to May). The plant spreads through vegetative growth and extension of underground rhizome. Shoots are produced irregularly along the entire extent of rhizome. Many of the shoots flower in late summer (August to September) before senescing (Harrison,1982). In other studies *Z. japonica* has been reported as a short-lived perennial (Bigley and Harrison,1986).

4.2 Zonation of seagrasses

The pattern of seagrass zonation can be compared to zonation of marine algae (Chapman, 1973), salt marsh vegetation (Vince and Snow,1984), and mangrove systems (Rabinowitz, 1978) in terms of the roles of abiotic and biotic structuring forces. Transplant or removal studies have indicated that the location of intertidal species is not only determined by ranges of physiological tolerance but is also infuenced by plant-plant interactions (Lubchenco, 1978, 1980; Rabinowitz, 1978). The mechanisms involved in these competitive interactions are not always understood.

Patterns of zonation in seagrass species have been reported by den Hartog (1973). The zonation of certain seagrasses is ascribed to a progressive successional process of replacement. In den Hartog's estimation, however, *Zostera* species are the initial as well as the terminal stage of seagrass succession.

Zostera marina inhabits the lower intertidal to upper subtidal region of soft sediment coastal shores. *Zostera japonica* is found in the mid intertidal region with a region of overlap with *Z. marina* into the lower intertidal. The upper limit of *Z. marina* distribution in monospecific populations has been accredited to stress associated with desiccation. *Zostera marina* is reported to be incapable of withstanding extreme heat occurring during summer low tides (McRoy and McMillan, 1977; Drew, 1979; Wetzel and Neckles, 1986). Shallow tidal waters at Roberts Bank may reach up to 35° C. At persistent water temperatures above 35° C photosynthetic activity is arrested (Short, 1980). The vigor and vegetative growth of *Z. marina* is affected by desiccation during exposure to air at low tide (Strawn, 1961; Ibarra-Obano and Huerta-Tamayo, 1987). The thin patchy cuticle layer (Tomlinson, 1980) permits rapid evaporation but similarly enables rehydration when tidal waters return.

The lower limit of *Zostera marina* distribution has been related to light attenuation (Backman and Barilotti, 1976; Dennison and Alberte, 1985; Dennison 1987). With increasing water depth, light penetration decreases. It has been reported that with increasing depth or reduced light penetration the density of *Z. marina* shoots decreases. Eventually a depth will be reached at which *Z. marina* shoots receive insufficient intensities or photoperiods of light at the appropriate intensity for survival (Dennison, 1987).

The same general explanation of distribution limitations is applicable to *Zostera japonica*. The factor determining the upper limit of *Zostera japonica* has been accredited to desiccation, temperature extremes, and salinity fluctuations (Bigley, 1981). The lower limit of *Z. japonica* is presumably also determined by light.

The overlap in the present distribution of the two species along the intertidal gradient can be attributed to an overlap in their physiological ranges of tolerance. The "preferred" habitats and life histories of the two species differ sufficiently that neither species will replace the other along the full extent of its present intertidal range (Harrison 1982). Both species, however, are able to survive, grow and reproduce within the 100 m region in which their present distributions overlap.

Populations of *Zostera marina* and *Zostera japonica* are found in temperate coastal waters of Japan and have been reported to form discrete zones or patches. *Zostera marina* occurs in deeper waters with a range of +10 cm to a depth of -180 cm MLW (mean low water) while *Zostera japonica* is in the shallow intertidal. Between the monospecific zones is a zone of patches of both species (K. Aioi, personal communication, 1989).

4.3 Study sites and description of vegetation zones

The Roberts Bank study area (Fig. 2) is located 30 km south of Vancouver and approximately 5 km south of the lower arm of the Fraser River (49 02'N;123 08'W). The Roberts Bank coalport was constructed in 1969 and enlarged in 1981-83, to the north of the existing Tsawwassen ferry terminal (Fig. 3). The coalport causeway deflects the sediment-laden waters of the Fraser River creating an area leeward of the causeway with improved water clarity. This man-made embayment encloses an area that was covered by approximately 400 ha of seagrass vegetation in 1984. The area is subject to mixed semi-diurnal tides with waters from the Strait of Georgia flooding and draining the embayment twice daily. The salinity of these waters ranges from a winter maximum of 28‰ S to a spring and summer minimum of 15-20‰ S coinciding with the Fraser River freshet (Moody, 1978). Salinities recorded at the Roberts Bank study site during a low tide in the summer of 1987 ranged from 22-23‰ S. The temperature of waters in

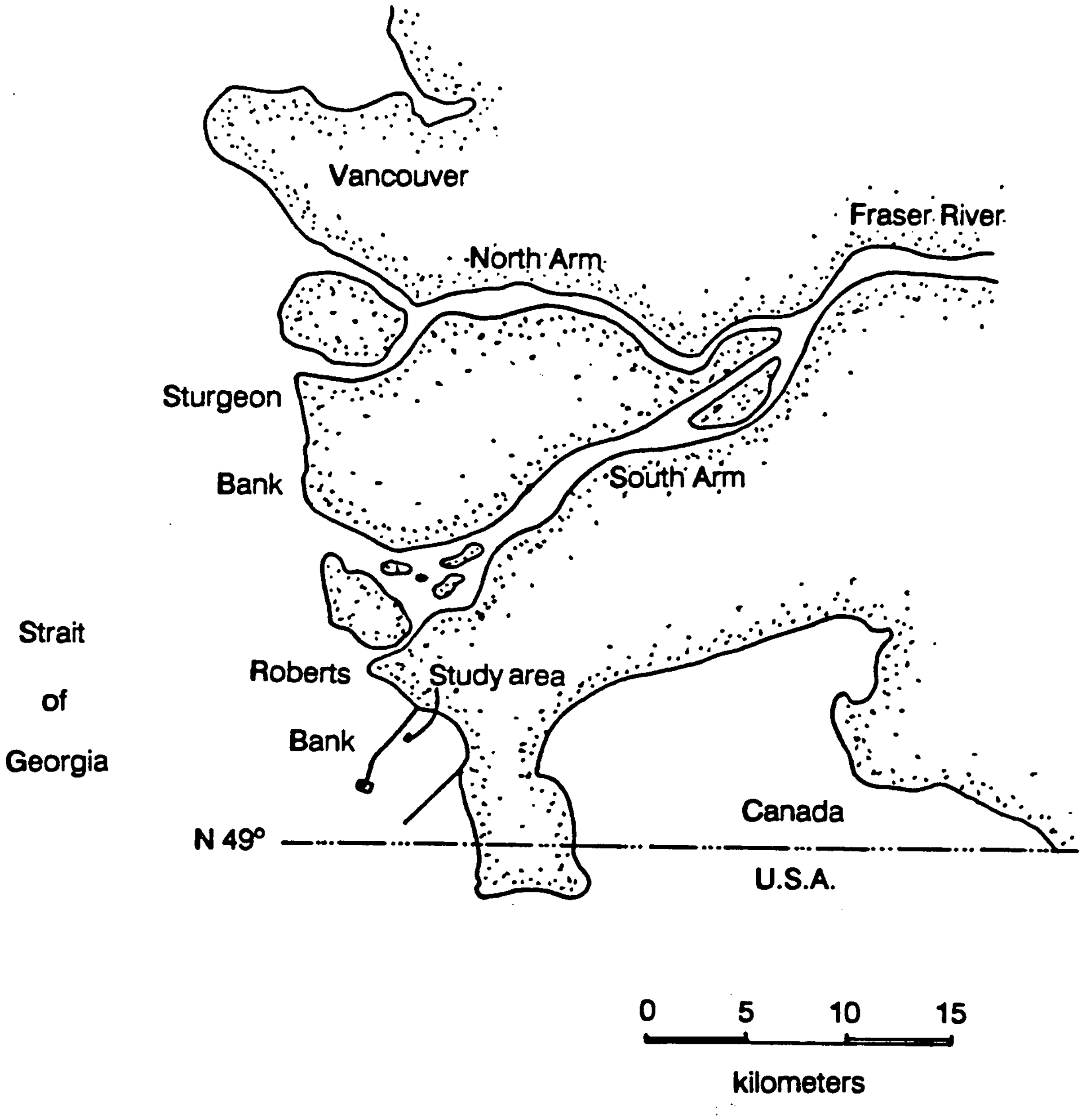

Fig. 2 Map of Fraser River estuary with location of study area on the Roberts Bank foreshore (From Bigley, 1981).

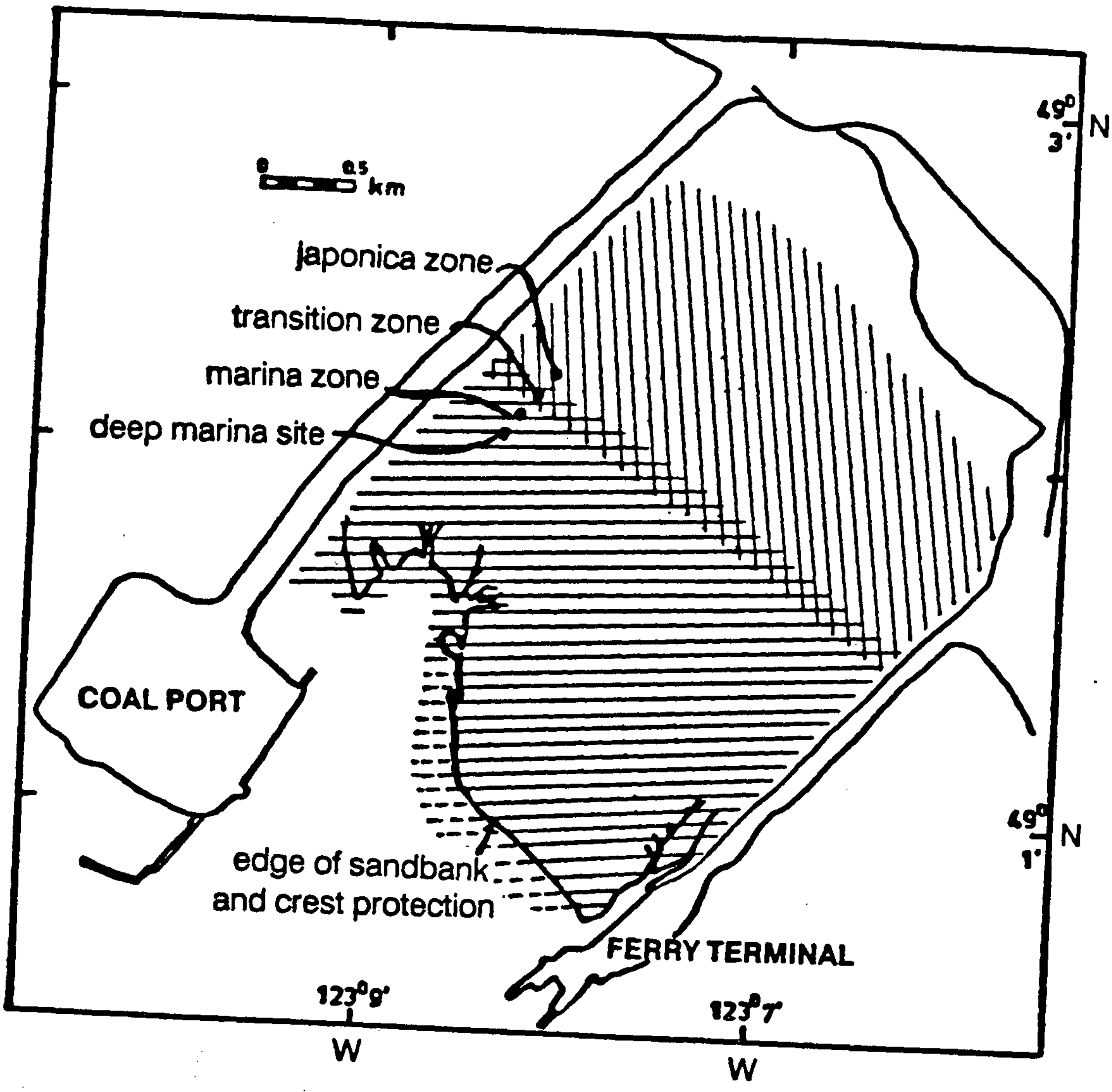

Fig. 3 General map of seagrass cover at Roberts Bank study area indicating approximate locations of sample and experimental sites, (☰) *Zostera marina* cover, (||||) *Zostera japonica* cover.

the Strait of Georgia range between 7° C in the winter and 18° C in the summer (Harrison, 1982). During a summer low tide which will persist for approximately five hours the shallow waters may reach temperatures of 22-34° C (personal observation).

A rip-rap dyke was constructed in early 1982 at the seaward margin of the seagrass bed to reduce erosion of dendritic drainage channels and the adjacent seagrass beds. The dyke has the effect of retarding drainage of the embayment. The area will typically not drain to the same extent as adjacent non-enclosed sites before the tide turns. Waters flow around the dyke into the embayment until the water levels rise above the dyke and the site quickly floods with incoming seawater. The surge of incoming tide waters and the delayed drainage process creates a lagoon-like habitat.

Zostera marina is native to the Pacific west coast. Prior to the construction of the Roberts Bank causeway a seagrass bed extended from below the Canada-USA border through the study site and beyond to the northwest (Harrison 1984). Portions of the seagrass population that were destroyed during the coalport development have since been replanted. The coverage of *Zostera marina* has greatly expanded through vegetative growth primarily because of the improved water clarity (Harrison, 1987).

Zostera japonica was first recorded in 1977 at Roberts Bank (Harrison and Bigley, 1982). A non-native species, *Z. japonica* was introduced to North America from Japan. Since the 1930's *Z. japonica* has colonized many suitable sites along the west coast of Washington and Oregon States, in Puget Sound, Juan de Fuca Strait and the southern Strait of Georgia. The patches of *Z. japonica* vegetation that initially appeared have since expanded. *Zostera japonica* is typically an annual at Roberts Bank but occasionally vegetative shoots will survive the winter.

The population is primarily maintained through reestablishment in the spring with seed germination (Bigley and Harrison 1986).

Progressively, the patchy coverage of both *Zostera marina* and *Zostera japonica* converged (Fig. 3). Since the construction of the coalport until 1983 the coverage of seagrasses has advanced towards the shore at the rate of about 25 m yr^{-1} (Beak-Hinton 1977; Harrison, 1987). As of 1987, the most landward zone of *Z. japonica* extends from the mid intertidal to the upper reaches of the lower intertidal region (+1 to +3 m relative to lowest low water) where its distribution overlaps with that of *Z. marina* (+2 to -1 LLW)(Harrison,1984). At the furthest landward extent of the *Z. marina* vegetation isolated patches of *Z. marina* are evident but by August these patches may be surrounded by annual *Z. japonica* vegetation. The region populated primarily by *Z. japonica* will be referred to as the "japonica zone". The region of overlap in the two species distributions will be referred to as the "transition zone" and the monospecific population of *Z. marina* will be referred to as the "marina zone".

In 1987 three sites were established in the study area, one in each of the vegetation zones. These sites were approximately 65 m apart in a line perpendicular to the tidal flow. The embayment drains gradually over a period of 2-3 hours with a receding tide. At low tide a difference of 3 cm in water depth was recorded between the japonica zone site and the transition zone site and a further difference of only 1.4 cm to the marina zone site. The surge of incoming waters reaches each site within 4-6 minutes of the next; thus the critical period of exposure in terms of heat stress is shorter by 4 minutes in the transition zone versus the japonica zone. Conversely the reduction of light that occurs with water coverage will be effective for 4 minutes less in the japonica zone than in the transition zone for every tidal change during daylight hours. The differences and hence the intertidal gradient in terms of elevation and total time of exposure or conversely coverage by waters which exceed 1 m depth at high tide are slight.

In 1988 an additional site was established a further 65 m seaward of the marina zone site. This site will be referred to as the "deep marina site". The conditions in this site are subtidal; the vegetation is covered by 6 cm of water at all times including during the lowest summer tides.

5 DESCRIPTION OF SEAGRASS GROWTH IN THREE VEGETATION ZONES AT ROBERTS BANK -1987

5.1 INTRODUCTION

The first step in determining whether significant interspecific interactions occur between *Zostera marina* and *Zostera japonica* is the comparison of monospecific populations of *Z. marina* and *Z. japonica* with populations of each species that occur in a mixed stand. One objective of this study is to describe the monospecific population of *Z. marina* in terms of population dynamics, morphological characters, phenological development, and biomass distribution and to compare it with the transition population. The null hypothesis is that no differences exist in the characters described between *Z. marina* populations from the two zones. Similarly the transition population of *Zostera japonica* will be described and compared with the monospecific population. The null hypothesis is that the two *Z. japonica* populations will not differ in population dynamics, morphological characters, phenological development or biomass distribution.

Growth of clonal plants such as *Zostera marina* and *Zostera japonica* is a function of the production of lateral shoots or ramets. Hence the density of the seagrass vegetation was used to measure population development. The morphological characters described included vegetative shoot, flowering shoot and rhizome dimensions. Vegetative shoots consist of a flattened bundle of green strap-like leaves, enclosed at the base by the outer leaf sheath which in turn encloses the developing rhizome. For the purposes of this study, the vegetative shoot includes all green leaf and sheath material and the developing rhizome to the first apparent bulges of root primordia. The primary meristem of vegetative shoots may develop into a sexually reproductive inflorescence. The development of an inflorescence is characterized by a stiff cylindrical stalk, with small leaves (5-10 cm) arising at each node. Spathes develop along the many ts branches of the reproductive shoot, with each spathe bearing 10 to 15 male and female flowers. The flowering shoot with the extended internode length is typically longer than vegetative shoots. The term "flowering shoot" is used to refer to the shoots involved in sexual reproduction with characteristic inflorescence, spathes, flowers, and seeds, to avoid confusion with asexual reproduction that occurs through lateral branch formation. The rhizome material described includes all belowground material that remains in the sample after the shoots have been cut from behind the root primordia and roots have been clipped away. It was anticipated that those characters that were significantly different between populations would indicate a response to environmental conditions, including the presence or absence of neighbours of another species.

In terrestrial systems plants which live under stressful conditions are apt to distribute a greater proportion of biomass to sexual reproduction (Gadgil and Solbrig, 1972; Harper, 1977). Seeds that are broadcast increase the probability that the propagules will encounter a favourable habitat for growth. If one assumes that the transition zone is a stressful environment for *Zostera marina*, representing the upper limit of its distribution, then the portion of aboveground biomass distributed to reproductive effort should be greater in the *Z. marina* population in the transition zone than in the marina zone. Similarly the partitioning of aboveground biomass in *Zostera japonica* populations may be associated with stress imposed by the abiotic or biotic environment.

The survival "strategy" of the plants must include a high degree of flexibility in development as expressed by morphological and phenological variation. Changes occur in the pattern of vegetative branching, in morphological features, and the distribution of biomass to flowering structures in response to seasonal changes in the environment. The many features of a plant's morphology and phenology are integrated to produce a "suitable" plant form for the environmental conditions encountered. Comparison of individual characters at particular times using *t*-tests is useful in searching for indications of a response. Many of the morphological characters may be correlated hence the morphological data might be better represented by a single summary character, probably reflecting plant size. Multivariate analysis can provide an integrated view of the plants and their response to the environment.

5.2 METHODS

In each of the three vegetation zones two 7 x 7 m plots were established for sampling of the aboveground vegetation, belowground rhizome material and for monitoring of flowering shoot development. Two plots in each region of vegetation cover were used to confirm that the subsequent measures would be representative of a zone of either mixed or monospecific population, and not of an isolated patch. Five previously determined random samples were collected from each plot for a total of ten samples in each zone for each sampling time. The samples included all aboveground shoots and loose material from within a 25 x 25 cm (625 cm^2) quadrat. The samples were transported to the laboratory at U.B.C. where, in the following two to three days, all shoots and green loose leaves were cleaned of epiphytes. The number of shoots per sample was counted and then the length of the shoots, the individual leaf lengths and widths were measured. The samples were oven-dried at 60 °C for at least 3 days, after which they were weighed. Harvested samples were collected every four weeks from May 13 to October 31, 1987. Sample times have been coded throughout as T1, T2, T3, T4, T5, T6, T7. Table 1 lists the date of each sample and their corresponding code for the descriptive measures portion of this thesis (section 5).

Table 1 Dates of sampling for descriptive population measures.

Date 1987	Vegetative measures	Flowering shoot measures	Rhizome measures
May 13	T1	T1	T1
May 26		T1+	
June 10	T2	T2	
June 24		T2+	
July 7	T3	T3	
July 22		T3+	
August 5	T4	T4	T4
August 21		T4+	
September 3	T5	T5	
September 19		T5+	
October 3	T6	T6	
October 16		T6+	
October 31	T7	T7	T7

\+ two weeks following time code indicated

From the harvested samples the number and proportion of flowering shoots were recorded. The mean length of the flowering shoots and the mean number of spathes per shoot were calculated. Additional measures which were taken biweekly consisted of repeat visits to permanent sample sites and will be described later.

Often leaves became detached from their shoots between the time they were collected and measured in the lab. This loose leaf material was measured and recorded separately from the measures of intact vegetative shoots. Since leaf material was not always entire, leaf segments were measured and a total per sample was recorded. A comparison of the measured leaf length, detached and attached to the shoot, could be made between zones. Table 2 lists the direct measures and means calculated for aboveground material in each sample.

Table 2 Aboveground measures and calculated parameters.

Number of vegetative shoots*	Number of flowering shoots*
Mean shoot length*	Mean length flowering shoots*
Mean number of leaves/shoot*	Mean number of spathes/shoot*
Mean leaf width*	Dry weight of flowering shoots*
Mean leaf length/shoot*	Mean flowering shoot dry weight
Mean shoot area	Length of loose leaf material
Dry weight of shoots*	Length of loose leaves/shoot*
Mean shoot dry weight	Mean width of loose leaves*
Total loose leaf area	Dry weight of loose leaf material*

* morphological characters included in principal component analysis

The total dry weight of vegetative shoot and loose leaf material for each sample was calculated as a percent of the total aboveground biomass in each sample. The percent of biomass distributed to vegetative shoots and the percent flowering shoots were then compared between zones.

After determining that the two plots within each zone where not significantly different in terms of population dynamics and mean shoot length, the data from the two plots within each zone were combined. Comparisons of population densities and morphological characters were made on the basis of vegetation zones. Data were included in the analyses if they conformed to the following criteria: samples from the marina zone were included if they contained only *Zostera marina* shoots, transition zone samples were included if they contained both *Z. marina* and *Zostera japonica* shoots, and japonica zone samples were included if they contained only *Z. japonica* shoots.

The population numbers, morphological characters and biomass data were analyzed at three levels. Initially, means for each character for each sample time were compared between the monospecific and mixed zones. The Bayesian approach to the two sample *t*-tests (testing equality of means) may be used when variances are unknown or unequal (Lindley, 1965; Hicks, 1982; Walpole, 1982). With many or repeated *t*-tests there is an increased chance of incorrect inference, but the procedure is still useful in searching for structure in the data and for suggesting hypotheses worthy of further study (University of Michigan, 1976).

The second level of analyses involved a principal component analysis (PCA) of the multivariate data. The characters in the original data set are reduced to a new set of uncorrelated multivariate characters. The 13 characters incorporated into the PCA included the numbers of shoots and spathes, linear measures of length and width (cm), and dry weight measures (g)(Table 2). Non-linear measures of shoot and leaf material area were omitted because of a lack of independence from other variables and nonlinear relationships (Pimental, 1979 p.60). Each sample could then be described by a single score along a multivariate principal component axis. Each axis would describe a certain proportion of the variation in the multivariate data set. With each additional axis incorporated into further analyses a more complete multivariate summary of the data is attained. Analyses of variance were performed on the scores for each of the first five axes for each sample time.

The third level of analysis involved a multivariate analysis of variance (MANOVA) performed on the first five principal components (PC1-PC5) at each time period.

All analyses were performed on the MTS operating system on the Amdahl 5860 mainframe computer at the University of British Columbia. Programs used in the analyses were MIDAS (University of Michigan; 1976) for *t*-tests, ANOVA, PCA, and MANOVA. Mean values were accepted to be significantly different at the probability level of $P \leqslant 0.05$.

Belowground rhizome samples were collected with the aboveground vegetation at three sample times (T1,T4, and T7). At T1 all *Zostera marina* shoots in samples designated to be harvested at T4 and T7 had a plastic-coated wire twisted behind the first node with root primordia protrusions. The shoots were resettled into the sediments with only the excess length of wire exposed. Similarly at T4 the samples designated to be harvested at T7 were tagged a second time. The exhumed rhizomes were cleaned of sediment, measured (Table 3), dried at 60 °C for at least 5 days and weighed. *Zostera japonica* rhizomes proved too fragile to withstand handling during tagging.

Table 3 Belowground measures and calculated parameters.

Total rhizome length	Mean lateral branch angle
Number of nodes	Rhizome extension (number of nodes, length) between T1,T4,&T7)
Mean internode length	
Number of lateral branches	Number connected ramets/plant

The number of terminal shoots in each sample was calculated by subtracting the number of lateral branches in the sample from the total number of shoots collected. The total number of aboveground shoots (vegetative plus flowering) was divided by the number of terminal shoots, either vegetative or flowering, to calculate the number of connected shoots per plant.

In each plot, sample sites were randomly designated for the monitoring of flowering shoot development. Ten samples in each of the three zones were monitored every two weeks for the development of inflorescences, spathes, flowers and seeds. The values recorded included the total number of flowering shoots per 10 samples in each zone. The percent of shoots flowering was calculated from these data as was the mean number of flowering shoots per sample, the mean number of spathes per flowering shoot, the number of seeds per flowering shoot and the number of seeds produced per square metre. Since the data collected were totals for 10 samples in each zone, statistical tests of differences between zones were not possible.

Seed cores of 7.7 cm diameter and 10 cm depth were collected in areas adjacent to all three stations on June 24 and August 22, 1987. Samples were also collected at three additional sites; the first was 150 m from the Roberts Bank causeway in line with the deep marina zone, the second was 100 m seaward of the marina zone station in the deep marina zone and the third site was 2 km landward from the japonica zone site approximately 1.3 km from shore. Three replicate sediment samples for each of the six sites were sifted and the numbers of each seed type found were recorded. The mean number of seeds per site was then converted to a value per 0.1 m^2. Viability tests using tetrazolium chloride were performed only on *Zostera japonica* seeds, because they were abundant.

5.3 RESULTS

5.3.1 *Zostera marina* vegetative shoot measures

There was no indication ($P \leqslant 0.05$) of a difference between the density of *Zostera marina* shoots in the marina zone compared to the density of *Z. marina* shoots in the transition zone (Table 4, Fig. 4).

Only once (at T1) was there a difference between zones in the number of leaves per vegetative shoot (Table 4). The mean number of leaves per shoot was consistently between 3 and 5 but occasionally shoots had as many as 10 leaves. Following dissection, these shoots proved to contain newly formed lateral shoots nestled within the sheath. Frequently shoots had 6 or 7 leaves, with the older, epiphyte-covered tattered leaves remaining attached to the shoots.

The mean length of *Zostera marina* shoots was greater in the marina zone than in the transition zone at T1, T4, T6, and T7 (Table 4, Fig. 5).

Table 4 Comparison of the *Zostera marina* vegetative shoot characters between the marina zone (MZ) and transition zone (TZ); means (±SD) for each zone, N total number of samples. The Bayesian probability that one mean is greater than the other is given and the significance (SIGN.) at 0.05 level is represented as SIG = significant or NS = not significant. A dash indicates insufficient data were available for analysis.

TIME	ZONES				N	PROBABILITY	SIGN.
	MARINA		TRANSITION			MZ < or > TZ	
Number vegetative shoots/625 cm^2							
T1	9.1	(5.1)	8.0	(4.3)	18	0.6769	NS
T2	7.7	(3.7)	5.8	(3.8)	17	0.8257	NS
T3	9.1	(3.9)	8.2	(5.0)	15	0.2778	NS
T4	8.6	(3.9)	8.1	(4.1)	18	0.5861	NS
T5	7.1	(3.7)	7.7	(4.6)	17	0.6010	NS
T6	7.3	(2.1)	9.8	(4.3)	13	-	-
T7	6.0	(3.4)	5.3	(2.9)	15	0.6630	NS
Mean number of leaves/shoot							
T1	3.8	(0.5)	3.1	(0.7)	18	0.9760	SIG
T2	4.1	(0.6)	4.1	(0.9)	17	0.5386	NS
T3	3.7	(0.6)	3.6	(0.6)	15	0.6310	NS
T4	4.5	(0.6)	4.2	(0.9)	18	0.7120	NS
T5	4.6	(1.4)	3.9	(0.8)	17	0.8644	NS
T6	4.1	(0.5)	4.2	(0.5)	13	-	-
T7	3.8	(0.6)	4.3	(1.3)	15	0.3709	NS
Mean shoot length (cm)							
T1	66.8	(16.3)	48.7	(13.3)	18	0.9849	SIG
T2	66.9	(29.3)	72.2	(11.9)	17	0.6657	NS
T3	72.6	(17.9)	59.7	(8.2)	15	0.9344	NS
T4	63.2	(8.2)	51.5	(12.9)	18	0.9746	SIG
T5	68.9	(6.8)	46.4	(9.2)	17	0.9999	SIG
T6	72.5	(3.1)	65.1	(14.5)	13	-	-
T7	69.7	(14.4)	49.4	(8.5)	15	0.9922	SIG

Table 4 continued

TIME	ZONES				N	PROBABILITY	SIGN.
	MARINA		TRANSITION			MZ < or > TZ	
Mean leaf length/shoot (cm)							
T1	139.0	(48.3)	82.9	(25.4)	18	0.9946	SIG
T2	179.3	(36.2)	154.8	(53.2)	17	0.8461	NS
T3	164.9	(47.7)	123.9	(25.9)	15	0.9597	SIG
T4	153.5	(30.1)	129.9	(39.9)	18	0.8977	NS
T5	169.5	(20.2)	112.3	(36.4)	17	0.9988	SIG
T6	163.0	(26.4)	155.2	(36.1)	13	-	-
T7	123.2	(66.9)	94.5	(35.9)	15	0.8223	NS
Mean leaf width (cm)							
T1	0.58	(0.07)	0.56	(0.08)	18	0.7318	NS
T2	0.63	(0.05)	0.63	(0.08)	17	0.5983	NS
T3	0.61	(0.06)	0.58	(0.04)	15	0.8570	NS
T4	0.56	(0.07)	0.54	(0.05)	18	0.7671	NS
T5	0.56	(0.04)	0.55	(0.05)	17	0.6359	NS
T6	0.55	(0.02)	0.52	(0.06)	13	-	-
T7	0.58	(0.09)	0.52	(0.08)	15	0.8561	NS
Mean shoot area (cm^2)							
T1	95.4	(44.6)	50.6	(18.1)	18	0.9913	SIG
T2	124.9	(30.4)	117.3	(47.7)	17	0.6461	NS
T3	111.7	(37.2)	79.5	(17.6)	15	0.9595	SIG
T4	94.2	(25.7)	76.9	(26.1)	18	0.8977	NS
T5	102.5	(15.7)	67.0	(24.6)	17	0.9971	SIG
T6	93.6	(16.2)	87.7	(25.7)	13	-	-
T7	86.4	(39.7)	57.6	(25.7)	15	0.9217	NS
Mean shoot weight (g)							
T1	0.47	(0.18)	0.26	(0.09)	18	0.0058	SIG
T2	0.58	(0.19)	0.50	(0.21)	17	0.7783	NS
T3	0.63	(0.19)	0.43	(0.12)	15	0.9748	SIG
T4	0.48	(0.14)	0.36	(0.12)	18	0.9553	SIG
T5	0.54	(0.08)	0.29	(0.09)	17	0.998	SIG
T6	0.53	(0.15)	0.57	(0.19)	13	-	-
T7	0.55	(0.23)	0.36	(0.11)	15	0.9536	SIG

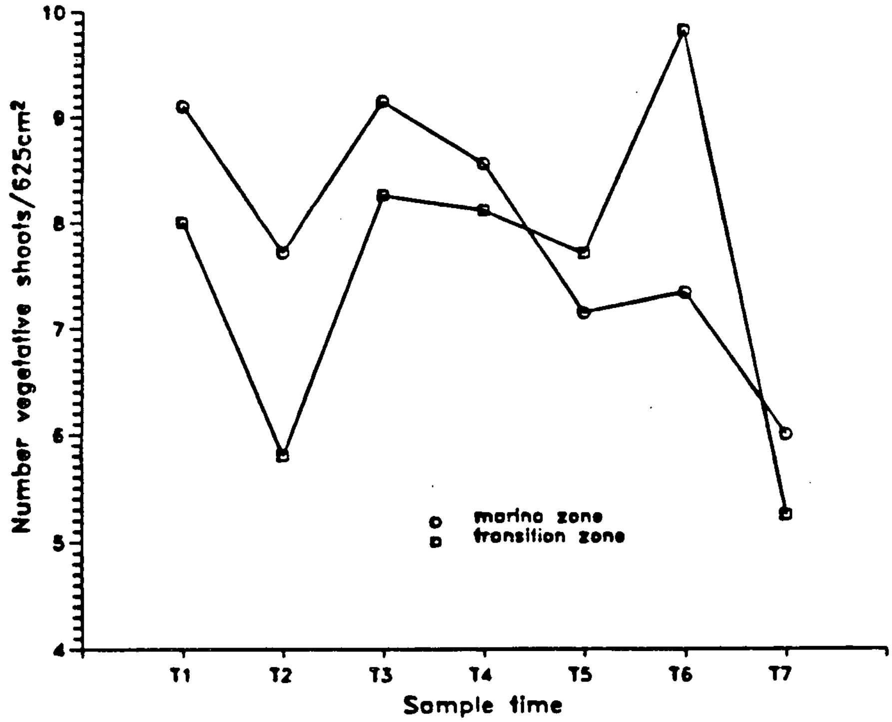

Fig. 4 Density of *Zostera marina* shoots at marina zone and transition zone sites during the 1987 sampling period.

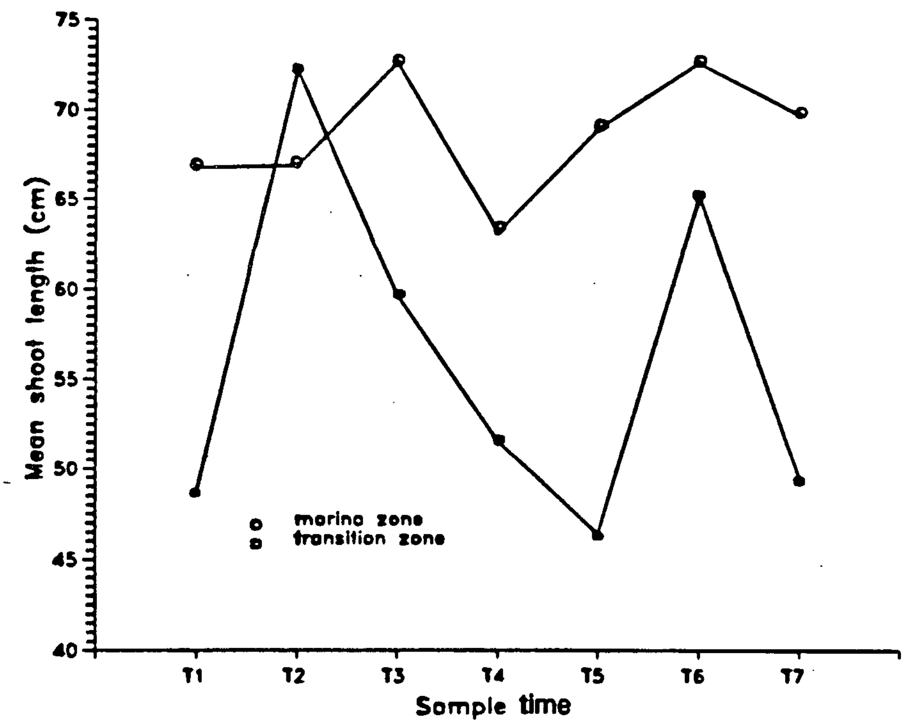

Fig. 5 Mean length of *Zostera marina* shoots at marina zone and transition zone sites during the 1987 sampling period.

The variable of mean total length of leaves per shoot is a function of the number of leaves per shoot and shoot length while shoot area is a function of both these characters as well as leaf width. Since the number of leaves per shoot and the mean leaf width were not highly variable, both the mean total leaf length and the mean shoot area corresponded directly with the mean leaf length per shoot. Significant differences for these two parameters were found between zones at T1, T3, and T5 (Table 4). In each case the length of leaf material or the total shoot area was greater in the marina zone than in the transition zone.

The mean weight per shoot in the marina zone was also greater than in the transition zone at T1, T3, T4, T5 and T7 (Fig. 6). The range in mean vegetative shoot weight was larger in the transition zone than in the marina zone.

Differences between the two populations of *Zostera marina* are evident at various sample times but are not consistent. The differences in mean vegetative shoot length and mean shoot weight persist for only 1 to 3 sample periods. The data indicates that *Z. marina* shoots in the marina zone tend to be of greater size than the transition zone population with a narrower range of variability in the morphological parameters which were measured.

5.3.2 *Zostera japonica* vegetative shoot measures

In contrast, there is a striking difference in the population growth of *Zostera japonica* shoots in the transition zone compared to the japonica zone (Table 5, Fig. 7). The transition population density increased little while in the japonica population showed an exponential rate of growth until T4. Unfortunately the *Z. japonica* samples collected at T5 were not processed quickly enough and therefore no accurate estimate of shoot numbers in the japonica zone was obtained for that sample time.

Differences in *Zostera japonica* morphological characters were less consistent (Table 5). Shoot (Fig. 8) and total leaf length, and hence shoot area

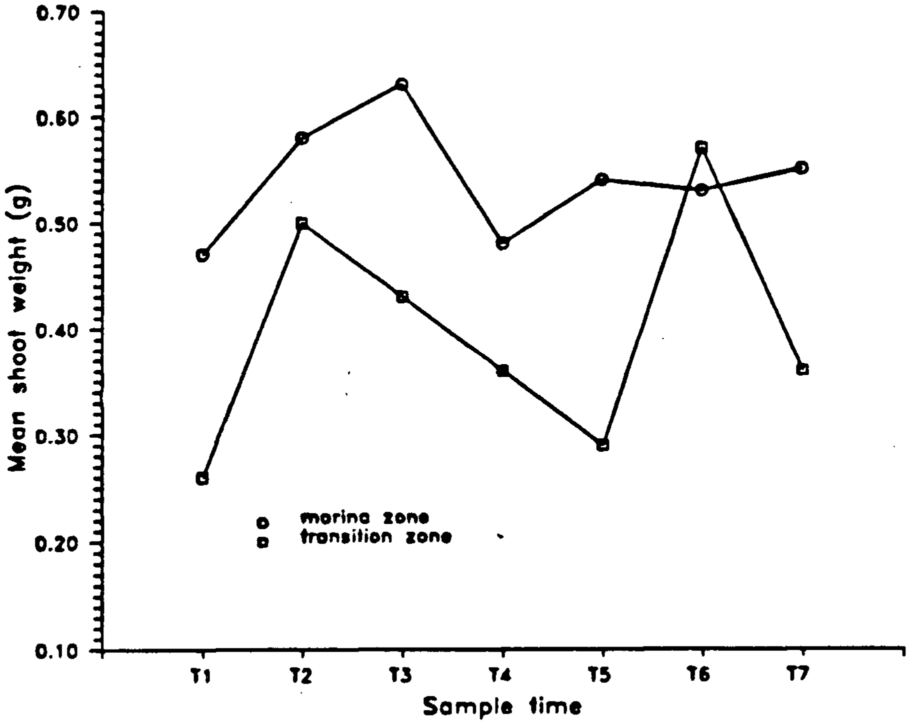

Fig. 6 Mean weight of *Zostera marina* shoots at marina zone and transition zone sites during the 1987 sampling period.

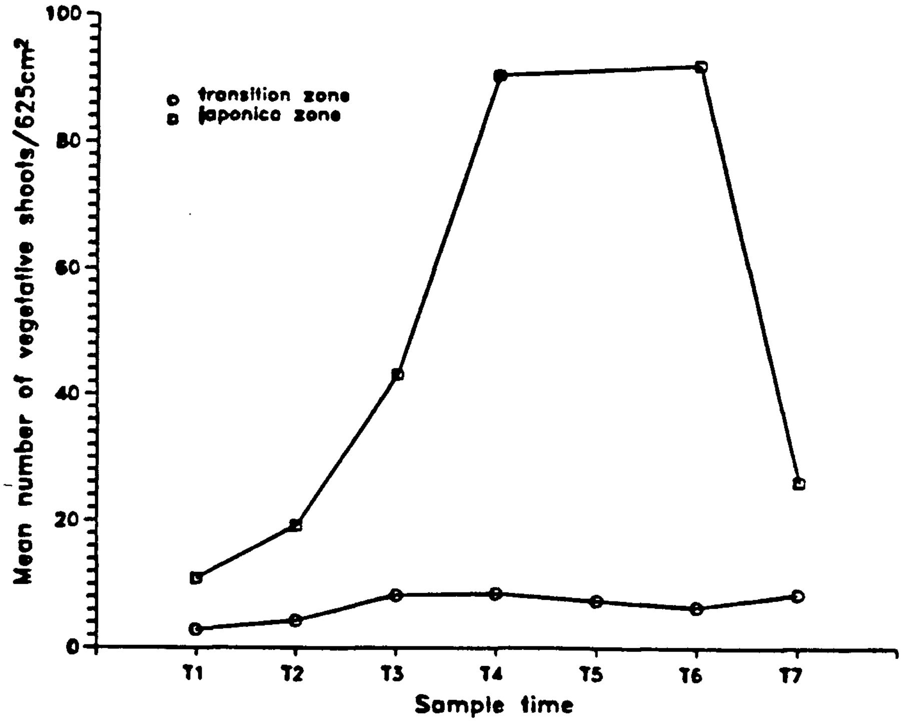

Fig. 7 Density of *Zostera japonica* shoots at transition zone and japonica zone sites during the 1987 sampling period.

Table 5 Comparison of the *Zostera japonica* vegetative shoot characters between the transition zone (TZ) and japonica zone (JZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	TRANSITION		JAPONICA			TZ < or > JZ	
Number vegetative shoots/625 cm^2							
T1	2.9	(2.2)	10.9	(8.5)	18	0.9907	SIG
T2	4.3	(3.7)	19.1	(12.5)	23	0.9975	SIG
T3	8.3	(6.7)	43.0	(14.3)	21	1.0000	SIG
T4	8.6	(9.8)	90.5	(40.0)	20	0.9999	SIG
T5	7.5	(9.3)	-	-	21	-	-
T6	6.5	(7.1)	92.1	(54.7)	27	0.9997	SIG
T7	8.5	(8.1)	26.1	(8.5)	19	0.9996	SIG
Mean number of leaves/shoot							
T1	2.8	(0.6)	2.4	(0.9)	18	0.7983	NS
T2	2.2	(1.2)	2.4	(0.8)	23	0.7136	NS
T3	2.3	(0.8)	2.6	(0.4)	21	0.8315	NS
T4	2.8	(0.8)	2.2	(0.2)	20	0.9756	SIG
T5	1.7	(0.0)	-	-	21	-	-
T6	2.3	(1.0)	3.0	(0.3)	27	0.9949	SIG
T7	1.6	(1.2)	2.3	(0.3)	19	0.9355	NS
Mean shoot length (cm)							
T1	19.3	(9.7)	10.0	(2.5)	18	0.9831	SIG
T2	11.9	(6.9)	10.3	(1.0)	23	0.7878	NS
T3	21.7	(7.8)	12.8	(1.8)	21	0.9989	SIG
T4	22.2	(7.0)	12.3	(1.7)	20	0.9992	SIG
T5	14.3	(6.5)	-	-	21	-	-
T6	17.9	(10.9)	16.8	(1.5)	27	0.6732	NS
T7	8.8	(6.4)	11.3	(1.2)	19	0.8643	NS
Mean leaf length/shoot (cm)							
T1	31.4	(19.4)	12.9	(5.9)	18	0.9827	SIG
T2	19.5	(13.4)	13.3	(3.5)	23	0.9322	NS
T3	33.9	(27.8)	17.3	(5.3)	21	0.9601	SIG
T4	34.1	(13.5)	15.3	(1.5)	20	0.9991	SIG
T5	18.3	(11.0)	-	-	21	-	-
T6	29.8	(22.3)	29.8	(4.7)	27	0.5006	NS
T7	9.9	(8.5)	11.4	(1.5)	19	0.6992	NS

Table 5 continued

TIME	ZONES				N	PROBABILITY	SIGN.
	TRANSITION		JAPONICA			TZ < or > JZ	
Mean leaf width (cm)							
T1	0.15	(0.04)	0.11	(0.04)	18	0.9450	NS
T2	0.11	(0.06)	0.11	(0.03)	23	0.5238	NS
T3	0.16	(0.02)	0.15	(0.01)	21	0.9147	NS
T4	0.16	(0.03)	0.14	(0.02)	20	0.9820	SIG
T5	0.14	(0.04)	0.08	(0.04)	21	-	-
T6	0.11	(0.05)	0.11	(0.01)	27	0.5892	NS
T7	0.08	(0.05)	0.09	(0.01)	19	0.8930	NS
Mean shoot area (cm^2)							
T1	5.03	(3.87)	1.75	(1.12)	18	0.9734	SIG
T2	2.69	(2.71)	2.49	(2.62)	23	0.4720	NS
T3	6.40	(5.19)	2.87	(0.86)	21	0.9747	SIG
T4	5.85	(3.03)	2.19	(0.47)	20	0.9979	SIG
T5	2.91	(1.85)	-	-	21	-	-
T6	4.30	(4.13)	3.36	(0.73)	17	0.8122	NS
T7	1.13	(1.16)	1.20	(0.17)	19	0.5758	NS
Mean shoot weight (g)							
T1	0.044	(0.054)	0.005	(0.005)	18	0.9586	SIG
T2	0.012	(0.011)	0.007	(0.005)	23	0.8972	NS
T3	0.023	(0.022)	0.013	(0.005)	21	0.9079	NS
T4	0.038	(0.027)	0.010	-	20	0.217+33	SIG
T5	0.010	(0.010)	-	-	21	-	-
T6	0.029	(0.020)	0.024	(0.009)	27	0.7852	NS
T7	0.010	(0.009)	0.010	-	19	0.5000	NS

and to a lesser extent shoot weight (Fig. 9), generally were greater in the transition than the japonica population.

At each time when significant differences occurred the mean length of *Z. japonica* shoots from the transition zone was 9 to 10 cm longer, with twice the mean leaf length and three times the mean shoot area of those sampled in the japonica zone.

5.3.3 Harvested flowering shoot measures

Few differences were found in the flowering shoot components of the two *Zostera marina* populations (Table 6). Flowering shoots were present for a longer period (until T5) in the transition zone.

The development of spathes began earlier in the marina zone. The maximum mean number of spathes recorded for these samples occurred at T3. In the transition zone spathes were not observed until T2 but maturing spathes remained in the population at least 4 weeks longer than in the marina zone (until T5). The maximum number of spathes per transition zone flowering shoot coincided with the maximum in the marina zone.

Zostera japonica flowering shoots developed in both the transition zone and the japonica zones by T2 (Table 7). The mean number of flowering shoots per sample was always greater in the japonica zone (significantly more from T4 to T7). Few other differences were found.

5.3.4 Loose leaf material measures

Only rarely were any differences observed for *Zostera marina* loose leaf measures (Table 8), but generally there was more *Z. japonica* loose leaf material in the japonica population than in the transition population (Table 9).

The ratio of loose leaf material to shoot leaf length (Table 10) represents a relative proportion of leaf material that detaches during harvesting, transportation to the lab and processing. Note the high ratio value at T5 for *Z. japonica* shoots

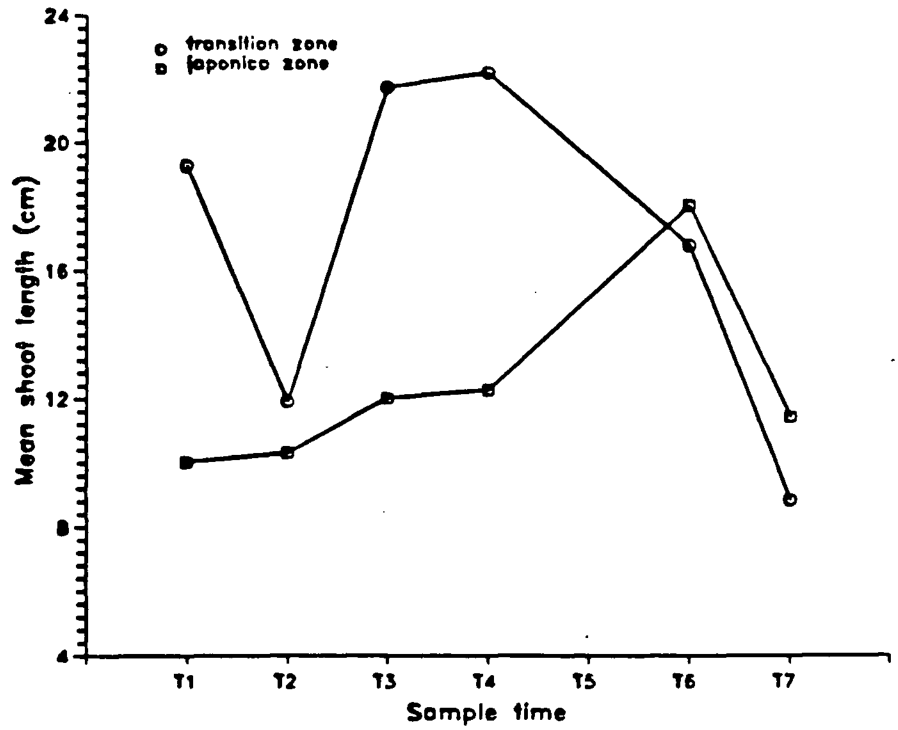

Fig. 8 Mean length of *Zostera japonica* shoots at transition zone and japonica zone sites during the 1987 sampling period.

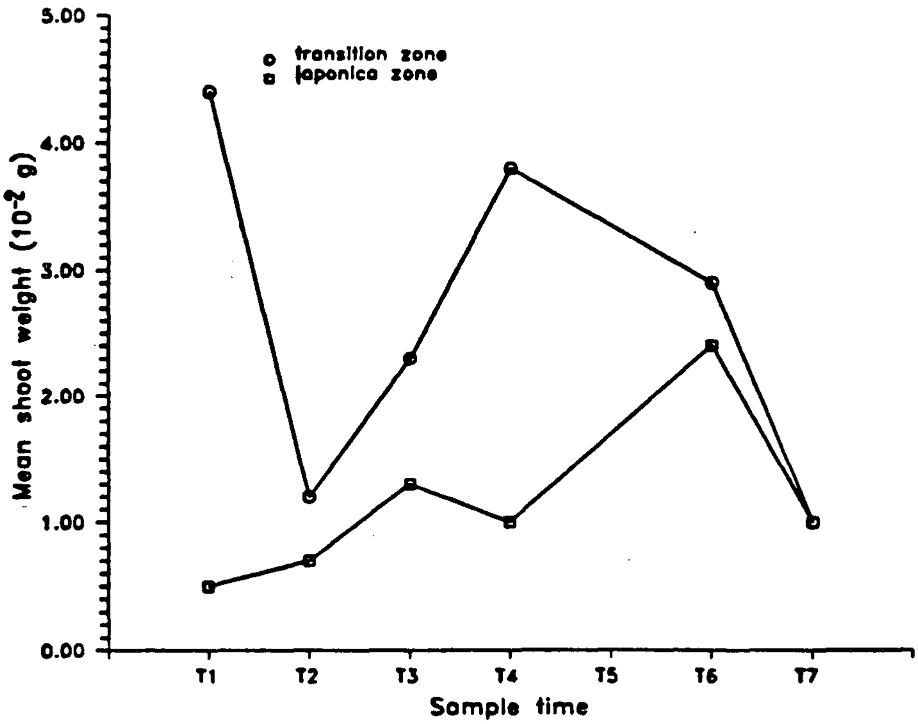

Fig. 9 Mean weight of *Zostera japonica* shoots at transition zone and japonica zone sites during the 1987 sampling period.

Table 6 Comparison of the *Zostera marina* harvested flowering shoot measures between the marina zone (MZ) and transition zone (TZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	MARINA		TRANSITION			MZ < or > TZ	
Mean number flowering shoots/625 cm^2							
T1	2.0	(1.8)	1.0	(1.4)	18	0.8811	NS
T2	0.7	(0.8)	0.4	(0.5)	17	0.8098	NS
T3	1.0	(1.0)	0.4	(0.5)	15	0.9048	NS
T4	1.3	(1.0)	0.1	(0.3)	18	0.9961	SIG
T5	0	-	0.3	(0.3)	17	-	-
T6	0	-	0	-	13	-	-
T7	0	-	0	-	15	-	-
Percent shoots flowering							
T1	16.8	(15.0)	9.2	(11.1)	18	0.8677	NS
T2	10.6	(14.4)	6.8	(9.5)	17	0.7154	NS
T3	11.6	(14.5)	5.1	(8.8)	15	0.8248	NS
T4	15.9	(12.6)	2.2	(6.7)	18	0.9907	SIG
T5	0	-	3.3	(10.5)	17	-	-
T6	0	-	0	-	13	-	-
T7	0	-	0	-	15	-	-
Mean flowering shoot length (cm)							
T1	40.0	(25.1)	10.8	(11.9)	18	0.9954	SIG
T2	36.9	(39.4)	21.4	(31.1)	17	0.7897	NS
T3	31.5	(35.3)	19.2	(36.5)	15	0.7274	NS
T4	42.3	(29.1)	7.0	(21.1)	18	0.9917	SIG
T5	-	-	4.3	(13.6)	17	-	-
T6	-	-	-	-	13	-	-
T7	-	-	-	-	15	-	-
Mean number spathes/flowering shoot							
T1	1.5	(1.6)	0	-	18	-	-
T2	5.0	(6.3)	2.1	(4.2)	17	0.8350	NS
T3	5.4	(6.5)	7.4	(11.9)	15	0.6439	NS
T4	2.3	(2.1)	0.3	(1.0)	18	0.9832	SIG
T5	-	-	0.2	(0.7)	17	-	-
T6	-	-	-	-	13	-	-
T7	-	-	-	-	15	-	-

Table 7 Comparison of the *Zostera japonica* harvested flowering shoot measures between the transition zone (TZ) and japonica zone (JZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	TRANSTIION		JAPONICA			TZ < or > JZ	
Mean number flowering shoots/625 cm^2							
T1	0	-	0	-	18	-	-
T2	0.6	(1.9)	0.8	(1.3)	23	0.6012	NS
T3	1.9	(3.4)	2.7	(3.1)	21	0.7011	NS
T4	2.7	(4.3)	7.4	(5.4)	20	0.9700	SIG
T5	2.5	(2.6)	22.2	(15.9)	21	0.9969	SIG
T6	3.2	(4.4)	13.4	(10.8)	27	0.9910	SIG
T7	1.6	(1.1)	6.6	(5.6)	19	0.9847	SIG
Percent shoots flowering							
T1	0	-	0	-	18	-	-
T2	4.2	(10.4)	3.4	(5.7)	23	0.5775	NS
T3	12.4	(15.1)	4.5	(4.5)	21	0.9319	NS
T4	15.7	(19.8)	7.5	(5.1)	20	0.8817	NS
T5*	27.8	(30.2)	-	-	12	-	-
T6	29.7	(30.2)	11.8	(8.4)	27	0.9793	SIG
T7	34.7	(38.3)	19.9	(16.8)	19	0.8360	NS

* No valid count of number of vegetative shoots in japonica zone samples was obtained with which to calculate percent value.

TIME	TRANSTIION		JAPONICA		N	PROBABILITY	SIGN.
Mean flowering shoot length (cm)							
T1	-	-	-	-	18	-	-
T2	3.1	(7.6)	6.7	(8.9)	23	0.8334	NS
T3	15.9	(16.8)	14.8	(8.1)	21	0.5722	NS
T4	20.2	(17.9)	17.3	(6.4)	10	0.6773	NS
T5	20.2	(12.8)	18.5	(2.8)	21	0.6723	NS
T6	16.7	(13.7)	16.7	(6.3)	27	0.5035	NS
T7	13.3	(5.9)	15.9	(6.8)	19	0.7890	NS
Mean number spathes/flowering shoot							
T1	-	-	-	-	18	-	-
T2	0.2	(0.6)	0	-	23	-	-
T3	1.6	(1.9)	1.3	(1.0)	21	0.6569	NS
T4	2.2	(2.3)	2.8	(1.5)	20	0.7364	NS
T5	2.5	(1.9)	2.3	(0.6)	21	0.5780	NS
T6	1.9	(1.5)	2.1	(0.8)	27	0.7192	NS
T7	1.7	(1.3)	2.1	(0.9)	19	0.7463	NS

Table 8 Comparison of *Zostera marina* loose leaf measures between the marina zone (MZ) and transition zone (TZ). Refer to legend on Table 4 for indentification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	MARINA		TRANSITION			MZ < or > TZ	
Mean length of loose leaf material (cm)/sample							
T1	564.2	(426.7)	461.6	(192.9)	18	0.7370	NS
T2	604.8	(365.1)	441.3	(224.7)	17	0.8323	NS
T3	714.9	(379.4)	451.2	(359.9)	15	0.8869	NS
T4	308.9	(148.9)	381.0	(426.7)	18	0.6753	NS
T5	248.7	(226.6)	368.1	(312.6)	17	0.7975	NS
T6	258.6	(117.7)	239.6	(190.2)	13	-	-
T7	221.7	(129.8)	85.9	(59.5)	15	0.9785	SIG
Mean width of loose leaf material (cm)							
T1	0.65	(0.05)	0.59	(0.09)	18	0.9144	NS
T2	0.64	(0.05)	0.63	(0.08)	17	0.6421	NS
T3	0.61	(0.06)	0.61	(0.09)	15	0.5219	NS
T4	0.62	(0.07)	0.58	(0.05)	18	0.9038	NS
T5	0.61	(0.06)	0.50	(0.19)	17	0.9350	NS
T6	0.61	(0.04)	0.47	(0.18)	13	-	-
T7	0.59	(0.06)	0.48	(0.19)	15	0.9074	NS
Mean area of loose leaf material (cm^2)/sample							
T1	369.1	(285.2)	272.7	(115.7)	18	0.8168	NS
T2	463.7	(178.6)	277.4	(123.4)	17	0.9745	SIG
T3	437.8	(208.1)	312.3	(204.0)	15	0.8524	NS
T4	197.8	(92.2)	242.5	(281.1)	18	0.6670	NS
T5	157.5	(156.6)	204.5	(179.6)	17	0.7017	NS
T6	159.4	(84.3)	170.2	(232.2)	13	0.7017	NS
T7	136.7	(82.6)	48.4	(34.7)	15	0.9810	SIG

Table 9 Comparison of *Zostera japonica* loose leaf measures between thetransiton zone (TZ) and japonica zone (JZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	TRANSITION		JAPONICA			TZ < or > JZ	
Mean length of loose leaf material (cm)/sample							
T1	28.1	(44.9)	119.3	(120.0)	18	0.9724	SIG
T2	44.7	(120.0)	158.1	(93.1)	23	0.9870	SIG
T3	225.9	(300.7)	773.9	(304.9)	21	0.9993	SIG
T4	243.9	(326.9)	1306.9	(691.0)	20	0.9994	SIG
T5	339.1	(422.4)	-	-	21	-	-
T6	71.6	(92.1)	700.9	(307.1)	27	0.9999	SIG
T7	32.1	(31.5)	77.8	(31.2)	19	0.9950	SIG
Mean width of loose leaf material (cm)							
T1	0.16	(0.04)	0.10	(0.05)	12	-	-
T2	0.14	(0.05)	0.11	(0.03)	13	-	-
T3	0.15	(0.03)	0.15	(0.03)	19	0.5875	NS
T4	0.17	(0.02)	0.15	(0.02)	17	0.9825	SIG
T5	0.16	(0.01)	-	-	17	-	-
T6	0.15	(0.04)	0.16	(0.01)	22	0.8341	NS
T7	0.12	(0.02)	0.12	(0.02)	16	0.6020	NS
Mean area of loose leaf material (cm^2)/sample							
T1	4.8	(8.5)	14.7	(16.3)	18	0.9317	NS
T2	7.8	(46.3)	118.3	(51.8)	23	0.9986	SIG
T3	37.3	(46.3)	118.3	(51.8)	21	0.9986	SIG
T4	43.4	(57.9)	198.0	(116.6)	20	0.9982	SIG
T5	50.5	(59.2)	-	-	21	-	-
T6	10.9	(14.9)	113.5	(46.6)	27	1.0000	SIG
T7	3.9	(4.3)	9.3	(4.3)	19	0.9874	SIG

in the transition zone. The bulk of the harvest from the japonica zone may have indirectly effected the transition zone samples during transportation.

Table 10 Ratio of loose leaf material (cm)/shoot leaf length (cm)

	Zone	T1	T2	T3	T4	T5	T6	T7
Z. marina	MZ	0.51	0.47	0.59	0.28	0.21	0.22	0.57
	TZ	0.85	0.61	0.49	0.29	0.58	0.15	0.19
Z. japonica	TZ	0.18	0.24	0.97	0.74	3.26	0.37	0.28
	JZ	1.18	0.74	1.16	0.96	-	0.33	0.31

5.3.5 Aboveground biomass distribution

The *Zostera marina* data indicate that at T2, T3, and T4 a greater proportion of aboveground biomass is distributed to production of flowering shoots in the marina zone than in the transition zone (Table 11) but only T4 is significant.

In the *Zostera japonica* data a greater proportion of biomass was distributed to sexual reproduction after T2 in the transition zone population rather than the japonica zone (Table 12) but only T6 is significant.

5.3.6 Multivariate analysis of descriptive data

The first principal component of *Zostera marina* data was highly correlated (correlation values not shown) with dry weight measures, length of flowering shoots and length of loose leaf material and accounted for 32% of the total variation (Table 13). When analyses of variance were performed on the principal component scores for *Zostera marina* at each sample time significant ($P \leq 0.05$) differences between the marina zone and transition zone populations were generally present (Table 14). MANOVA performed on principal component scores of the *Zostera marina* data revealed significant differences for T4 and to a

Table 11 Comparison between percent of aboveground biomass distributed to *Zostera marina* flowering shoots in the marina zone (MZ) and transition zone (TZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	MARINA		TRANSITION			MZ < or > TZ	
T1	12.4	(18.4)	15.4	(34.5)	18	0.5823	NS
T2	10.6	(16.2)	6.3	(10.1)	17	0.7208	NS
T3	12.1	(12.6)	10.7	(19.0)	15	0.5638	NS
T4	13.5	(11.8)	2.8	(8.2)	18	0.9728	SIG
T5	0	-	2.4	(7.2)	17	-	-
T6	0	-	0	-	13	-	-
T7	0	-	0	-	15	-	-

Table 12 Comparison between percent of aboveground biomass distributed to *Zostera japonica* flowering shoots in the transition zone (TZ) and japonica zone (JZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN.
	TRANSITION		JAPONICA			TZ < or > JZ	
T1	0	-	0	-	18	-	-
T2	4.9	(11.3)	7.2	(11.8)	23	0.6671	NS
T3	22.2	(26.9)	12.1	(9.5)	21	0.8603	NS
T4	24.9	(26.5)	18.7	(8.8)	20	0.7492	NS
T5	36.2	(28.1)	24.6	(11.7)	21	0.8840	NS
T6	34.5	(29.6)	19.4	(11.5)	27	0.9592	SIG
T7	41.0	(33.3)	31.7	(16.0)	19	0.7702	NS

Table 13 Principal component analysis of 13 morphological characters of *Zostera marina*. The percent variation is the amount of variation in the multivariate data set which is explained by each component. Listed are the coefficients for each character for the first five principal components.

	Component				
	PC1	PC2	PC3	PC4	PC5
Variation (%)	32.74	19.02	16.82	9.83	5.46
Cumulative	32.74	51.76	68.58	78.41	83.87
Number of vegetative shoots	0.212	-0.069	-0.510	0.310	0.166
Mean number of leaves per vegetative shoot	0.044	-0.357	0.322	0.428	0.077
Mean length of vegetative shoots	0.225	-0.414	0.068	-0.132	0.049
Mean leaf length per shoot	0.235	-0.448	0.268	0.075	-0.019
Mean leaf width	0.197	-0.263	0.301	-0.411	-0.230
Number of flowering shoots	0.287	0.292	0.141	0.161	0.441
Mean flowering shoot length	0.345	0.222	0.291	0.112	0.122
Mean number of spathes per flowering shoot	0.272	0.289	0.200	0.055	-0.45
Length of loose leaf material per shoot	0.352	0.036	-0.347	-0.129	-0.271
Mean width of loose leaf material	0.185	0.040	0.008	-0.585	0.584
Dry weight of vegetative shoots	0.310	-0.309	-0.286	0.225	0.140
Dry weight of flowering shoots	0.344	0.326	0.217	0.183	-0.011
Dry weight of loose leaf material	0.396	0.011	-0.266	-0.179	-0.249

Table 14 Significance values from analyses of variance and multivariate analysis of variance of principal component scores for *Zostera marina* populations from the marina and transition zones.

	Significance at each sample time						
	T1	T2	T3	T4	T5	T6	T7
ANOVA							
PC1	0.035*	0.064	0.155	0.031*	0.192	0.747	0.008*
PC2	0.312	0.712	0.363	0.742	0.007*	0.925	0.195
PC3	0.225	0.709	0.820	0.134	0.316	0.467	0.738
PC4	0.312	0.356	0.949	0.300	0.776	0.009*	0.026*
PC5	0.105	0.361	0.673	0.005*	0.094	0.578	0.614
MANOVA							
PC1-5	0.168	0.625	0.514	0.034*	0.051	0.127	0.139

* = $P \leqslant 0.05$

lesser extent T5 (Table 14). At these times PC1, the axis that represented the greatest proportion of the variation in the multivariate data set, correlated with length and dry weight of vegetative leaves and shoots.

The first principal component of the multivariate *Zostera japonica* data accounted for 41% of the total variation and was strongly correlated (correlation values not shown) with measures of dry weight, the numbers of vegetative and flowering shoots and the total length of loose leaf material (Table 15). Analyses of variance performed on the principal component scores at each time period indicated differences between the transition and japonica populations in at least one principal component at all but T5 (Table 16). The data set was incomplete for *Zostera japonica* samples at T5 and therefore could not be used in the multivariate analyses. When the multivariate analysis of variance was performed using the principal components (PC1-PC5) at each time period, significant differences were evident between zones at all but T1 (excluding T5).

5.3.7 Belowground rhizome measures

There were no significant differences between the marina and transition populations of *Zostera marina* in all rhizome parameters tested (Table 17).

The negative value for the number of connected shoots per plant calculated for the marina zone at T7 is indicative that shoots have been lost and only the branch stub remained. Individual plants that were carefully dug up in the vicinity of the sampling stations indicated that typically there are two connected shoots per plant but there may be as many as 6 or 7.

All shoots that were evident within the region of the designated 625 cm^2 sample quadrats were tagged. After samples were collected and processed, it was confirmed that 99.6% of the shoots included in the samples had been tagged (270/271). Further, 13.5% (20/148) of the shoots collected at T7 had double tags. Of the tags placed in the field, 91% were retrieved, indicating that this is an

Table 15 Principal components analysis of 13 morphological characters of *Zostera japonica*. The percent variation is the amount of variation in the multivariate data set which is explained by each component. Listed are the coefficients for each character for the first five principal components.

	Component				
	PC1	PC2	PC3	PC4	PC5
Variation (%)	41.52	22.81	12.49	7.83	4.14
Cumulative	41.52	64.33	76.82	84.65	88.79
Number of vegetative shoots	0.364	0.051	-0.321	-0.115	0.111
Mean number of leaves per vegetative shoot	0.071	-0.465	-0.173	0.015	-0.044
Mean length of vegetative shoots	0.069	-0.521	0.150	0.094	-0.044
Mean leaf length per shoot	0.037	-0.529	0.008	0.230	-0.012
Mean leaf width	0.089	-0.445	0.182	-0.415	0.037
Number of flowering shoots	0.362	0.049	-0.071	0.397	-0.176
Mean flowering shoot length	0.247	0.084	0.564	0.063	0.153
Mean number of spathes per flowering shoot	0.254	0.113	0.502	0.107	0.369
Length of loose leaf material per shoot	0.347	0.062	-0.161	-0.392	0.371
Mean width of loose leaf material	0.263	0.025	0.284	-0.397	-0.747
Dry weight of vegetative shoots	0.351	-0.025	-0.304	0.166	-0.155
Dry weight of flowering shoots	0.356	0.024	0.050	0.425	-0.155
Dry weight of loose leaf material	0.388	0.038	-0.178	-0.239	0.167

Table 16 Significance values from analyses of variance and multivariate analysis of variance of principal component scores for *Zostera japonica* populations from the japonica and transition zones.

	Significance at each sample time						
	T1	T2	T3	T4	T5	T6	T7
ANOVA							
PC1	0.762	0.080	0.031*	0.006*	-	0.000*	0.002*
PC2	0.022*	0.668	0.063	0.000*	-	0.891	0.296
PC3	0.195	0.720	0.018*	0.013*	-	0.000*	0.845
PC4	0.290	0.005*	0.001*	0.000*	-	0.386	0.684
PC5	0.219	0.000*	0.806	0.019*	-	0.071	0.118
MANOVA							
PC1-5	0.087	0.000*	0.000*	0.001*	-	0.000*	0.002*

* = $P \leqslant 0.05$

Table 17 Comparison of *Zostera marina* rhizome measures between the marina zone (MZ) and transition zone (TZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES MARINA		TRANSITION		N	PROBABILITY MZ < or > TZ	SIGN
Mean internode length (cm)							
T1	2.1	(0.5)	1.9	(0.6)	18	0.6935	NS
T4	1.2	(0.3)	1.1	(0.1)	18	0.7876	NS
T7	1.3	(0.2)	1.1	(0.3)	13	0.8286	NS
T1-T4	1.2	(0.7)	1.2	(0.3)	16	0.6082	NS
T4-T7	1.2	(0.3)	1.1	(0.4)	12	0.5399	NS
Mean length of rhizome grown (cm)							
T1-T4	6.9	(3.5)	8.2	(2.7)	16	0.7694	NS
T4-T7	7.1	(2.9)	6.2	(2.3)	12	0.6999	NS
Mean number nodes produced							
T1-T4	5.8	(1.3)	7.3	(2.3)	16	0.9097	NS
T4-T7	5.9	(0.9)	5.4	(0.9)	12	0.7845	NS
Mean number lateral branches /625cm^2 sample							
T1	6.5	(3.9)	5.9	(4.0)	18	0.6219	NS
T4	5.3	(4.2)	7.4	(3.1)	18	0.8654	NS
T7	4.2	(2.8)	3.3	(3.0)	13	0.6896	NS
Mean lateral branch angle (°)							
T1	44.6	(8.6)	50.1	(17.7)	18	0.7747	NS
T4	43.9	(20.0)	44.4	(8.3)	18	0.5292	NS
T7	47.5	(12.0)	63.0	(7.5)	11	-	-
Number connected shoots /plant							
T1	2.3	(0.7)	3.2	(2.7)	18	0.8055	NS
T4	3.9	(3.8)	1.7	(4.9)	18	0.8298	NS
T7	-1.2	(3.9)	1.3	(3.2)	10	-	-

effective means of identifying or marking shoots for demographic or morphometric studies.

The *Zostera japonica* rhizome measures of mean internode length, mean lateral branch angle and number of connected shoots per plant did not differ between the transition zone and japonica zone samples (Table 18). At T4 selected *Z. japonica* plants in the vicinity of the sample plots that were carefully removed from the sediments typically had 4 to 10 shoots arising from a single rhizome. Breakage of the delicate *Z. japonica* rhizomes may have affected the calculation of the number of connected shoots.

Significant differences were found in the mean number of lateral branches per sample between the transition zone and japonica zone samples. The greater number of lateral branches in the japonica zone at T4 resulted in the large difference in the number of vegetative shoots at this time (see section 5.3.2).

5.3.8 Permanent site flowering shoot measures

Flowering *Zostera marina* shoots were evident from the initiation of sampling on May 13 (T1) until September 19 (T5+) in the marina zone but only until August 21 (T4+) in the transition zone (Table 19). The maximum mean number and percentage of flowering shoots occurred at the same time in the two populations. A secondary peak in the graph of transition population occurred six weeks later (Fig. 10). The data collected from the permanent site indicate a greater overall proportion of the *Z. marina* shoots are in flower in the transition zone, compared with in the marina zone which is contrary to the data derived from the harvested shoot samples.

The development of spathes on the flowering shoots occurred over a longer period of time in the marina zone. The maximum mean number of spathes per flowering shoot in the marina zone occurred at T3+ (July 26), while the maximum in the transition zone occurred four weeks earlier at T2+ (June 24).

Table 18 Comparison of *Zostera japonica* rhizome measures between the transition zone (TZ) and japonica zone (JZ). Refer to legend on Table 4 for identification of symbols.

TIME	ZONES				N	PROBABILITY	SIGN
	TRANSITION		JAPONICA			TZ < or > JZ	
Mean internode length (cm)							
T1	1.6	(0.4)	1.4	(0.3)	8	-	-
T4	1.5	(0.4)	1.3	(0.2)	19	0.8979	NS
T7	1.1	(0.4)	0.9	(0.2)	17	0.8867	NS
Mean number lateral branches /625 cm^2 sample							
T1	0.	-	2.0	(1.4)	13	-	-
T4	2.1	(2.4)	27.7	(14.2)	21	0.9999	SIG
T7	7.1	(4.5)	19.0	(9.5)	17	0.9964	SIG
Mean lateral branch angle (°)							
T1	-	-	-	-	-	-	-
T4	84.3	(5.1)	66.4	(7.7)	14	-	-
T7	71.0	(2.3)	72.6	(5.3)	16	0.7776	NS
Number connected shoots /plant							
T1	1.0	-	1.2	(0.2)	13	-	-
T4	1.5	(0.7)	1.4	(0.2)	20	0.5890	NS
T7	1.9	(1.9)	2.5	(8.2)	17	0.5860	NS

Table 19 *Zostera marina* permanent site flowering shoot data from the marina zone (MZ) and transition zone (TZ).

TIME	MZ	TZ	MZ	TZ
	Mean number flowering shoots/625cm^2		Percent shoots flowering	
T1	0.4	1.1	4.2	12.1
T1+	0.8	1.8	8.7	20.7
T2	0.4	0.7	4.9	10.8
T2+	0.5	0.7	5.9	8.9
T3	0.3	0.6	3.2	6.7
T3+	0.1	1.1	0.01	11.8
T4	0	0.2	0	2.4
T4+	0.1	0.1	0.01	1.3
T5	0.5	0	6.6	0
T5+	0.3	0	0.04	0
T6	0	0	0	0
T6+	0	0	0	0
T7	0	0	0	0
	Mean number spathes/flowering shoot		Mean number seeds/flowering shoot	
T1	3.3	-	-	-
T1+	1.6	2.9	-	-
T2	3.5	5.1	-	-
T2+	6.8	14.6	23.6	33.5
T3	12.0	12.2	28.7	23.8
T3+	13.0	4.4	31.0	4.9
T4	-	6.0	-	-
T4+	8.0	-	-	-
T5	4.2	-	1.4	-
T5+	3.3	-	5.3	-
T6	-	-	-	-
T6+	-	-	-	-
T7	-	-	-	-
	Number seed produced/m^2			
T1	-	-		
T1+	-	-		
T2	-	-		
T2+	189	374		
T3	138	229		
T3+	49	86		
T4	-	-		
T4+	-	-		
T5	11	-		
T5+	26	-		
T6	-	-		
T6+	-	-		
T7	-	-		

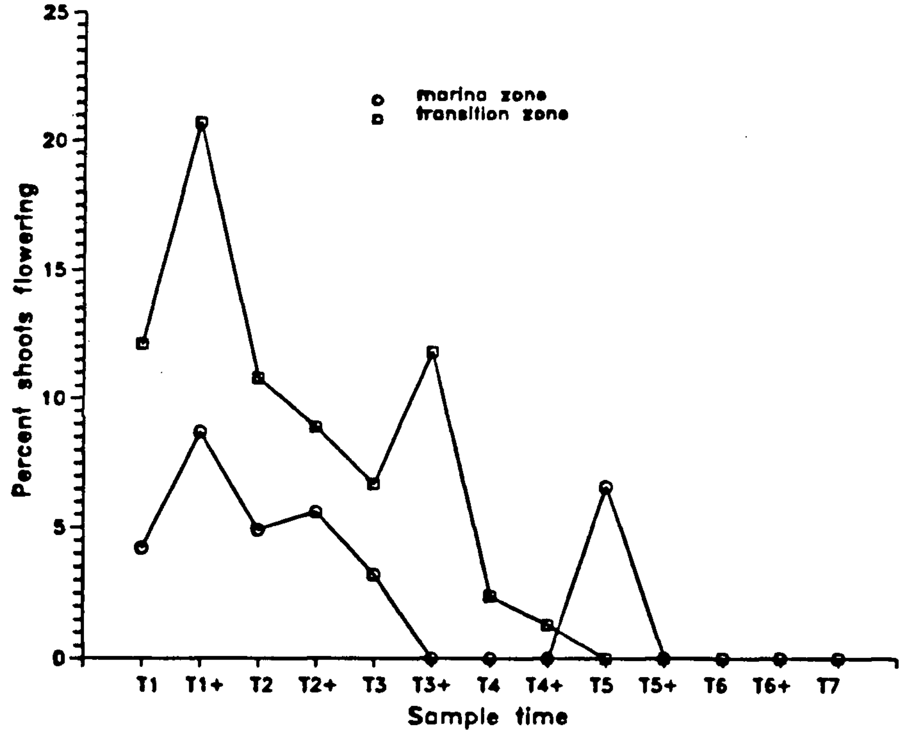

Fig. 10 Percent of flowering shoots in *Zostera marina* populations at the marina zone and transition zone sites during the 1987 sampling period.

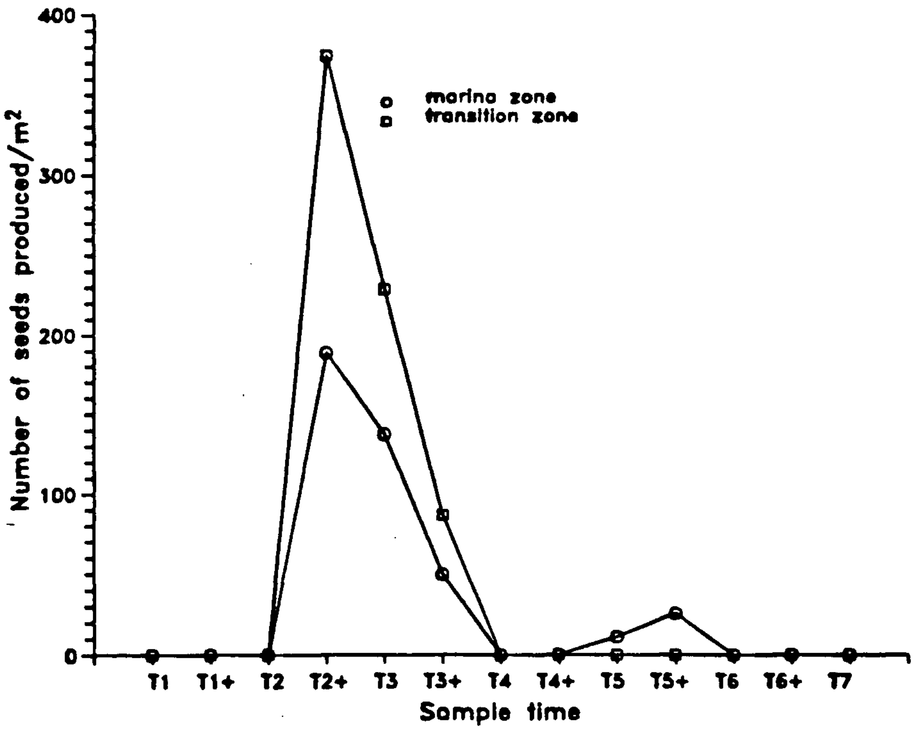

Fig. 11 Number of *Zostera marina* seeds produced in situ per square metre during the 1987 sampling period.

The maximum mean number of seeds per flowering shoot coincided with the maximum mean number of spathes in each zone. The greatest numbers of seeds were produced (per square metre) at T2+ in both zones. The seed output in the transition zone was almost twice as great as in the marina zone (Fig. 11).

Zostera japonica flowering shoots appeared four weeks earlier in the japonica zone (T2, June 10) than in the transition zone (T3, July 7, Table 20). Also, a greater number of *Z. japonica* flowering shoots appeared in the japonica zone than in the transition zone. Despite the low maximum mean number of flowering shoots in the transition zone 12.8% of the low density *Z. japonica* population in the transition zone was in flower at T5. In comparision the monospecific *Z. japonica* population in the japonica zone with a relatively high overall density reached a maximum of 17.3% of the population in flower at T6+ (Oct. 16)(Fig. 12).

The development of spathes in the *Zostera japonica* populations coincided with the appearance of flowering shoots (Table 20). The *Z. japonica* flowering shoots in the transition zone had a greater number of spathes and a greater number of seeds per flowering shoot than in the japonica zone but the larger number of flowering shoots in the japonica zone, in total, contributed over twice the number of seeds/m^2 as in the transition zone (Fig. 13).

5.3.9 <u>Seeds collected from sediments</u>

The first seed sample collected on June 24 coincides with sample T2+. At this time the peak of *Zostera marina* flowering shoot development had passed, (Table 10) and the maximum numbers of seeds per square metre were evident on flowering shoots in both the transition zone and the marina zones, and had not yet been shed. It is not surprising, therefore, that few *Z. marina* seeds were found in these samples (Table 21). By August (T4+) the numbers of *Z. marina* seeds in the sediment samples has increased in the marina, deep marina and transition

Table 20 *Zostera japonica* permanent site flowering shoot data from the transition zone (TZ) and japonica zone (JZ).

TIME	TZ	JZ	TZ	JZ
Mean number flowering shoots/625 cm^2			Percent shoots flowering	
T1	0	0	0	0
T1+	0	0	0	0
T2	0	0.3	0	1.5
T2+	0	0.4	0	1.3
T3	0.3	1.6	3.5	3.6
T3+	0.1	1.7	1.2	2.5
T4	0.5	3.4	5.5	3.6
T4+	0.5	4.2	5.8	4.4
T5	1.1	7.1	12.8	7.2
T5+	0.9	10.5	11.4	10.3
T6	0.4	12.9	5.8	12.3
T6+	0.6	12.4	7.4	17.3
T7	0.6	2.9	6.5	10.0
Mean number spathes/flowering shoot			Mean number seeds/flowering shoot	
T1	-	-	-	-
T1+	-	-	-	-
T2	-	1.7	-	-
T2+	-	1.5	-	-
T3	0.3	1.2	-	0.3
T3+	2.0	1.5	-	-
T4	2.0	2.8	0.8	0.3
T4+	5.2	4.0	6.2	1.5
T5	2.6	2.8	0.6	0.5
T5+	5.3	2.6	8.9	0.8
T6	3.0	3.0	2.8	1.5
T6+	4.8	3.0	7.8	1.6
T7	2.8	1.9	1.2	0.2
Number seeds produced/m^2				
T1	-	-		
T1+	-	-		
T2	-	-		
T2+	-	-		
T3	-	6		
T3+	-	-		
T4	6	18		
T4+	50	102		
T5	11	56		
T5+	128	136		
T6	18	328		
T6+	75	326		
T7	11	11		

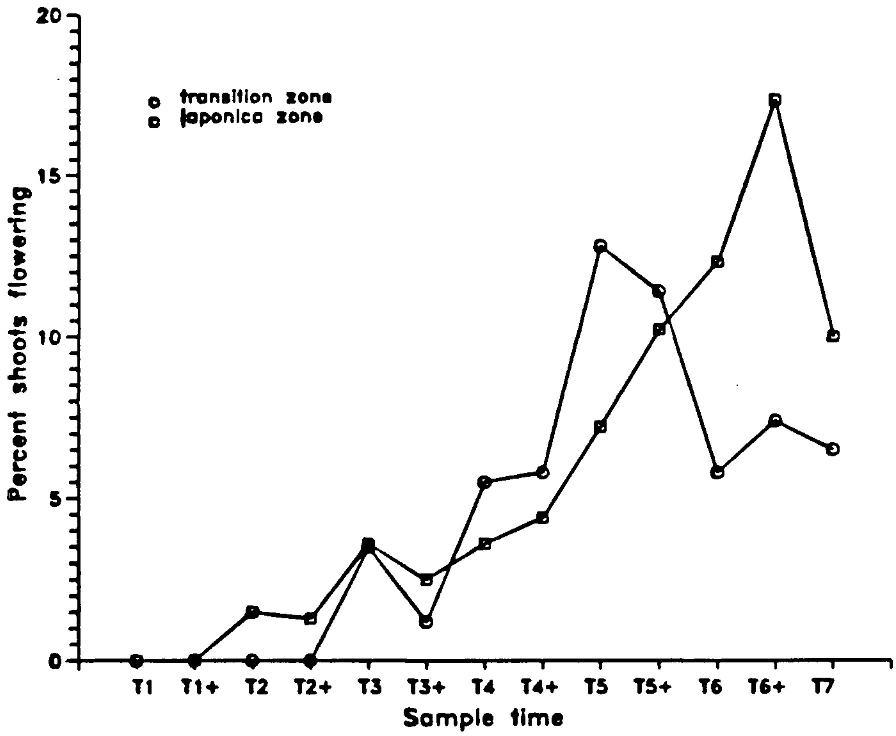

Fig. 12 Percent of flowering shoots in *Zostera japonica* populations at the marina zone and transition zone sites during the 1987 sampling period.

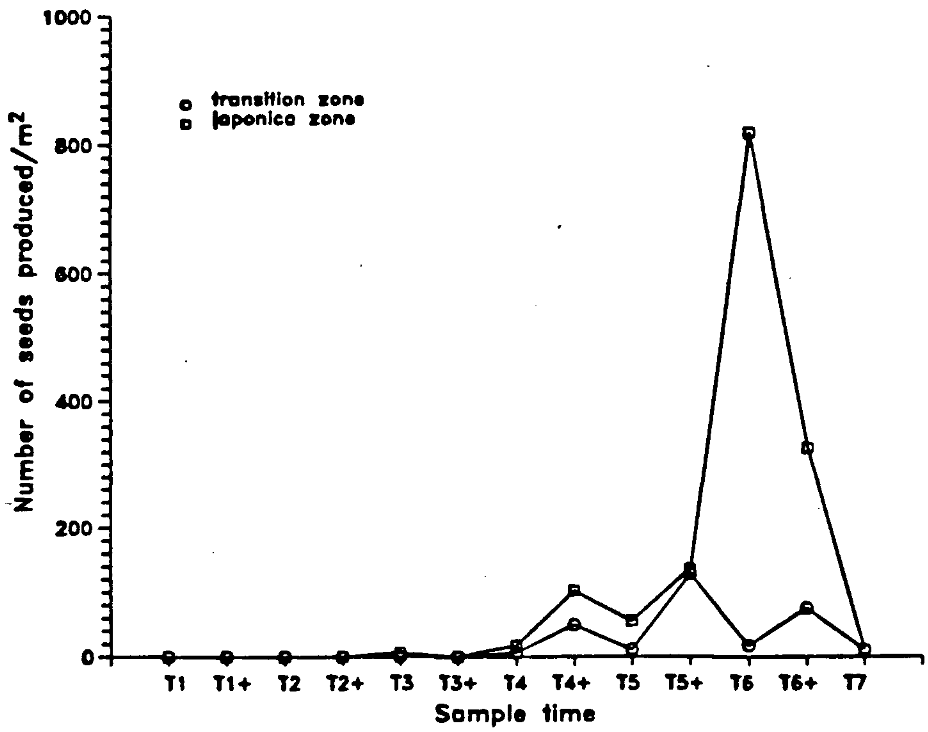

Fig. 13 Number of *Zostera japonica* seeds produced in situ per square metre during the 1987 sampling period.

Table 21 Data on seeds collected from sediment cores.

SAMPLE SITE	June 24(T2+)	August 22(T4+)
Number of *Zostera marina* seeds/0.1 m^2		
causeway site	0	0
deep marina zone	36	43
marina zone	7	14
transition zone	0	43
japonica zone	0	0
landward site	0	0
Number of *Zostera japonica* seeds/0.1m^2		
causeway site	36	0
deep marina zone	7	0
marina zone	63	36
transition zone	143	150
japonica zone	57	229
landward site	429	136

causeway site -located 150 m from causeway in line with deep marina zone site; sparse *Z. marina* cover
deep marina zone -located 100 m seaward of the marina zone sample site; primarily *Z. marina* cover
marina zone -primarily *Z. marina* vegetation cover
transition zone -mixed *Z. marina* and *Z. japonica* cover
japonica zone -primarily *Z. japonica* cover
landward site -located 2 km from japonica zone site and approximately 1.3 km from shore; *Z. japonica* cover

zones, clearly reflecting the recent addition of seeds from this season's flowering shoots. The sediment samples from the causeway, japonica zone and landward sites still did not contain any *Z. marina* seeds by August.

Zostera japonica seeds were found at all six sites in June (Table 21). The greatest numbers of seeds where found at the landward site and the transition zone site. The August sediment samples from the causeway, deep marina zone and marina zone sites contained fewer or no *Z. japonica* seeds. In the transition zone the number of seeds in the sediment samples remained constant and in the japonica zone there was a dramatic increase in number of seeds. At the landward site the number of seeds decreased. Of the 42 *Z. japonica* seeds subjected to the tetrazolium chloride test, 88% stained positive indicating that they were viable.

5.4 DISCUSSION

The presence or absence of *Zostera japonica* in the understory had no effect on the population growth of *Zostera marina*. The environmental conditions which would possibly affect the initiation of lateral branching and ramet formation were consistent between zones.

Morphological characters of the *Zostera marina* vegetative shoots such as mean shoot length and mean shoot weight differed between zones on a consistent basis. Shoots from the marina zone population were typically longer and had a correspondingly greater biomass than shoots from the transition zone. The principal components analysis and multivariate analysis of variance confirmed that differences do exist at T4 between the marina and transition zone populations and to a lesser extent at T5. Although ramet development had not been affected by location along the intertidal gradient the morphological characters of mean shoot length and mean shoot weight indicate a plastic response to some aspect of their environment.

Despite the occurrence of significant differences between zones in *Zostera japonica* population sizes differences found between zones in individual vegetative shoot characters did not persist for more than two sample dates. The transition zone population could generally be described as having longer shoots with a greater shoot area and weight than shoots from the japonica zone. The multivariate analyses included the population numbers which strongly biased the comparison of the monospecific and mixed population characters and therefore the highly significant differences in these analyses reflected the marked difference in population sizes. The relatively low population numbers of *Z. japonica* shoots under a *Z. marina* canopy were due to either differing abiotic or biotic environmental conditions (refer to section 4.3). The suppression of lateral branching in *Z. japonica* rhizomes in the transition zone may be due to a modification of the environment by the presence of *Z. marina*.

The observation that both *Zostera marina* and *Zostera japonica* have longer or bigger shoots in the more seaward location indicates that the size of the seagrasses may be related to water depth. Evidence supporting this observed trend was provided by Phillips (1972) in a comparison of subtidal samples of *Z. marina* with intertidal samples. The subtidal plants had longer and wider shoots than the intertidal plants.

The seaward populations of both species generally had a greater percent biomass per sample allocated to sexual reproduction, although the differences were significant at only one time for each species. The developmental processes associated with initiation of sexual reproductive structures are often triggered by photoperiod or light quality that would be modified by the everchanging levels of tidal waters (Vince-Prue, 1986; Smith, 1986). *Zostera marina* and *Zostera japonica* may both be responding to a similar environmental cue related to position on the tidal gradient in triggering biomass allocation to sexual reproduction.

Two methods were used to estimate the flowering shoot component of the seagrass populations and the results do not agree in all cases. Data collected from sites that were repeatedly monitored should be interpreted with caution, particularly the data collected for the longer *Zostera marina* flowering shoots. During sampling, quadrats were put in place and the shoots which originated in the quadrat were pulled in while any shoot whose base was outside the sample quadrat was pulled away and not counted. Flowering shoots may detach before they are mature during this process. In harvested samples, when it was apparent that the flowering shoots belonged to the sample they were included. With repeated measures of permanent plots the detached shoots could be lost and subsequent measures could be inaccurate. The flowering shoot data collected from permanent sites for both *Z. marina* and *Z. japonica* indicate a reduction in numbers of flowering shoots per sample compared with the harvested samples in the same zones. With the *Z. japonica* data the discrepancy in numbers of flowering shoots did not affect the relative abundance of flowering shoots between zones. A greater number of *Z. japonica* flowering shoots were found in the japonica zone than in the transition zone by both methods. With the *Z. marina* data, however, the harvested shoot data indicated that more flowering shoots were produced in the marina zone than in the transition zone. The opposite was indicated by the permanent site data, although in either case there was no overall significant difference. Kentula (1983) also indicated a greater number of flowering shoots occurred in a site +1.1 m MLW than at a site slightly higher at +1.2 m MLW, but no tests for significant differences were performed. While Kentula's results do not confirm the validity of the harvested shoot data over the data collected from permanent sites it is an indication that this may be the case.

The two sets of data do agree as to the timing of flowering shoot development but the biweekly monitoring of the permanent sites provides a more detailed survey of the progression in flowering shoot development. The peak in the number of *Zostera marina* flowering shoots ocurred in mid-May regardless of zone. Phillips (1972) reported the presence of flowering shoots in Puget Sound, Washington intertidal seagrass beds from April to August, with no indication of maximum occurrence of flowering shoots. Kentula (1983) from her work in Netarts Bay, Oregon indicated that a site located +1.1 m MLW had a peak in flowering shoot density on June 29 and a more landward site located +1.4 m MLW on August 24. The difference between the maximum flowering shoot density observed in this study and that reported by Kentula may be related to environmental site conditions resulting in a plastic shift of phenological development but has not been distinguished in either study from possible genotypic differences.

The maximum numbers of *Zostera japonica* flowering shoots were evident during a period from September through to mid-October. The harvested shoot data indicated that the peak in *Z. japonica* flowering occurred earlier in the japonica zone (September 7) than in the transition zone (October 3). The maximum number of spathes per flowering shoot occurred on September 7 in the transition zone and on August 5 in the japonica zone. Bigley (1981) recorded a maximum in *Z. japonica* inflorescences (spathes) per flowering shoot in August of 1980 at a site 2 km landward of the japonica zone site at Roberts Bank. Despite the 2 km distance between the japonica zone site in the present study and the site from which Bigley collected his data, both indicated maximum numbers of spathes per flowering shoots in August. The one month difference in maximum spathe development between the japonica zone and transition zone sites may be related to biotic interactions rather than a shift of phenological development associated with environmental conditions along the tidal gradient.

The occurrence of flowering shoots was extremely variable from one sample to the next, as is evident in the large standard deviation values in the harvested flowering shoot data. Initially, amongst the vegetative shoots of either *Zostera marina* or *Zostera japonica* a small number of flowering shoots appeared in patches. It was possible that the development of flowering shoots was related to the density of vegetation but no correlation was found between the density of shoots in each sample and the number of flowering shoots. An alternative explanation for the observed patchiness can be adapted from work on terrestrial plants. Shoots that are at the correct developmental phase for floral induction are sensitive to photoperiod. The perception of daylength is attributed to leaves (Vince-Prue 1986). Induction also takes place in the leaf which leads to the production and release of a chemical stimulus which will move to the apex to stimulate the meristem into floral development. In seagrasses floral stimulating chemicals produced in the long vertical leaves could be pulled by gravity to the developing meristem nested within the shoot. Some of this chemical may pass through the leaky cuticle to the surrounding waters. Other nearby shoots may then be secondarily induced to flower. No specific floral hormone or florigen has been isolated in terrestrial plants and a chemical stimulus would be just as difficult to detect in an aquatic marine system. Watson (1984) gave a similar explanation for the observed phenomenon of group flowering in tanks of water hyacinth. He speculated that mutual induction of flowering was initiated by hormones that had leaked into the growth medium from the initial flowering individuals. The initial perception of photoperiod of an adequate length for floral induction by the seagrasses may vary along the tidal gradient and hence the initiation of floral development would also be staggered.

The differences in loose leaf material ratios may be a reflection of the efficiency with which the shoot samples were processed. The *Zostera japonica* samples from the transition zone were processed before the japonica zone samples. At T1 and T2 when the numbers of shoots in each sample were relatively low the samples were processed either 1 or 2 days after collection. Later in the summer, the process of measuring samples took longer as the number of shoots in each sample increased. Processing the shoots 3 or 4 days after collection may have resulted in a greater number of leaves detaching from the shoots. At T5 it was not possible to process the japonica zone population until 8 days after collection and many of the leaves had detached.

Flowering shoots have been reported to detach with immature seeds still enclosed in the spathes. As the shoots are carried by the water currents the mature seeds would be shed (Keddy 1987). In this study, however, *Zostera marina* seeds were not found in regions where there was no *Z. marina* vegetation cover; therefore the seeds of *Z. marina* plants did not appear to be widely dispersed. *Zostera japonica* seeds were found in all sample stations even where no *Z. japonica* vegetation cover existed, indicating that *Z. japonica* seeds are more widely dispersed than those of *Z. marina*.

The maximum number of *Zostera japonica* seeds from the sediments in the *Z. japonica* populations (August sample) coincided with the maximum numbers of flowering shoots present. The seed bank was therefore being added to from the early maturing flowering shoots of the current season. It is likely that substantially more seeds would continue to be added to the seed bank. A proportion of the seed-laden shoots would be dispersed away from the parent vegetation while the seeds shed in situ would initiate the next spring's population of seedlings in the same site.

The general null hypothesis that *Zostera marina* populations do not differ between zones was rejected. Various morphological features such as mean shoot length were found to be statistically different between the marina and transition populations. The population dynamics of the two populations are not, however, statistically different. Neither was the phenological development of *Z. marina* flowering shoots significantly affected by location on the tidal gradient, and only at one time was there a significant difference in the percent biomass allocated to flowering shoots between zones. While differences in individual morphological characters were found, the behaviour of *Z. marina* in the marina and transition zones was very similar.

The null hypothesis that *Zostera japonica* populations of the transition zone and japonica zones do not differ was strongly rejected primarily on the basis of population dynamics. Individual morphological characters also differed at various times. The phenological development of flowering shoots, however, was not greatly affected by position on the tidal gradient and similarly little difference was found between the percent biomass allocated to flowering shoots in the transition zone as compared to the japonica zone.

6 TRANSPLANT EXPERIMENTS -1987, 1988

6.1 INTRODUCTION

There are at least two possible causes for the observed differences in morphology and phenology of *Zostera marina* and *Zostera japonica* among samples from the three vegetation zones. The first are differences in the abiotic environment at different locations along the intertidal gradient. The slope of the sandflat is very gradual and although the elevation differences between adjacent zones are slight, environmental parameters such as total time of water coverage and maximum temperature at low tide may be of considerable consequence to seagrass growth (Strawn, 1961; Short, 1980). A second possible cause of the observed differences may be the presence or absence of a neighbour of another closely related species. The differences could then be interpreted as morphologically or phenologically plastic responses to a competitor. In order to discriminate between these two possible causes a series of transplant studies were undertaken.

The objective of this part of the study was to determine whether monospecific patches of both *Zostera marina* and *Zostera japonica* vegetation respond to environmental conditions along the intertidal gradient. The use of monospecific patches eliminates the possible effect of interaction between species. The number of shoots/m^2 and mean shoot lengths were two population characters that previously (section 5) were found to vary between zones; those characters were monitored in the transplant patches. The null hypotheses are:

i) the initiation of lateral branching and development of *Zostera marina* shoots are not affected by location along the intertidal gradient,

ii) the mean length of *Z. marina* shoots is not affected by location along the intertidal gradient,

iii) the initiation of lateral branching and development of *Zostera japonica* shoots are not affected by location along the intertidal gradient, and

iv) the mean length of *Z. japonica* shoots is not affected by location along the intertidal gradient.

6.2 METHODS

In the spring of 1987, one 4 x 5 m site was located in each of the three identified vegetation zones: marina zone, transition zone, and japonica zone. All aboveground vegetation and rhizome material was cleared from the sites. Monospecific *Zostera marina* patches measuring 25 x 25 cm (625 cm^2) including aboveground vegetation, rhizomes, and roots with adhering sediments were collected from the marina zone on July 7, 1987. Ten patches were transplanted into each of the cleared sites in the transition and japonica zones, and ten patches were replanted in the marina zone site as a control for the effects of transplantation. Similarly *Zostera japonica* samples were collected from the japonica zone, replanted into the japonica zone site as a control and transplanted into the transition and marina zones.

All 60 transplant patches were monitored at four-week intervals beginning July 8 through to September 21 and then at irregular intervals until June 14, 1988 (Table 22). The number of shoots that remained or had arisen from each transplant sample was recorded. At two monitoring dates (July 22 and September 22, 1987) the transplants were also subsampled for measures of shoot length. Fifteen haphazardly selected shoots were recorded and used to calculate mean shoot lengths for each patch.

Table 22 Dates of sampling for transplant experiments initiated in 1987 and 1988.

	1987 transplant	1988 transplant
T0	July 8	
T1	July 22	May 29
T2	August 21	June 27
T3	September 21,22	July 25
T4	February 13, 1988	August 24
T5	March 14	September 21
T6	April 8	
T7	June 14	

New transplants were undertaken on May 29 1988 (T1). Again a site was cleared in each of the three vegetation zones identified the previous summer. An additional fourth site was included in 1988, located approximately 60 m seaward of the marina zone and was referred to as the "deep marina zone" site. All vegetation including rhizome material was removed from the four cleared sites and in the process the sediments became mixed. The patches of transported vegetation consisted of a 625-cm^2 mat of monospecific vegetation, rhizome, and roots with adhering sediments to a depth of 10 cm. Ten *Zostera marina* patches collected from the deep marina zone were transported to the japonica, transition, and marina zones. At each site the patches were planted in previously determined random positions. Ten patches were also replanted in the deep marina site as a control for the effects of transplanting. Similarly patches of *Zostera japonica* were removed from the japonica zone and relocated at each of the four sites. In the japonica zone and deep marina zone sites an additional ten *Z. japonica* patches were transplanted. To each of these additional transplants 15 artificial *Zostera marina* shoots made from green plastic strips were randomly placed within a 50 x 50 cm area centered over the transplanted patches (see section 7.2 for details on artifical shoot dimensions).

The 1988 transplants were monitored five times during the summer at four-week intervals (Table 22). The numbers of vegetative and flowering shoots that originated from each transplanted patch were recorded as well as the length of 15 haphazardly chosen shoots in each patch. In addition, adjacent natural vegetation was randomly sampled beginning at T2 (June 27). The number of shoots (vegetative and flowering) in a 625-cm^2 quadrat and the lengths of 15 haphazardly chosen shoots were recorded for each patch of natural vegetation.

The mean shoot length of transplanted samples was converted to a percentage of the mean shoot length of adjacent natural vegetation. The conversion removes the effect of seasonal changes and permits an appraisal of the effect of transplantation on shoot length. The deep marina zone was the donor site for transplanted *Zostera marina* shoots and therefore if there were no effects of transplantation on shoot length a value of 100% would be expected for replanted shoots in the deep marina zone.

ANOVA was used to test for differences among transplant samples and among random samples of natural vegetation zones. Other comparisons of transplant samples with natural vegetation and with samples under plastic shoot canopies were analysed with Student's *t*-tests.

6.3 RESULTS

6.3.1 1987 *Zostera marina* transplants

The growth pattern of *Zostera marina* transplants initiated in 1987 is illustrated in Figure 14. At no time were there any significant differences in the mean number of shoots among zones (Table 23). The *Z. marina* transplants originating from the marina zone continued to branch and increase or decrease in

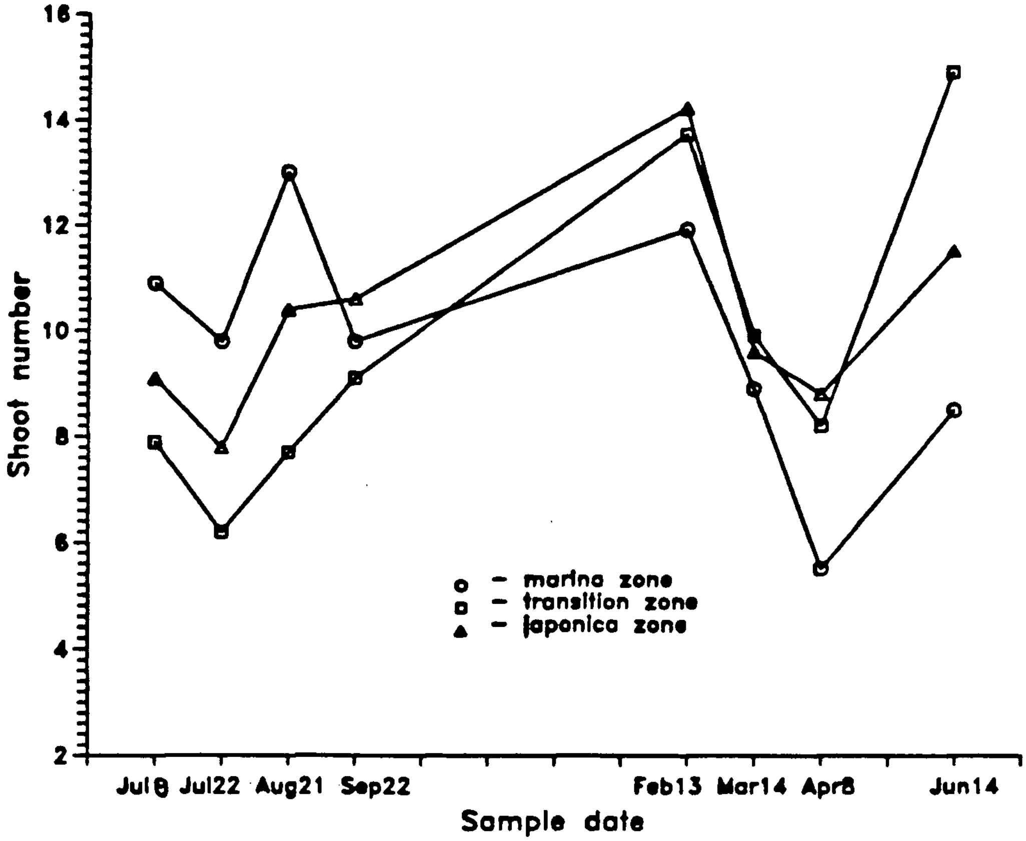

Fig. 14 Mean number of *Zostera marina* shoots per transplant patch in three zones from July 8, 1987 to June 14, 1988.

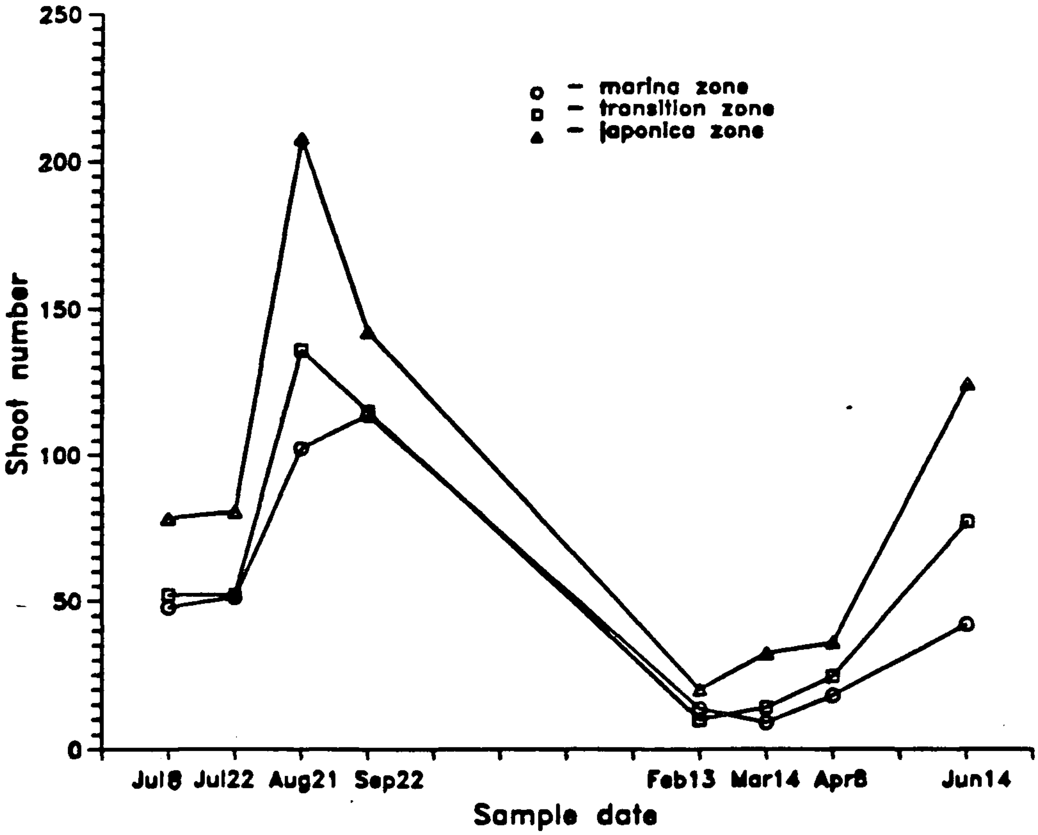

Fig. 15 Mean number of *Zostera japonica* shoots per transplant patch in three zones monitored from July 8, 1987 to June 14, 1988.

Table 23 Means (±SD) and summary of ANOVA for number of shoots and shoot length in *Zostera marina* transplants initiated in 1987. In each zone, marina zone (MZ), transition zone (TZ), and japonica zone (JZ), 10 transplanted patches were monitored and 15 shoots were measured. Significance (SIGN) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean Number of Shoots

TIME	ZONE	MEAN	(±SD)	F-STAT	P	SIGN.
	MZ	10.9	(4.7)			
T0	TZ	7.9	(4.4)	1.3134	0.2855	NS
	JZ	9.1	(3.2)			
	MZ	9.8	(3.2)			
T1	TZ	6.2	(4.4)	2.3562	0.1141	NS
	JZ	7.8	(3.4)			
	MZ	13.0	(7.8)			
T2	TZ	7.7	(7.8)	1.4448	0.2534	NS
	JZ	10.4	(4.9)			
	MZ	9.8	(4.4)			
T3	TZ	9.1	(7.4)	0.16735	0.8468	NS
	JZ	10.6	(5.1)			
	MZ	11.9	(5.2)			
T4	TZ	13.7	(7.4)	0.28009	0.7579	NS
	JZ	14.2	(8.6)			
	MZ	11.9	(5.2)			
T5	TZ	9.9	(9.2)	0.047969	0.9532	NS
	JZ	9.6	(7.5)			
	MZ	5.5	(5.3)			
T6	TZ	8.2	(7.7)	0.61179	0.5497	NS
	JZ	8.8	(7.9)			
	MZ	8.5	(7.3)			
T7	TZ	14.9	(13.1)	0.86192	0.4336	NS
	JZ	11.5	(11.5)			

Mean Shoot Length (cm)

TIME	ZONE	MEAN	(±SD)	F-STAT	P	SIGN.
	MZ	53.2	(11.6)			
T1	TZ	47.1	(14.3)	1.3106	0.2862	NS
	JZ	55.7	(10.4)			
	MZ	46.4	(4.4)			
T3	TZ	35.2	(13.8)	4.5424	0.0199	SIG
	JZ	37.8	(3.9)			

number of shoots in a similar manner regardless of their location. The abiotic environmental parameters associated with the three zones did not result in a significant change in the growth pattern of *Z. marina* plants.

The mean length of *Zostera marina* shoots was not significantly different at T1 (May 13, 1987)(Table 23). This is to be expected as all plants had originated from the marina zone and until 2 weeks previous would have been exposed to a common environmental regime. By T3 (July 7, 1987) the *Z. marina* shoots sampled in the marina zone were significantly longer than those transplanted into the japonica zone. Although the branching and vegetative growth pattern of the *Z. marina* population was not affected by relocation, the mean shoot length was reduced in the 1987 transplants when located higher along the intertidal gradient.

6.3.2 1987 *Zostera japonica* transplants

Transplanted *Zostera japonica* samples in the marina and transition zones did not attain the same numbers of shoots as the replanted controls in the japonica zones (Fig. 15). Only at two sample dates, T3 (Sept. 22, 1987) and T4 (Feb. 13, 1988) when the populations were undergoing a seasonal decline in shoot number, were no significant differences evident (Table 24). Note that the mean number of shoots was greater initially in the japonica zone than the marina and transition zones and the rates of increase and decrease were also greater in the japonica zone compared to that of the transplanted samples. The growth of *Z. japonica* shoots in the japonica zone was more vigorous than in either the marina or transition zones.

In July 1987 (T1) the mean length of *Zostera japonica* shoots was greater in the marina and transition zones compared to the control transplants in the japonica zone (Table 24). By September (T3) these differences no longer existed.

Table 24 Means (±SD) and summary of ANOVA for number of shoots and shoot length in *Zostera japonica* transplants initiated in 1987. In each zone, marina zone (MZ), transition zone (TZ), and japonica zone (JZ), 10 transplanted patches were monitored and 15 shoots were measured. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean Number of Shoots

TIME	ZONE	MEAN	(±SD)	F-STAT	P	SIGN.
	MZ	47.7	(13.9)			
T0	TZ	52.1	(14.2)	12.306	0.0002	SIG
	JZ	78.3	(16.5)			
	MZ	51.2	(23.4)			
T1	TZ	57.1	(27.5)	4.1221	0.0274	SIG
	JZ	80.6	(21.4)			
	MZ	102.3	(29.1)			
T2	TZ	135.9	(66.3)	10.688	0.0004	SIG
	JZ	207.8	(53.9)			
	MZ	113.7	(21.1)			
T3	TZ	114.9	(26.0)	2.8406	0.0759	NS
	JZ	142.0	(39.8)			
	MZ	13.5	(18.9)			
T4	TZ	10.0	(7.1)	1.3633	0.2729	NS
	JZ	19.9	(12.0)			
	MZ	9.0	(11.9)			
T5	TZ	14.0	(11.9)	9.0639	0.0010	SIG
	JZ	32.3	(14.6)			
	MZ	17.9	(14.9)			
T6	TZ	24.4	(13.2)	4.7788	0.0167	SIG
	JZ	35.9	(11.2)			
	MZ	42.1	(49.3)			
T7	TZ	77.2	(34.2)	6.3071	0.0057	SIG
	JZ	124.3	(76.0)			

Mean Shoot Length (cm)

TIME	ZONE	MEAN	(±SD)	F-STAT	P	SIGN.
	MZ	17.9	(3.6)			
T1	TZ	17.0	(1.0)	11.721	0.0002	SIG
	JZ	13.1	(1.7)			
	MZ	16.2	(1.5)			
T3	TZ	14.6	(1.9)	2.0423	0.1493	NS
	JZ	15.6	(2.0)			

6.3.3 1988 *Zostera marina* transplants

The numbers of *Zostera marina* shoots originating from the patches transplanted in 1988 were not statistically different among the four zones at any sample date (Table 25, Fig. 16). In contrast with the 1987 transplant results, the mean length of *Z. marina* shoots in the 1988 transplants initially differed among transplant sites at T1 (Fig. 17). By T2 (1987) this difference was no longer evident (Table 25).

The random samples of natural vegetation adjacent to the transplants undertaken in the 1988 transplant study differed among the zones in both *Zostera marina* shoot density and mean shoot length only at T2 (Table 26). Interestingly, while both the deep marina and marina natural populations decreased in shoot density from T2 to T5, the transition population exhibited an increase in mean shoot density. There is a large variance in the transition zone samples which impedes any statistical separation of means. The lack of differences among the random samples of natural vegetation from each zone for most of the study period indicates that no differences in shoot density and mean shoot length were to be expected in the *Z. marina* transplant samples.

The patches of *Zostera marina* responded to the procedure of transplantation with a decrease in shoot lengths. At all times the mean shoot lengths of transplants from all zones were less than the mean length of shoots in the deep marina natural population which served as the donor site (see Table 27 for mean values, no test for significance performed for these comparisons). In the deep marina zone, where the effect of environmental changes would be minimal compared to transplants into other zones, a significant difference between the transplanted patch and the neighbouring vegetation occurred at all times (Table 27). The shoots in the natural assemblage of vegetation were consistently 7-20 cm longer (mean shoot length) than transplanted shoots. A similar difference was

Table 25 Summary of ANOVA for mean numbers of shoots and mean shoot length in *Zostera marina* and *Zostera japonica* transplants initiated in 1988. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean number of *Zostera marina* shoots

TIME	N	F-STATISTIC	P	SIGN.
T1	40	2.1514	0.1108	NS
T2	40	1.5331	0.2226	NS
T3	40	2.3747	0.863	NS
T4	40	2.2192	0.1027	NS
T5	40	0.71471	0.5497	NS

Mean *Zostera marina* shoot length (cm)

TIME	N	F-STATISTIC	P	SIGN.
T1	40	3.6846	0.0206	SIG
T2	38	3.1280	0.2849	NS
T3	40	0.70508	0.5553	NS
T4	40	1.1156	0.3556	NS
T5	40	1.2815	0.2954	NS

Mean number of *Zostera japonica* shoots

TIME	N	F-STATISTIC	P	SIGN.
T1	40	1.1450	0.3441	NS
T2	40	3.8416	0.0175	SIG
T3	40	1.5039	0.2300	NS
T4	40	2.1711	0.1084	NS
T5	40	0.2389	0.8686	NS

Mean *Zostera japonica* shoot length (cm)

TIME	N	F-STATISTIC	P	SIGN.
T1	40	1.7286	0.1785	NS
T2	40	1.1917	0.3267	NS
T3	40	2.9635	0.0449	SIG
T4	40	1.5865	0.2096	NS
T5	40	0.6598	0.5821	NS

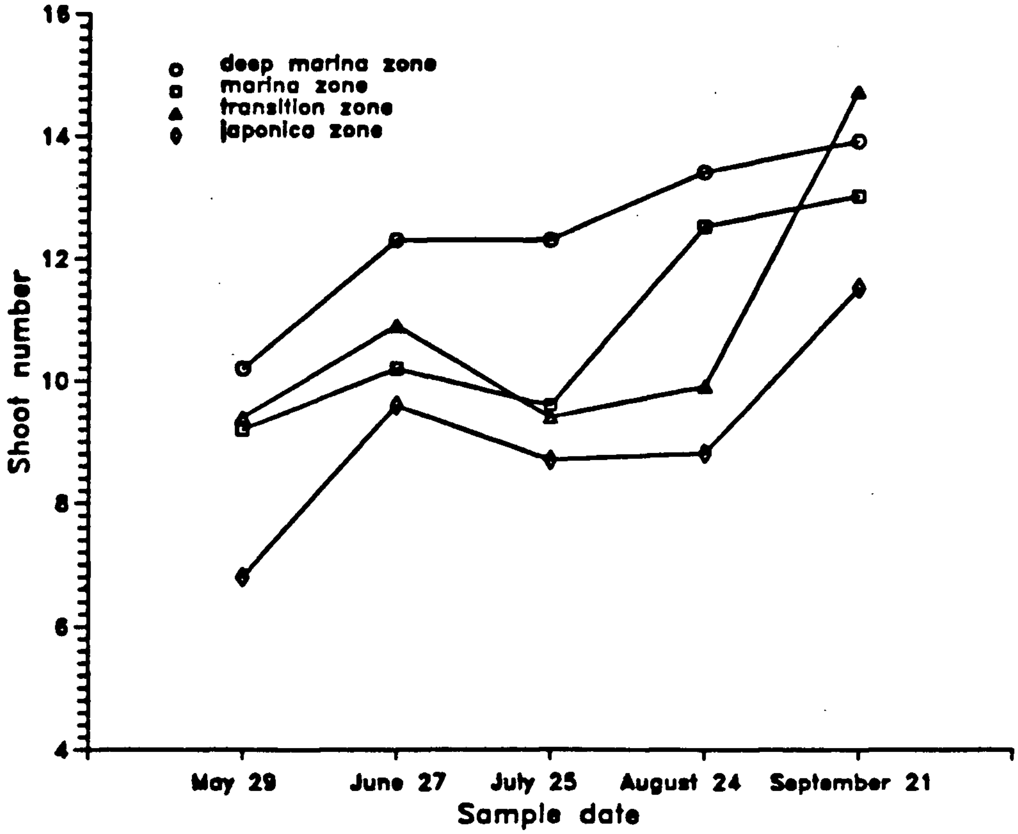

Fig. 16 Mean number of *Zostera marina* shoots per transplant patch in four zones monitored from May 29 to September 21, 1988.

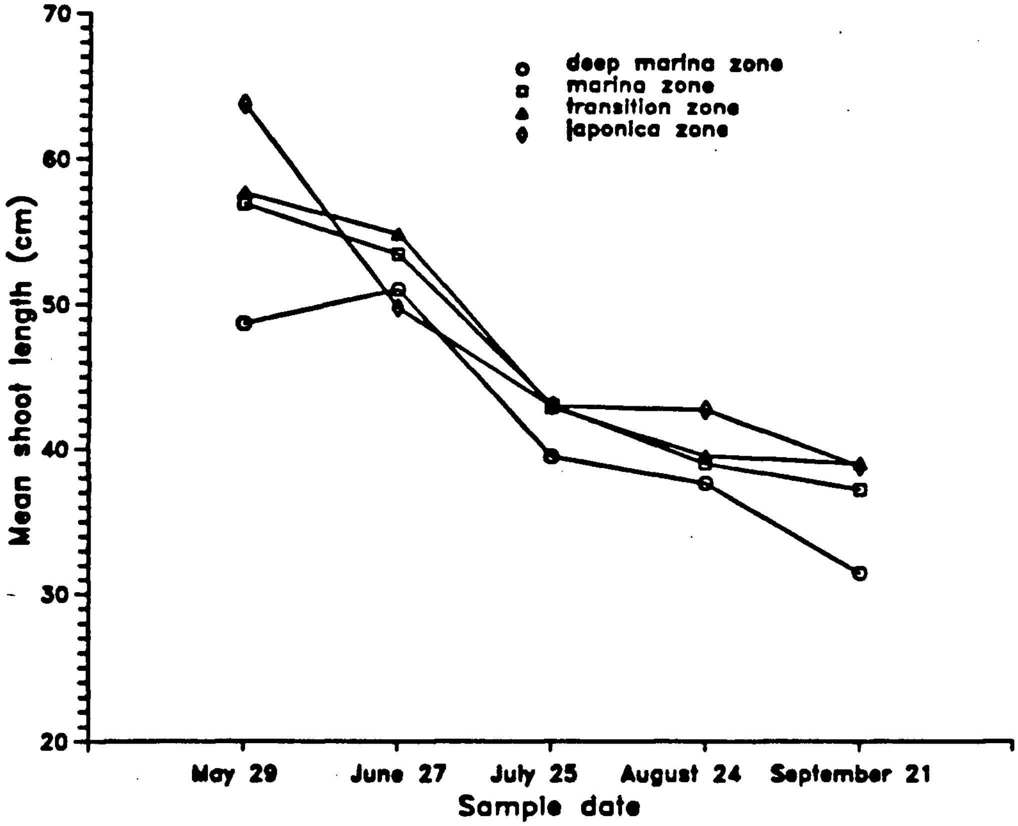

Fig. 17 Mean length of *Zostera marina* shoots in four transplant zones monitored from May 29 to September 21, 1988.

Table 26 Means (±SD) and ANOVA summary for number of shoots/625 cm^2 and shoot length in random samples of natural *Zostera marina* vegetation from deep marina zone (DMZ), marina zone (MZ), and transition zone (TZ) adjacent to transplants initiated in 1988. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean number of *Zostera marina* shoots/625 cm^2

TIME	ZONE	MEAN	(±SD)	N	F-STAT	P	SIGN.
	DMZ	11.5	(5.8)				
T2	MZ	7.8	(4.7)	30	5.2219	0.0121	SIG
	TZ	4.6	(3.6)				
	DMZ	6.5	(2.6)				
T3	MZ	7.2	(3.8)	30	0.96329	0.3944	NS
	TZ	5.0	(4.2)				
	DMZ	7.8	(2.8)				
T4	MZ	6.8	(5.1)	30	0.96329	0.3944	NS
	TZ	9.5	(8.1)				
	DMZ	7.8	(2.9)				
T5	MZ	4.3	(2.6)	30	1.3571	0.2744	NS
	TZ	12.1	(17.9)				

Mean *Zostera marina* shoot length (cm)

TIME	ZONE	MEAN	(±SD)	N	F-STAT	P	SIGN.
	DMZ	58.2	(5.9)				
T2	MZ	55.1	(9.2)	27	3.6043	0.0428	SIG
	TZ	46.2	(13.3)				
	DMZ	59.4	(12.5)				
T3	MZ	48.7	(7.3)	27	3.2029	0.0585	NS
	TZ	53.7	(6.7)				
	DMZ	55.7	(12.3)				
T4	MZ	46.2	(9.7)	28	3.1424	0.0606	NS
	TZ	56.5	(6.5)				
	DMZ	66.3	(9.2)				
T5	MZ	52.5	(22.7)	29	1.7234	0.1982	NS
	TZ	55.9	(17.2)				

Table 27 Means (±SD) and test results for *Zostera marina* shoot length between transplants initiated in 1988 and random samples of adjacent natural vegetation. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Deep marina zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	51.1	(4.6)	58.2	(5.9)	19	8.4078	0.0100	SIG
T3	39.5	(9.4)	59.4	(12.5)	20	16.207	0.0008	SIG
T4	37.7	(6.9)	55.7	(12.3)	20	16.191	0.0008	SIG
T5	35.2	(7.5)	66.3	(9.2)	20	68.413	0.0000	SIG

Marina zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	53.5	(3.0)	55.1	(9.2)	19	0.2650	0.6133	NS
T3	43.1	(6.9)	48.7	(7.3)	20	3.1002	0.0953	NS
T4	39.0	(5.9)	46.2	(9.7)	20	3.9644	3.9644	NS
T5	37.3	(5.6)	52.5	(22.7)	20	4.2247	0.0546	NS

Transition zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	54.9	(6.8)	46.2	(13.3)	18	3.2635	0.0897	NS
T3	42.9	(5.1)	53.7	(6.7)	17	14.010	0.0020	SIG
T4	39.6	(6.5)	56.5	(6.5)	18	30.031	0.0001	SIG
T5	43.1	(6.3)	55.9	(17.1)	19	4.9437	0.0400	SIG

Japonica zone

TIME	TRANSPLANT	
T2	49.8	(8.8)
T3	43.1	(3.6)
T4	42.8	(6.3)
T5	38.9	(6.5)

* No natural *Zostera marina* was present in the japonica zone for comparison

found in the transition zone, but in the marina zone mean lengths of *Z. marina* transplants were the same as in the randomly sampled natural vegetation.

6.3.4 <u>1988 *Zostera japonica* transplants</u>

The population growth curves of the monospecific *Zostera japonica* transplants in 1988 (Fig. 18) were similar to that depicted by the japonica population in section 5. Note that the deep marina population attained the greatest population size at T4 (August 24). Significant differences were found among the zones in mean shoot number at T2 and mean shoot length at T3 (Table 25), but there were no apparent trends of transplant samples in one zone developing greater shoot number or longer shoots than in another.

The natural density of *Zostera japonica* shoots was always significantly different among the four zones (Table 28). No *Z. japonica* shoots were found in the deep marina zone and few were found in the marina zone. There were substantially more *Z. japonica* shoots naturally located in the transition and the japonica zones. No significant differences were found, however, in the mean lengths of *Z. japonica* shoots (Table 28).

In the marina zone the randomly sampled *Zostera japonica* shoots from adjacent vegetation were consistently longer than the transplanted *Z. japonica* but significant ($P \geqslant 0.05$) differences in mean shoot length were noted only at T2 and T3 (Table 29). The same was true in the transition and japonica zones, where significant differences in the mean shoot length between natural and transplant samples were found at T2, T3 and T5. In the japonica zone the randomly sampled natural population continued to increase in shoot length after T4 and was significantly longer at T5 than the declining shoot length of the transplanted population.

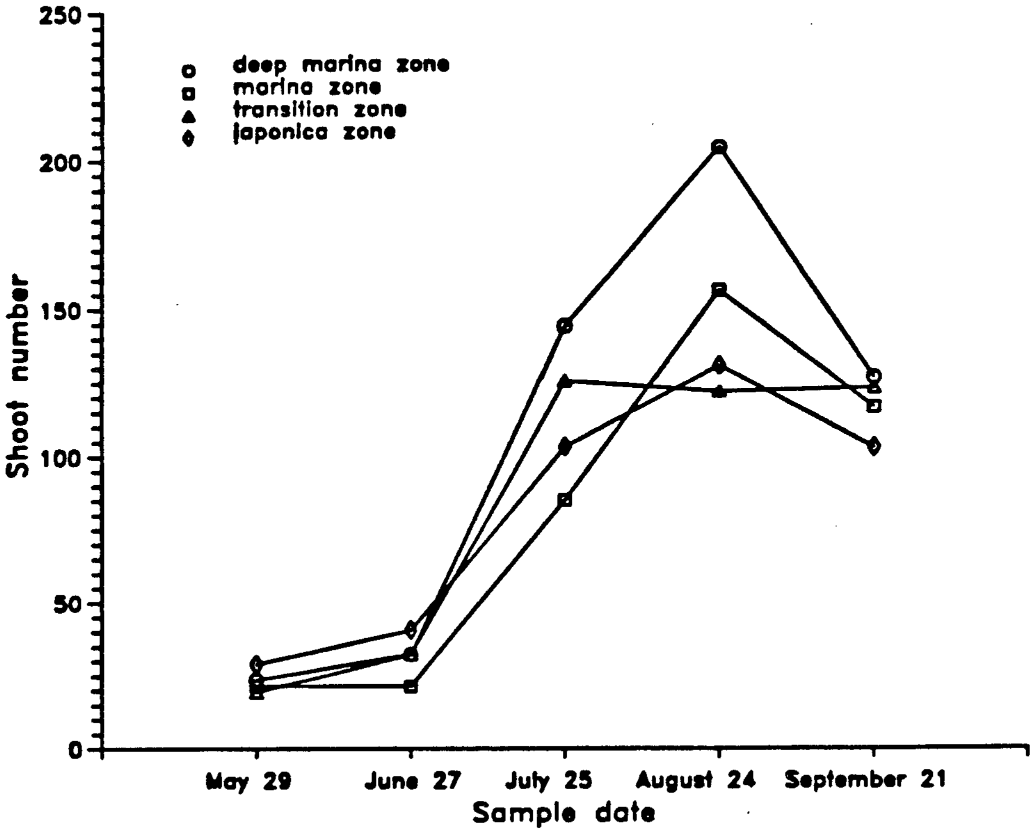

Fig. 18 Mean number of *Zostera japonica* shoots per transplant patch in four zones monitored from May 29 to September 21, 1988.

Table 28 Means (±SD) and ANOVA summary for number of shoots/625 cm^2 and shoot length in random samples of natural *Zostera japonica* vegetation from marina zone (MZ), transition zone (TZ), and japonica zone (JZ) adjacent to transplants initiated in 1988. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Number of *Zostera japonica* shoots/625 cm^2

TIME	ZONE	MEAN	(±SD)	N	F-STAT	P	SIGN.
	MZ	1.2	(0.9)				
T2	TZ	20.3	(13.8)	30	5.4431	0.0103	SIG
	JZ	22.5	(22.3)				
	MZ	4.1	(5.6)				
T3	TZ	24.4	(28.5)	30	3.9586	0.0311	SIG
	JZ	32.6	(24.5)				
	MZ	4.7	(5.9)				
T4	TZ	42.2	(31.4)	30	14.020	0.0001	SIG
	JZ	65.6	(27.9)				
	MZ	3.0	(5.4)				
T5	TZ	20.4	(9.8)	30	57.160	0.0000	SIG
	JZ	51.8	(13.8)				

Mean *Zostera japonica* shoot length (cm)

TIME	ZONE	MEAN	(±SD)	N	F-STAT	P	SIGN.
	MZ	15.9	(4.2)				
T2	TZ	16.6	(5.7)	27	2.4582	0.1069	NS
	JZ	12.4	(1.7)				
	MZ	19.1	(6.4)				
T3	TZ	17.8	(5.7)	25	2.9637	0.0725	NS
	JZ	13.7	(2.4)				
	MZ	14.4	(3.3)				
T4	TZ	21.3	(10.4)	27	2.1564	0.1376	NS
	JZ	16.6	(3.3)				
	MZ	16.6	(5.2)				
T5	TZ	20.6	(4.2)	25	1.1464	0.3360	NS
	JZ	19.8	(4.0)				

Table 29 Means (±SD) and test results for *Zostera japonica* shoot length between transplants initiated in 1988 and random samples of adjacent natural vegetation. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Deep marina zone

TIME	TRANSPLANT	
T2	12.1	(1.4)
T3	15.0	(2.8)
T4	14.9	(2.6)
T5	16.9	(2.8)

* No natural *Zostera japonica* was present in the deep marina zone for comparison

Marina zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	12.0	(2.9)	16.4	(4.1)	18	6.69417	0.0180	SIG
T3	13.7	(1.7)	18.7	(5.9)	17	7.4411	0.0156	SIG
T4	14.2	(1.6)	14.7	(3.1)	17	0.20598	0.6564	NS
T5	16.1	(2.4)	17.0	(4.6)	15	0.2746	0.6091	NS

Transition zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	11.9	(1.6)	16.3	(5.9)	20	5.1574	0.0357	SIG
T3	12.8	(1.9)	18.1	(6.0)	20	6.8732	0.0185	SIG
T4	16.1	(2.9)	21.8	(10.8)	20	2.6173	0.1231	NS
T5	15.7	(3.7)	20.8	(4.9)	20	6.5902	0.0194	SIG

Japonica zone

TIME	TRANSPLANT		NATURAL		N	F-STAT	P	SIGN.
T2	10.7	(0.9)	12.4	(1.7)	29	4.0684	0.0290	SIG
T3	14.9	(1.4)	13.7	(2.4)	30	7.8558	0.0020	SIG
T4	16.3	(2.8)	16.6	(3.3)	30	1.5781	0.2248	NS
T5	15.1	(2.1)	19.8	(4.0)	30	15.231	0.0000	SIG

6.3.5 Response to transplantation

The conversion of transplant mean shoot length to a percent of the length of natural vegetation further indicated that transplantation negatively effected shoot length. For *Zostera marina* the transplants in the deep marina zone showed the greatest negative effect of transplantation, but in all three zones transplants became shorter than natural plants (Table 30).

Zostera japonica samples transplanted into the marina zone increased in mean shoot length relative to the natural vegetation throughout the growing season (Table 30). *Zostera japonica* shoots transplanted into the transition zone consistently remained 24-29% shorter than the adjacent natural *Z. japonica* vegetation. The control shoots replanted in the japonica zone developed a mean shoot length 86-109% of that of the natural population until T5 when the mean transplant shoot length in the japonica zone was 23% less than that of the natural population.

6.3.6 Response to imposed artificial shoots

The imposition of a canopy of plastic green shoots had no effect on the number of *Zostera japonica* shoots arising from a transplant in the deep marina zone (Table 31). In the japonica zone, however, there were significantly fewer *Z. japonica* shoots under a canopy of plastic shoots at T3, T4, and T5. Plastic shoots had no initial effects on the mean length of transplanted shoots at T1 (Table 31). By T2 the transplanted shoots under the plastic canopies were significantly longer than the control in both zones. At T3 in the japonica zone the artificial canopy had no effect and thereafter the control transplants were longer. A similar reversal of the effect of the artificial shoots occurred in the deep marina zone but not until the last sampling date.

Table 30 Relative mean length of transplanted *Zostera marina* and *Zostera japonica* shoots calculated as a percent of mean length of natural adjacent vegetation for each zone. Control indicates vegetation patches that were replanted into the donor sites and +plastic indicates the *Z. japonica* controls which had plastic shoots imposed.

Zostera marina

TIME	DEEP MARINA ZONE control	MARINA ZONE	TRANSITION ZONE
T2	88	97	119
T3	67	89	80
T4	68	85	70
T5	54	71	77

Zostera japonica

TIME	MARINA ZONE	TRANSITION ZONE	JAPONICA ZONE control	JAPONICA ZONE +plastic
T2	73	72	86	100
T3	73	71	109	134
T4	96	74	99	86
T5	95	76	77	64

Table 31 Comparison of *Zostera japonica* number of shoots and shoot length between transplant patches (TRANSP) and transplant patches with plastic shoots imposed (+PLASTIC). Means are given for the japonica zone (JZ) and deep marina zone (DMZ). In each zone 10 transplanted patches were monitored and 15 shoots were measured. The Bayesian probability (see section 5.2 for description) that one mean is greater than the other is given and the significance at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean Number of *Zostera japonica* Shoots

TIME	ZONE	TRANSP	+PLASTIC	PROBABILITY TRANSP < or > +PLASTIC	
T1	JZ	23.6	21.7	0.6851	NS
	DMZ	28.8	26.8	0.5427	NS
T2	JZ	32.3	24.9	0.8736	NS
	DMZ	40.6	47.5	0.8159	NS
T3	JZ	144.4	64.8	0.9751	SIG
	DMZ	103.4	102.0	0.5244	NS
T4	JZ	205.0	74.0	0.9973	SIG
	DMZ	130.9	90.7	0.9164	NS
T5	JZ	127.1	38.0	0.9988	SIG
	DMZ	103.4	64.4	0.9494	NS

Mean Length of *Zostera japonica* shoots (cm)

TIME	ZONE	TRANSP	+PLASTIC	PROBABILITY TRANSP < or > +PLASTIC	
T1	JZ	10.9	11.1	0.6267	NS
	DMZ	11.5	11.4	0.5751	NS
T2	JZ	12.1	13.9	0.9861	SIG
	DMZ	10.7	12.8	0.9877	SIG
T3	JZ	15.0	17.5	0.9486	NS
	DMZ	14.9	18.4	0.9880	SIG
T4	JZ	14.9	12.6	0.0669	SIG
	DMZ	16.3	14.3	0.9114	NS
T5	JZ	16.9	13.8	0.9638	SIG
	DMZ	15.1	12.6	0.9853	SIG

6.4 DISCUSSION

In the transplants undertaken in both 1987 and 1988 *Zostera marina* exhibited a similar pattern of ramet production regardless of the location along the environmental gradient and although significant differences were found in mean shoot length among zones, the differences were not consistent over time. *Zostera marina* at Roberts Bank appears to be relatively insensitive to the variation in environmental conditions which correspond to each site. In contrast, Phillips (1972) described differences in shoot density and length in intertidal and subtidal *Z. marina* populations of Puget Sound. Reciprocal transplants between an intertidal site and a subtidal site indicated that leaf dimensions such as the mean length of leaves and leaf width are plastic and vary according to location on the tidal gradient (Phillips, 1972). Backman (1984) also concluded from several common garden experiments that the observed variation in morphology along spatial gradients was partially due to phenotypic plasticity. It appears that in this study at Roberts Bank the environmental cues, whether abiotic light conditions or conditions mediated by neighbours, that may trigger lateral branch formation and variation in leaf length are not sufficiently varied among transplant sites. If the populations of *Z. marina* presently under study are capable of phenotypic variation in accordance with location on the tidal gradient it was not sufficiently expressed to be discerned as significant differences. Both null hypotheses i) that "the initiation of lateral branching and development of *Z. marina* shoots" and ii) that "the mean shoot length are not affected by location along the intertidal gradient" are accepted.

The monospecific samples of *Zostera japonica* exhibited a growth pattern similar to the monspecific *Z. japonica* population in the japonica zone described in section 5 (Descriptive study). All four transplanted populations initially produced lateral branches at a similar rate regardless of location on the tidal gradient. The null hypothesis iii) that "the initiation of lateral branching and development of *Z. japonica* shoots is not affected by location along the intertidal gradient" is accepted. The greatest population increase, although not statistically different, occurred in the deep marina zone. Transplanted *Zostera japonica* shoots did not differ in mean shoot length among the four transplant sites with one exception. Therefore there is no correlation of mean shoot length with position on the intertidal gradient, and the null hypothesis iv) that "the mean length of *Z. japonica* shoots is not affected by location along the intertidal gradient" is also accepted. Since there was no variation in *Zostera japonica* shoot number and length in response to location, differences that were noted between japonica and transition populations in section 5 must be related to the presence of *Zostera marina* in the transition zone. The suppression of lateral branch development in the transition population of *Z. japonica* clearly is due to the presence of *Z. marina* and is not related to abiotic environmental conditions associated with location on the tidal gradient. In those cases in the 1987 Descriptive study where significant differences occurred in the mean shoot length, the transition population was always longer, indicating that *Z. marina* enabled the understory *Z. japonica* shoots to attain or maintain greater shoot lengths.

The effect of the procedure of transplantation was measured by comparing transplanted samples with samples of natural vegetation in the same zone. This assumes that abiotic conditions of the position on the tidal gradient induce a set range of variation in morphological responses (as indicated by Phillips 1972). The lack of a significant difference between transplant samples and samples of natural vegetation would imply that transplantation had no lasting negative effect on plant growth. However, differences did occur. With one exception, natural *Zostera marina* shoots were always longer than transplant samples in that zone. Possible causes for this difference could be i) the stress of transplantation (Backman, 1984), ii) shoots in isolated transplant patches may be more prone to breakage by wave action and abiotic fluctuations associated with low tides, or iii) the transplanted rhizomes branched more frequently, resulting in greater numbers of younger shorter shoots.

The greatest discrepancy between transplanted *Zostera marina* and natural populations occurred in the deep marina zone. There the transplants, which were taken from the zone, attained only 54% of the mean shoot length of the natural population. Thus, contrary to expectation, the ability of *Z. marina* shoots to withstand transplantation was reduced with increasing depth along the tidal gradient. Since the measures of shoot number in the transplant samples were not restricted by area they could not be compared with the measures of shoot density (shoots/625cm^2) recorded for randomly sampled adjacent vegetation. But by comparing the slope of line segments in Figure 16 it appears that the rate of lateral shoot development is not greater in the deep marina zone transplants than in the other zones. Therefore, the shoots developing in the deep marina transplant site are not shorter because of a higher rate of branching.

Zostera japonica transplants typically showed a similar trend, i.e. shorter mean shoot lengths when compared to natural vegetation in the same zone. The *Z. japonica* transplants in the marina zone recovered totally from transplantation, whereas the transition and japonica populations attained only 76% and 77% of the mean shoot lengths of the natural populations respectively. The isolation of the transplants in patches would compound the effects of desiccation as compared to the adjacent stand of natural vegetation. The layering of shoots as they lay prostrate during a low tide reduces the area of each shoot exposed to the air and helps maintain moisture between shoots. Where the shoots are found in isolated patches, a greater proportion of each shoot's surface area would be exposed and subject to desiccation. The ability of *Z. japonica* transplants to recover to such a great extent in the marina zone compared to the transition and japonica zones could be related to the prevailing abiotic environmental conditions. Transplants in the transition and japonica zones would experience more desiccation associated with slightly longer periods of exposure. The ability of *Z. japonica* shoots to recover from transplantation appears to be ameliorated by the less desiccating conditions in the marina zone.

The green plastic shoots imposed on *Zostera japonica* transplants in the deep marina and japonica zones were intended to mimic *Zostera marina* shoots. If the plastic shoots effectively mimicked *Z. marina* shoots in their ability to alter the growth pattern of *Z. japonica* shoots, the understory *Z. japonica* shoot numbers would be much reduced under a plastic canopy. The plastic shoots had no effect on the deep marina zone transplants but did reduce the population growth of the japonica zone transplants. The effectiveness of the plastic canopy is therefore mediated by the exposure regime associated with the transplant site. Since the plastic shoots had no effect on lateral shoot development in the deep marina zone it is not likely that they effectively shaded the *Z. japonica* shoots in the isolated transplant patches. Possible explanations for the observed effects of plastic shoots on the *Z. japonica* understory are i) the plastic shoots increase the ambient water temperature during low tides sufficiently to reduce the growth rate of plants, or ii) the plastic strips may physically remove the shoots by slicing the shoots with their relatively sharp edges.

Zostera japonica shoots were longer under plastic canopies in both the japonica and deep marina zones up to and including T3 (July 25). After this time the plastic canopy had a negative effect on the mean length of *Z. japonica* shoots in the understory. This switch in plastic shoot performance occurred in both the japonica and deep marina zones. The environmental character or cue that regulates leaf length in *Z. japonica* shoots is modified by the plastic canopy and must be common in both zones. Both the japonica zone and deep marina zone populations under a plastic canopy declined in population numbers from T4 to T5. The general reduction in size could be explained if the plastic shoots remove the tips of longer leaves from the transplanted *Z. japonica* in the understory by the way in which they move or flip during a tide change.

7 MANIPULATION EXPERIMENT -1988

7.1 INTRODUCTION

It is possible that the mechanism by which the population growth of *Zostera japonica* is supressed under a canopy of *Zostera marina* is related to irradiance. Reduced irradiance under a *Z. marina* canopy reaching the understory *Z. japonica* may be considered a form of interference competition (Vance,1984). Measurements in the field indicated that 30 % of surface photosynthetically active radiation (PAR, 400-700 nm) penetrates to the sediment through 1.5 m of seawater and a canopy of *Z. marina* compared to 43% of surface PAR that reaches the sediment beneath a *Z. japonica* canopy. The reduction of available PAR may be responsible for suppressing lateral branch development or in some other way modifying the growth of *Z. japonica*.

Competition could also be occurring between *Zostera marina* and *Zostera japonica* for a limited supply of nutrients. *Zostera marina*, a perennial, is already established and absorbing nutrients from the sediments when the annual *Z. japonica* germinates, and commences rhizome extension and ramet production. At Roberts Bank, however, nutrients are not considered limiting (P. G. Harrison, personal communication). Run off drains waters from nearby farms and the waters from the Fraser River mix with those of the Strait of Georgia to regularly flood the Roberts Bank study site. Nutrients may be absorbed through the root system or they may be absorbed directly through the leaf surfaces (McRoy and Barsdate, 1970).

A third possible limiting resource for which the two species could be competing is space. Below the sediment surface horizontal rhizomes of both species penetrate the sediment with two bundles of fibrous roots at each node. These roots not only serve for nutrient uptake but more significantly act as an anchoring device in a substrate that is potentially very mobile. The interwoven network of rhizomes, roots and invertebrate tubeworm casings provide an effective anchor against the pull of tidal waters. Typically *Zostera japonica* rhizomes will occupy the upper 2 to 5 cm of the sediments whereas *Zostera marina* rhizomes will be 4 to 10 cm deep in the sediments. *Zostera japonica* seedlings may have difficulty in establishing in extremely thick mats of rhizome and those that do establish in the upper 2 to 5 cm may not be able to penetrate further than 5 cm with their roots and hence would be susceptible to uprooting and loss. Preemption of rooting space by *Z. marina* may inhibit the initial establishment of *Z. japonica* seedlings and thus be limiting the growth of the population of ramets.

Considering the responses of *Zostera japonica* to the presence of a *Zostera marina* canopy demonstrated in section 5 it is most likely that the responses were due to the irradiance limitation. Competition for nutrients and preemption of space may be of significance in the interaction between the two species, but both are difficult to manipulate and control in a field situation. Hence, a manipulation experiment was designed to test whether light reduction (shading) was the factor responsible for suppression of *Z. japonica* population growth. The primary objective of section 7 is to determine whether the transition zone *Z. japonica* population is suppressed or in some other way modified due to the shading effects of *Z. marina*. A second objective is to establish whether the morphological differences in *Z. japonica* shoot length noted in section 5 could be attributed to the presence of taller neighbours that served to protect the shorter *Z. japonica* shoots from breakage as was indicated for *Thalassia testudinum* and *Syringodium filiforme* by Williams (1987). No significant differences in *Z. japonica* shoot length were evident between zones in the Transplant Experiments (section 6) and therefore the differences observed in the Descriptive Study (section 5) must have been due in part to interactions with *Z. marina* neighbours. The null hypotheses in the manipulation experiment are:

i) the population growth of *Zostera japonica* is not inhibited by an irradiance-reducing canopy, and

ii) the mean length of *Z. japonica* shoots is not affected by the presence of taller seagrass neighbours.

7.2 METHODS

The experiment was done in the transition zone. In May of 1988 a site was chosen adjacent to the 1987 transition zone site. Both sites had similar densities of *Z. marina* shoots.

Artificial shoots were designed to mimic the light-shading ability of *Zostera marina* shoots while maintaining a vertical presence as a "protective" neighbour. Each artificial shoot consisted of three plastic strips 70, 70, and 50 cm long by 1 cm wide cut from rolls of medium-weight clear and green opaque plastic. The tip of each strip was dipped into a mixture of "Sista Multi-purpose Foam", an aerosol polyurethane foam, diluted with acetone, to create a float for the tip of each "leaf". The three plastic leaves were stapled and then secured to a 30-cm stainless steel rod (1.5 or 3.0 mm diameter) with plastic tie wraps. When tested in the lab for floatation the completely submerged artificial shoots behaved in a manner similar to *Z. marina* shoots by assuming a vertical position perpendicular to the sediment. When the water level was dropped, differences in shoot "posture" became apparent. The lacunae of *Z. marina* leaves provide buoyancy along the entire length of the leaf. The bases of the real shoots were perpendicular to the sediment, the shoots were vertical through the shallow water column with the remaining length of shoot spread over the water surface. In contrast, the bases of artificial shoots lay along the sediment with only the shoot tip extending vertically to the water's surface. In waters with a slight current equivalent to a receding tide at Roberts Bank the base of the real shoots would be angled diagonally, while the artificial shoots would have only the terminal tip angled diagonally. The differences in shoot behaviour would be evident only during periods of tidal flow when the water depth ranged from 10 to 70 cm. This difference in behaviour is confined to a short period, approximately 30 minutes, during the flow of waters from high tide to low tide and again from low tide to high tide. Divers visually inspected the performance of artificial shoots and verified that when the shoots were covered with more than 1 m of water they were difficult to distinguish from real *Z. marina* shoots. Measurements in the field indicated that with a water depth of 1.5 m 32% and 31% of surface PAR penetrates to the sediment under a clear plastic and green plastic canopy respectively as compared to 30% under a natural *Z. marina* canopy.

In the field a 10 x 7 m area was marked as the site for the manipulation experiment with coloured wooden stakes placed at 2-m intervals about the perimeter. Measuring tapes and rope were temporarily placed about the stakes to form a grid of 70 1-m^2 quadrats. All treatments consisted of a 1-m^2 quadrat with the central 50 x 50 cm portion of the quadrat subject to the manipulation. The 25-cm wide border around the central portion had all *Zostera marina* shoots regularly clipped to a height of 20 cm. This height was above the growing meristematic region of the shoot allowing the shoots to continue growing. This height was also equivalent to the seasonal mean height of *Zostera japonica* shoots from the transition zone during the previous growing season. Underground interactions would theoretically still be ongoing, but aboveground shading would no longer be a factor.

One of five treatments was randomly assigned to each 1-m^2 quadrat (Table 32). In treatment (A) all *Zostera marina* shoots in the 50 x 50 cm central portion of the quadrat were clipped below the first prominent node, behind the growing meristem, and replaced with 15 randomly placed clear plastic shoots. Light was thought to penetrate this artificial canopy to the developing *Z. japonica* population. Treatment (B) involved the replacement of *Z. marina* shoots in the centre of each treatment with 15 opaque green plastic shoots. Light penetration to the *Z. japonica* understory would be reduced. The third treatment (C1) was a control of undisturbed *Z. marina* and *Z. japonica* vegetation. In the fourth treatment (C2) all *Z. marina* shoots were removed from the centre of the quadrat with no replacements. The fifth treatment (C3) involved the removal of *Z. marina* shoots and replacement with anchors as a control for possible interactions of the anchor rods with the sediment or rhizomes and roots. Each treatment was replicated 15 times except the anchor control (C3) which was replicated 10 times.

Table 32 Manipulation experiment treatments

	TREATMENT	FUNCTION OF TREATMENT
A.	*Z. marina* shoots removed, and replaced with clear shoots	*Z. japonica* shoots will be protected, but not shaded
B.	*Z. marina* shoots removed, and replaced with opaque shoots	*Z. japonica* shoots will be both protected and shaded
C1.	natural mixed vegetation	control for effect of artificial shoots
C2.	*Z. marina* shoots removed	*Z. japonica* growth without *Z. marina* neighbours; no shading, no protection
C3.	*Z. marina* shoots removed, replaced with shoot anchors	control for effect of anchors on *Z. japonica* growth

The experimental site was monitored five times at four-week intervals from May 14 through September 7, 1988 (Table 33). To avoid edge effects the number of shoots in the 625 cm^2 central portion of each treatment was recorded, as was the length of 15 randomly chosen shoots from the sample. Large epiphytes that colonized the green plastic shoots by T2 were removed and also at every subsequent sample date. Epiphytes also colonized the clear plastic strips and required their replacement at each sampling date with clean clear plastic shoots.

Table 33 Dates of sampling for the manipulation experiment -1988.

T1	May 14
T2	June 13
T3	July 11
T4	August 7
T5	September 7

The natural vegetation surrounding the manipulation site was sampled randomly with a 625-cm^2 quadrat at T4 (August 8) and T5 (September 7). The number of shoots and mean shoot length ($n = 15$) of these samples were compared to the experimental control of natural vegetation (C1). The clipping of *Zostera marina* shoots in the border region and the removal of shoots within the treatments could possibly affect the growth of connected ramets in adjacent control quadrats. The validity of the control (C1) needed to be verified.

ANOVA was used to test for differences among treatments. Duncan's Multiple Range Test (ANOVAR program) was used to separate the treatment means when significant differences were found. Comparisons of the control (C1) with randomly sampled natural vegetation were analysed with Students' *t*-test.

7.3 RESULTS

The density of *Zostera japonica* shoots increased gradually in all treatments and controls in a similar manner up to August (Fig. 19). By August 7 (T4) no significant differences were found but the mean density of *Z. japonica* shoots was slightly greater where *Z. marina* had been removed and no artificial shoots or anchors were imposed (C2) than in the other treatments (Table 35). The treatments involving removal of *Z. marina* and replacement with either plastic shoots (A, B) or anchors (C3) appeared to have the same effect on *Z. japonica* population growth, while the natural *Z. marina* vegetation (C1) had the lowest population density at T4.

By September 7 (T5), ANOVA revealed a significant treatment effect (Table 35). Treatment B had fewer shoots in the understory than threatments A, C2, and C3 (Table 34). The density of *Z. japonica* shoots had declined from T4 (August 7) in the treatments where clear plastic shoots (A) or green plastic shoots (B) had been imposed. The population of *Z. japonica* under a natural *Z. marina* canopy (C1) remained at a constant density, whereas the density of *Z. japonica* shoots continued to increase in the anchor control (C3). In the treatment where *Z. marina* had been removed and not replaced (C2) the population of *Z. japonica* declined.

Table 34 Separation of treatment means for shoot density at T5 using Duncan's multiple-range test.

T5	GREEN PLASTIC (B)	NATURAL (C1)	CLEAR PLASTIC (A)	*Z. japonica* only (C2)	ANCHORS (C3)
$\bar{x}$	21.7	31.6	41.3	50.5	51.0

$\alpha = 0.05$

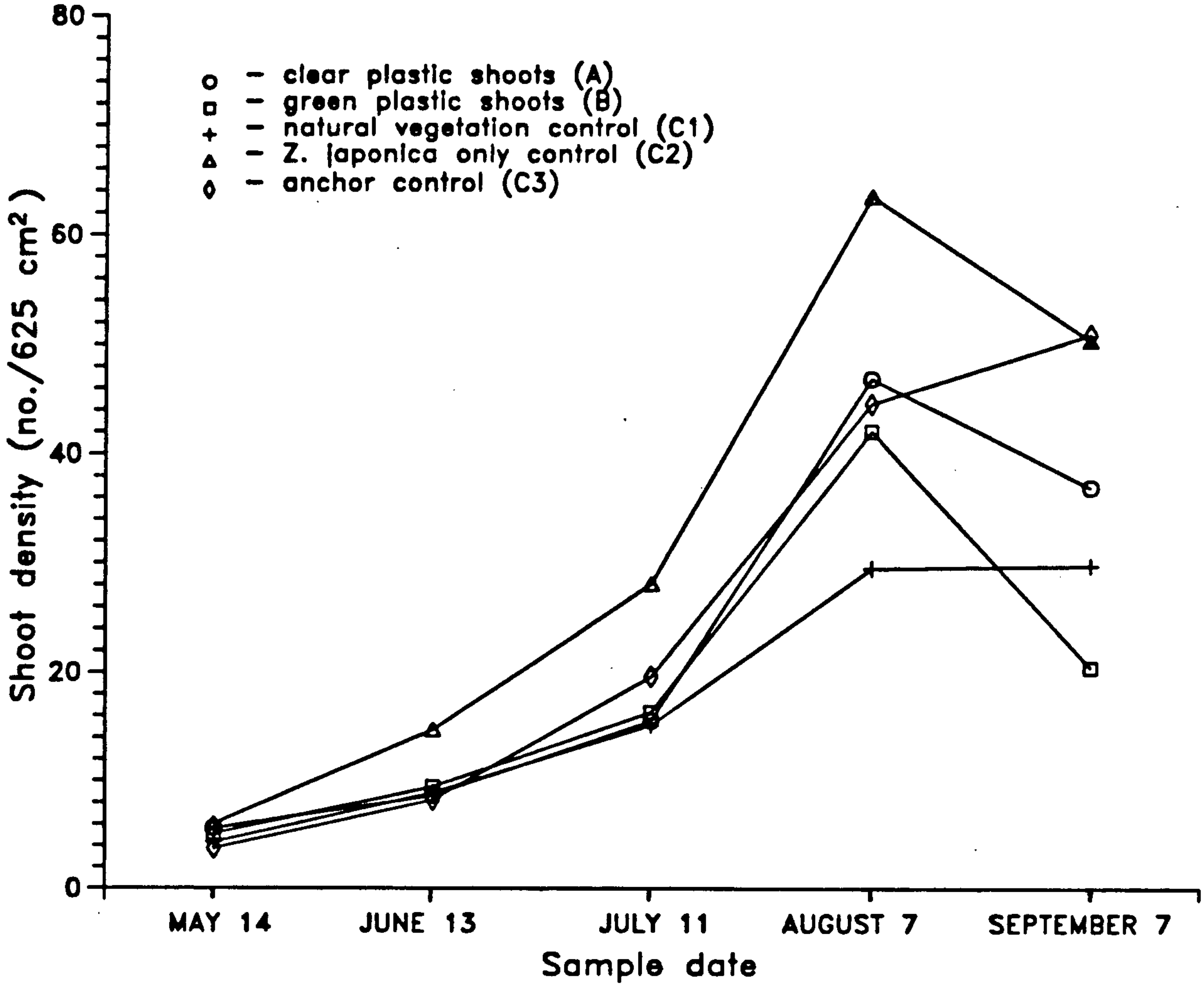

Fig. 19 Density of *Zostera japonica* shoots in five experimental manipulations monitored from May 14 to September 7, 1988.

Table 35 Summary of ANOVA for *Zostera japonica* mean numbers of shoots and mean shoot length in manipulations treatments. The total number of samples included in each analysis is identified under N. Significance (SIGN.) at 0.05 level is represented as SIG = significant difference or NS = not significant.

Zostera japonica shoots per 625cm^2

TIME	N	F-STATISTIC	P	SIGN.
T1	70	0.8565	0.4949	NS
T2	70	1.3427	0.2637	NS
T3	70	2.2381	0.0745	NS
T4	70	2.0109	0.1033	NS
T5	70	4.7077	0.0021	SIG

Mean *Zostera japonica* shoot length

TIME	N	F-STATISTIC	P	SIGN.
T1	67	0.9831	0.4230	NS
T2	70	1.4097	0.2406	NS
T3	70	0.3175	0.8653	NS
T4	69	1.3043	0.2779	NS
T5	70	4.7289	0.0021	SIG

The mean shoot length within each treatment increased at a similar rate from May through to August (Fig. 20). No significant ($P > 0.05$) differences were evident until September 7 (T5)(Table 35), when the presence of green artificial shoots had a negative effect on the mean length of *Z. japonica* shoots at T5. The length on understory shoots was less in treatment B than in treatments C2, C1, and C3 (Table 36).

Table 36 Separation of treatment mean for shoot length at T5 using Duncan's multiple-range test.

T5	GREEN PLASTIC (B)	CLEAR PLASTIC (A)	*Z. japonica* ONLY (C2)	NATURAL (C1)	ANCHORS (C3)
$\bar{x}$	13.5	16.4	17.4	17.6	19.2

$\alpha = 0.05$

Neither mean shoot density nor mean shoot length showed any significant difference between random samples of the natural *Zostera japonica* vegetation outside the treatment plots and the manipulation control (C1)(Table 37).

The numbers of *Zostera marina* shoots, however, were significantly greater in the manipulation control (C1) than in the surrounding natural vegetation at both T4 and T5, while the mean length of the *Z. marina* shoots showed no difference.

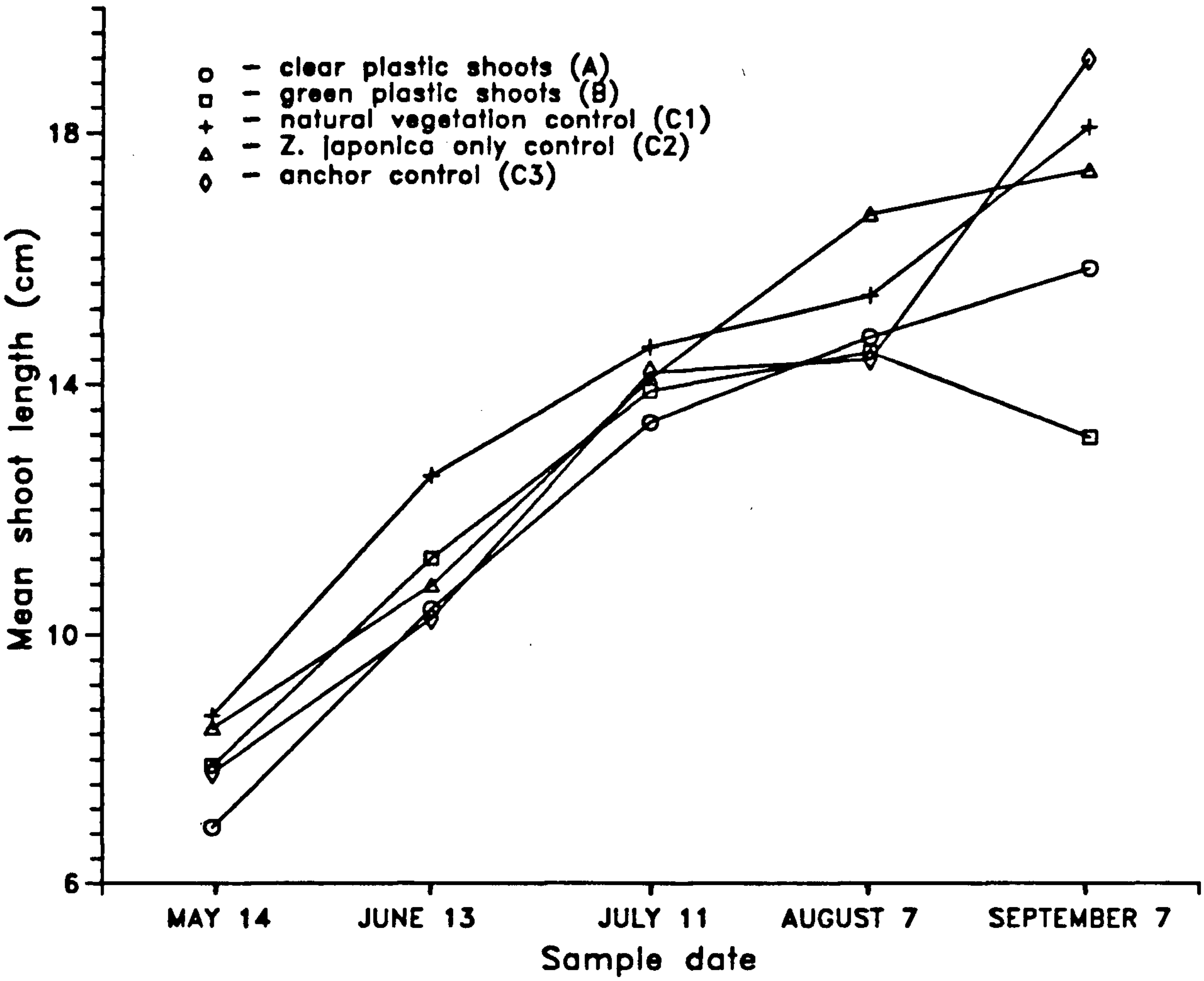

Fig. 20 Mean length of *Zostera japonica* shoots in five experimental manipulations from May 14 to September 7, 1988.

Table 37 Comparison of *Zostera japonica* and *Zostera marina* number of shoots per $625 cm^2$ and shoot length between manipulation control (C1) and random samples of adjacent natural vegetation. The total number of samples included in each analysis is identified under N. The Bayesian probability (see section 5.2 for description) that one mean is greater than the other is given and the significance at 0.05 level is represented as SIG = significant difference or NS = not significant.

Mean *Zostera japonica* shoots per 625 cm^2

TIME	CONTROL (C1)	NATURAL	N	SIGNIFICANCE CONTROL < or > NATURAL	
T4	63.5	39.6	45	0.9417	NS
T5	50.5	37.5	25	0.9056	NS

Mean *Zostera japonica* shoot length (cm)

TIME	CONTROL (C1)	NATURAL	N	SIGNIFICANCE CONTROL < or > NATURAL	
T4	16.7	16.9	45	0.5770	NS
T5	17.4	18.2	25	0.6909	NS

Mean *Zostera marina* shoots per 625 cm^2

TIME	CONTROL (C1)	NATURAL	N	SIGNIFICANCE CONTROL < or > NATURAL	
T4	9.2	5.1	45	0.9934	SIG
T5	8.0	3.5	25	0.9977	SIG

Mean *Zostera marina* shoot length (cm)

TIME	CONTROL (C1)	NATURAL	N	SIGNIFICANCE CONTROL < or > NATURAL	
T4	36.0	39.1	45	0.8608	NS
T5	39.0	44.0	25	0.9376	NS

7.4 DISCUSSION

The gradual increase in *Zostera japonica* population density from May to August is reminiscent of the monospecific population growth evident in the japonica zone of the Descriptive study (section 5) and in all zones of the Transplant experiments (section 6). In the manipulation experiment the *Z. japonica* population densities of the monospecific treatments (C2, C3) did not reach the maximum levels observed in the monospecific japonica zone (section 5). It appears that the summer maximum in monospecific patches of *Z. japonica* is dependent on the number of established seedlings and the size of an overwintering population. In the manipulation control (C1) the mean shoot density (4.3 shoots/625 cm^2) was lower initially than in the japonica zone population (10.9 shoots/625 cm^2) in the Descriptive study; therefore there was a lower potential for population increase.

The growth of *Zostera japonica* under a natural *Zostera marina* canopy (C1) or *Z. marina* replacements (A, B) was not suppressed to the same degree as occurred in the transition zone (section 5). In the manipulation experiment the borders around each treatment quadrat were clipped and would have permitted light to penetrate from the edges to the central portion, even in the control treatment (C1) where no *Z. marina* shoots were removed. The comparison of *Z. japonica* densities in the control (C1) with the sampling of adjacent natural vegetation indicated that although no significant difference was found, there appeared to be fewer shoots per 625 cm^2 in the natural continuous vegetation (Table 37). The light conditions under the *Z. marina* canopy in the manipulation experiment may not have been as limiting as in a natural continuous vegetation and therefore the *Z. japonica* population in the control treatment (C1) attained higher population densities than would be expected based on transition zone data from section 5.

During the period of population growth from May through to August no significant differences in shoot density were found, but there were consistently higher mean densities of *Z. japonica* in treatment C2 where no shoots or anchors had been imposed. By August 7, Figure 19 illustrates a trend of mean separation (although not significantly different) among treatments. The presence of anchors either with or without attached plastic shoots may have had a suppressive effect on the production of *Z. japonica* shoots by inhibiting growth and extension of *Z. japonica* rhizomes and roots. It also appears that the plastic shoots, either green opaque or clear, did not sufficiently mimic the natural *Z. marina* shoots in terms of their ability to suppress lateral shoot development during this period of population growth.

The decrease in density observed between August and September in those *Zostera japonica* populations under plastic canopies was similar to the decrease in shoot number of transplanted samples (section 6.3, refer to Table 31 for means). It is possible that the plastic shoots did not protect *Z. japonica* shoots, but rather facilitated the loss of *Z. japonica* shoots during periods of vigorous wave action during this period of population decline.

The manipulation experiment does not clearly demonstrate that the population growth of *Zostera japonica* is inhibited by a light-reducing canopy. The first null hypothesis (i) must therefore be accepted. The observed population growth and later population decline are a function of the changing abiotic environment and the innate schedules of phenological development. The population responses to the presence of *Zostera marina* neighbours or artificial shoots are dependent on the time at which the observations are made.

None of the treatments had any effect on the mean length of *Zostera japonica* shoots from May to August. The *Z. japonica* shoots were no longer when under a plastic canopy or a real *Z. marina* canopy than without. The decrease in *Z. japonica* shoot length under a green plastic canopy between August and September coincided with the decline in *Z. japonica* shoot density in the same treatments. Although the green plastic shoots had a negative effect on *Z. japonica* shoot length between August and September shoot, length was not affected at any time by a natural *Z. marina* canopy or the lack of a canopy (C2, C3). Therefore the null hypothesis ii) that the mean length of *Z. japonica* shoots is not affected by the presence of taller seagrass neighbours as tested by this experiment is accepted. It is erroneous to conclude, however, that *Z. marina* shoots played no role in protecting the understory from breakage or inducing greater production of leaf length. The relative isolation of the manipulated patches or treatment quadrats from an extensive meadow of taller *Z. marina* at Roberts Bank may have counteracted any protective role of *Z. marina* shoots. *Zostera japonica* shoot lengths were found to be significantly greater (at several times) in the mixed zone of continous vegetation than in the monospecific zone. Also a reduction in mean shoot length was evident in the transplant experiments (section 6.3, Table 29) indicating that isolation in patches can reduce *Z. japonica* shoot length compared to occupation in the *Z. marina* understory in a continuous meadow. This is in agreement with the interaction between *Thalassia testudinum* and *Syringodium filiforme* (Williams 1987) where the presence of *Thalassia* resulted in increased *Syringodium* lengths.

The increase in density of *Zostera marina* shoots in the natural vegetation control patches (C1) compared with the randomly sampled vegetation around the treatment area may have been a result of the careful clipping of *Z. marina* shoots in all treatment borders to a height of 20 cm. The removal of adjacent canopy had the effect of inducing greater lateral branch formation in the isolated patches of *Z. marina* in treatment (C1).

The manipulation experiment with the isolated patches of *Zostera marina* and artificial shoots did not adequately create the shade conditions intended and therefore was not a true test of the hypotheses. In comparisons with the results of sections 5 and 6 it became apparent that the patches of canopy did not effectively shade the understory and suppress lateral shoot development. Light could easily penetrate the centre of each canopied treatment from the non-canopied border and surrounding areas. Similarly, there was no evidence of *Z. marina* protecting *Z. japonica* shoots from breakage or inducing longer leaf lengths that were apparent in a continuous meadow. The results from the manipulation experiment must therefore be interpreted with caution and only in conjuction with the results of the previous sections of this thesis.

8.0 SUMMARY

The general objectives of this study were to describe *Zostera marina* and *Zostera japonica* vegetation that occurred at Roberts Bank and to investigate the processes determining the observed zonation. Abiotic environmental factors and interspecific competition between the two seagrasses were considered as two possible forces responsible for structuring the seagrass community. The following are general conclusions concerning the interactive biology of *Z. marina* and *Z. japonica*.

1. Population densities of *Zostera marina* were not affected by location in the intertidal zones studied which covered only the upper end of its distribution but included areas of pure *Z. marina*, and mixed *Z. marina* and *Z. japonica*.

2. Morphological variation of *Zostera marina* vegetation was not as clearly discernible using single discrete characters as was apparent in previous comparisons of intertidal with subtidal populations (i.e. Phillips, 1972). Shoots tended to be longer with a greater biomass in the marina zone than in the transition zone.

3. The population size of *Zostera japonica* shoots was significantly smaller under a *Zostera marina* canopy in the transition zone than in the monospecific japonica zone. Transplant results confirmed that adult *Z. japonica* are capable of attaining large population numbers in the four intertidal zones (sites) tested. The initially lower numbers of *Z. japonica* shoots under a *Z. marina* canopy may be due to fewer seedlings successfully establishing, or fewer adult *Z. japonica* surviving through the winter. During June and July the population numbers increase exponentially by rhizome extension and vegetative production of lateral shoots regardless of initial population numbers. Under a *Z. marina* canopy, however, development of lateral shoots is suppressed. Since transplants of adult *Z. japonica* shoots indicated no suppression of lateral shoot development under

the ambient light conditions associated with the deep marina zone, the presence of a *Z. marina* canopy must be competitively interfering with *Z. japonica* population growth.

4. Morphological variation of *Zostera japonica* between the monospecific japonica zone and the mixed transition zone was evident at various times, but overall the differences were inconsistent. Shoots tended to be longer with greater biomass in the more seaward transition zone than in the landward japonica zone. Since no significant differences in mean shoot length were found among monospecific *Z. japonica* transplants, the differences observed in the descriptive study were thought to have been due in part to the presence of *Zostera marina* neighbours. However, no direct evidence was obtained from the manipulation experiment to confirm that longer *Z. marina* protect *Z. japonica* shoots from breakage.

5. The artificial shoots designed for this experiment did not adequately mimic *Zostera marina* shoots. Although initial testing indicated that they did reduce PAR penetration to the sediment at high tide, their posture during low water reduced their effectiveness in shading the understory compared with natural *Z. marina* shoots. The artificial shoots frequently became laden with epiphytic macroalgae, diatoms, barnacles and mussels, thereby reducing buoyancy and decreasing their effectiveness as a shading canopy. In addition the relatively sharp edges of the plastic leaves were partially responsible for the reduction of *Zostera japonica* shoot lengths and population numbers during the period of natural population decline in September.

The differences between natural and artificial shoots in conjunction with the patch design of the manipulation experiment did not adequately create the conditions intended (see section 7.4). The results of the manipulation experiment must therefore be interpreted in conjuction with the results of the descriptive study and the transplant experiments.

6. *Zostera japonica* and *Zostera marina* coexist within a restricted range of the intertidal due in part to differences in their phenology. The maximum extent of the region of mixed vegetation and coexistence was not determined. The seaward limit of *Z. japonica* may be a function of seedling establishment and/or competitive interactions with *Z. marina*. This study has clearly indicated that adult *Z. japonica* are capable of thriving in the environmental conditions of the deep marina zone. The lower limit of the zone in which the two species coexist is therefore determined by biotic factors. The contention of this thesis is that shading by a *Z. marina* canopy is the primary mechanism of competition. Further study into the physiological response of *Z. japonica* to reduced PAR would supplement the work of this thesis. Indirect evidence also indicates that belowground interaction may be a factor in interfering with *Z. japonica* population growth (see section 7.4). To elucidate the factors limiting the coexistence of *Z. japonica* in the deeper intertidal the mechanisms of competitive interaction between *Zostera marina* and *Zostera japonica* in regards to seedling establishment and belowground interactions need to be further studied.

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